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Tick-Host Specificity[1]

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In this review, the various patterns of tick-host relationships are discussed in detail in order to answer the following questions (1957):
1. How, when and where did host specificity of each parasite group evolve?
2. How strict is specificity in each case?
3. Why and under what circumstances does specificity break down?

The authors present several definitions which characterize the various degrees of parasitic specificity existing today between ticks and their hosts.

Tick-host relationships are presented in relation to the life-cycle patterns and also to their appearance during the evolution of the various classes of terrestrial vertebrates. Special attention is paid to the ticks of mammals. A family-tree has been set up to display the families, subfamilies and genera of ticks.

As biologists, we seek to understand the patterns, details, and implications of host-parasite relationships. In opening the First Symposium on Host Specificity among Parasites of Vertebrates, MAYR (1957) asked: How, when, and where did host specificity of each parasite group evolve? How strict is specificity in each case? Why does specificity break down and under what circumstances?

This analytical review of tick-host relationships incorporates our current concepts of the complex subject and provides data and models which should help to answer the questions of MAYR (1957). The final answers await more comprehensive correlation of evolutionary and biological information.

As biomedical researchers, we are charged with the task of improving the quality of human life and welfare precisely, reducing risks of disease, irritation, and debilitation resulting from parasitism by ticks. We investigate the properties and behavior of each tick species that may affect the species role in enzootics and epizootics of agents infecting man and domestic and wild vertebrate animals. Indeed, contemporary cognizance of tick-host specificity derives largely, directly or indirectly, from results of biomedical-epidemiological studies... which abounded for some years during the post-World War II renaissance of biomedical and veterinary research. Knowledge thus obtained provides evidence indispensable for

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answering MAYR's questions. However, biological experience and insight warn us that data for medical and veterinary use are heavily biased to reflect human concern with the most versatile vector species. Overwhelming demands for mission-oriented research funds and results leave extensive areas of significant biological phenomena poorly investigated if at all.

«Important» (adaptable) tick species thrive in the modified environments offered by human activities and defy expensive efforts to control them. In the meantime, numerous biologically conservative species, closely tied to specific hosts, may continue to flourish or become less common, rare, or extinct as their host population densities and spatial ranges are reduced.

Today we shall begin to bring into biologically rational perspective the disparate data from studies of phenomena in nature and in tick-borne disease epidemiology. Unbiased data on tick-host specificity can be equally useful and supportive for the biologist, for answering MAYR's questions and for the epidemiologist to elucidate biomedical questions. Today's presentation is a preliminary overview of the kind of data required by the biologist, the epidemiologist, and the responder to MAYR on the subject of tick-host specificity.

Host specificity is defined, for this tick-orientated discussion, as an association between a tick species and a vertebrate species, or a clearly related vertebrate group, which is critical for reproduction and continued survival of populations of the tick species.

Ticks are large mites (Acarina). More than 200 families and 1,700 genera of mites have been described. Described and undescribed species of mites in the world today have been estimated to number close to one million. Within this vast galaxy of small organisms, the larger ticks account for only three families and few more than 800 species (Fig. 1). None of these species are known from true fossils.

The ticks evolved along two principal lines: Argasidae («argasids» or «soft-ticks», chief genera *Argas* and *Ornithodoros)* and Ixodidae («ixodids» or «hard ticks», 13 genera in 5 subfamilies) (Fig. 1). The basic differences between these families were reviewed by HOOGSTRAAL (1956, 1978) and in numerous other papers and textbooks.

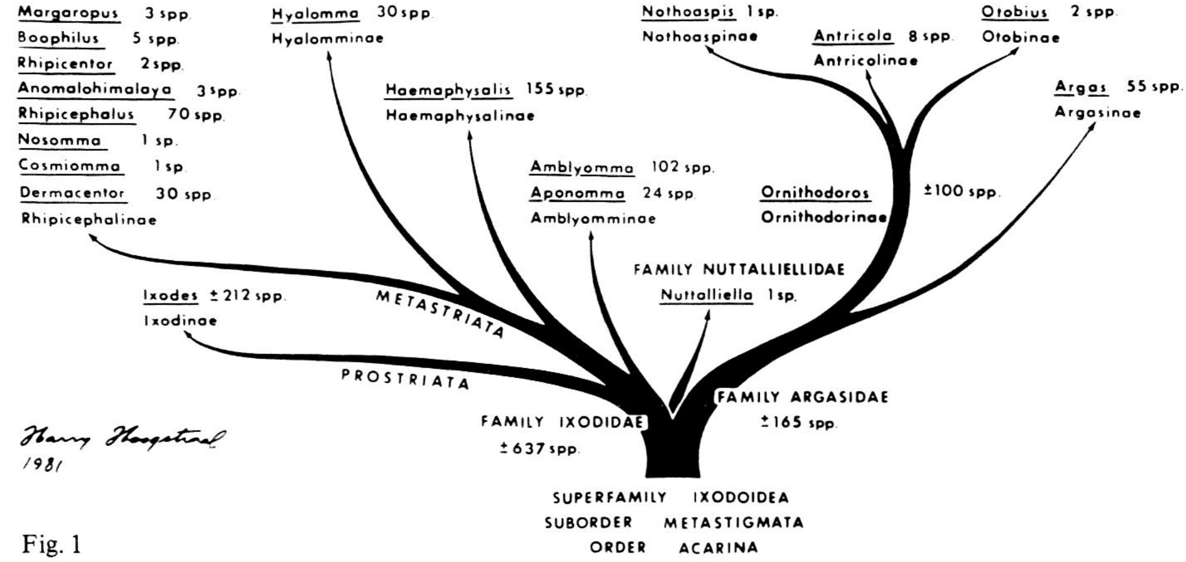

Fig. 1

Most Argasidae preserve basic late Mesozoic - early Tertiary biological patterns within a few remarkably conservative, highly specialized external body structure patterns. Argasid adaptations for survival with late Tertiary or Recent hosts, and in temperate climates, are expressed chiefly in diapause and longevity phenomena. Significant argasid life cycle adaptations occur only in a few *Ornithodoros* species and in the eleven species constituting the subfamilies Otobinae (2), Antricolinae (8), and Nothoaspinae (1).

In the Ixodidae, Prostriata (Ixodinae, *Ixodes)* structural properties are mostly those that are critically definitive of this family; some properties of secondary importance differ from those of Metastriata. *Ixodes* species, some with specialized biological characteristics, proliferated during the Tertiary. In the Metastriata (other genera of Ixodidae), the tropical-subtropical Amblyomminae (2 genera) retain more primitive late Mesozoic - early Tertiary biological and structural properties than other subfamilies. The tropical-temperate Haemaphysalinae (1 genus) also retain clearly primitive properties, but only in a small group of significant «indicator», relict-type species. During the Tertiary, numerous *Haemaphysalis* species coevolved along a distinctively specialized structural line with birds and mammals in much of the world except in the Nearctic and Neotropical, where there now are only five species. The Eurasian-African (Palearctic-Ethiopian) Hyalomminae (1 genus) retain significant primitive structural properties but most groups of *Hyalomma* became highly specialized biologically for survival in harsh environments with low population densities of hosts. The Rhipicephalinae (114 species in 8 genera) evolved most recently of all ixodid ticks as Eurasian-African parasites of mammals with few *Dermacentor* species in the Americas and no native representatives in Australia, New Guinea, or Madagascar. Rhipicephalinae are all tropical except one of the three African *Margaropus* species, both Asian *Anomalohimalaya* species, and several North American-Eurasian *Dermacentor* and Eurasian *Rhipicephalus* species.

A strict or limited degree of host specificity characterizes at least 700 of the 800 species of biologically and structurally conservative obligatory parasites constituting the superfamily Ixodoidea (HOOGSTRAAL, 1978). Indeed, host specificity is one of several important biological factors contributing to confining the ecological and geographical distribution and population densities of most tick species. The often repeated assertion that ticks lack host specificity is an ill-advised biological generalization.

Patterns of strict or limited host specificity, established through eons of host-parasite co-evolution in geographical and/or ecological isolation, may be broken when physiologically acceptable domestic or feral vertebrates, introduced by Recent human activities, intrude into the primeval host-parasite domain. This surrogate-host-parasite relationship often becomes so prevalent and economically important in exploited regions of chief concern to humans that we lose sight of original host-parasite relationships. Anthropocentric concern obscures recognition of biological and physiological properties that can be useful for developing integrated control measures against ticks.

Certain anomalies in recorded data have also contributed to incorrect or ambiguous host-specificity conclusions found in literature. When even the most host-discriminating (host-specific) tick is accidentally dislodged during the extended feeding process, its discriminatory senses are dullened or lost. The dislodged, partially fed tick, now intensely programmed to complete a bloodmeal, strives to feed wherever possible: on another tick, through a crack in wood, through the shell of a reptile egg, on an insect, or on any available vertebrate animal. Thus, host data are «loaded» by incidents of host-specific tick species feeding on predatory or scavenger vertebrates that have disturbed the feeding parasites while tearing their host apart. Human hunters (predators) similarly become tick-infested when handling and skinning game animals...and might suffer afterward from Rocky Mountain spotted fever, Colorado tick fever, tularemia, or other tick-transmitted disease agents. Milkmaids and herdsmen pick ticks from the animals in their charge and often drop the parasites on the ground. The dislodged ticks may rapidly resume feeding on the milkmaids and herdsmen. Recorded tick-transmitted Crimean-Congo hemorrhagic fever morbidity is high in these two occupational groups in the USSR.

Vertebrates that congregate in dense resting and/or breeding colonies (burrow or den-systems, caves, rookeries), or periodically revisit nesting or resting sites on the ground, ledges, or trees, are characteristically parasitized by strictly specific tick species. Moderately specific species may also infest some of these vertebrates. Wandering vertebrates, with (A) extensive home ranges, (B) generally low population densities, and (C) not congregating in specific sites for nesting or resting, are characteristically parasitized by species that have (A) «atypical» life cycles (1- or 2-host types) or (B) moderate or nonparticular host specificity. Where A, B, or C does not apply to a wandering vertebrate, more strictly host-specific ticks with 3-host cycles may characterize a tick-host relationship.

Most tick species of greatest importance in both human and veterinary medicine parasitize domestic cattle, yaks, buffalo, camels, sheep, goats, pigs, dogs, chickens, or pigeons. These ticks were already strictly or moderately host specific for the same vertebrate species, genera, or families before man domesticated the animals as food sources or as beasts of burden. Many of these parasites had already shown exceptional (for ticks) biological adaptability in life cycle adjustments for surviving on wandering wild animals (deer, antelopes, cattle, goats, sheep). Concentrated herds and flocks of sedentary domestic animals enhanced these ticks' chances for survival. Pastures, stone fences, vegetated windbreaks, stables, barns, caravansaries, bird cotes, houses, and irrigation in arid zones provided hosts and shelters further enhancing the ticks' ability to survive and multiply. Driving or transporting domestic animals to more or less distant areas, and making the new areas ecologically suitable for the animals as well as for the ticks, vastly increased the intercontinental and intracontinental geographic range of many tick parasites of domestic animals.

Our investigations of the tick faunas of the continents and islands of the world, and of the host preferences of immature and adult stages, external and internal structures in relation to hosts and environment, ecology, zoogeographical distribution, phylogeny, physiology, biochemistry, behavior, life cycles, dynamics, biosystematics, virus infections, etc., have led us to conclude that the Superfamily Ixodoidea arose as obligate parasites of Reptilia in the late Paleozoic or early Mesozoic (200 million years ago) (HOOGSTRAAL, 1978).

TICK LIFE CYCLES

Historical implications

To understand the nature of host specificity, we need to know, insofar as possible, the historical relationships between these parasites and their hosts both before and after man revolutionized the environments and faunal composition of the world in recent times. Different life cycle patterns evolved before the time of man and domestic animals where low host densities and wandering behavior made survival impossible for populations of ordinary 3-host ixodid ticks. Human animal husbandry practices are a boon to ticks with life cycles differing from the 3-host type. Deep appreciation of these patterns is essential to understanding all aspects of tick evolution, biology, host relationships, and epidemiological interactions. Knowledge of the basic life cycle patterns, first categorized by NUTTALL (1911a, b, 1913, 1915), and elaborated by HOOGSTRAAL (1956, 1978), BALASHOW (1968), and many others, was schematized by AESCHLIMANN (1977). These patterns are illustrated in Figs. 2 and 3.

Oviposition

All tick eggs are deposited off the host (Figs. 2, 3), except that *Argas (Microargas) transversus* oviposits on its Galapagos giant tortoise hosts (R. C. A. RICE; pers. commun.) (Table 1) and *Ixodes (Lepidixodes) kopsteini,* a parasite of Oriental and Ehtiopian bats, produces larvae from eggs hatching within the dead female. These unique episodes appear to be associated with host movements in search of food and the minute size of the ticks (the smaller the tick size, the more unusual are often the life cycle and structural properties).

Larval feeding

All argasid and ixodid larvae feed only once (or, subgenus *Ornithodoros,* not at all). The subgenus *Ornithodoros* inhabits burrows (warthogs, antbears, etc.) or scrapes (tortoises) to which hosts may return irregularly.

Multihost life cycle

The multihost pattern characterizing the family Argasidae (Fig. 2) represents primitive relationships between ticks and hosts (HOOGSTRAAL, 1978). Argasid nymphs undergo several instars and feed on an available host during each instar. Argasid adults feed several times, usually copulate several times, and females deposit a new egg batch after each full bloodmeal. These «endophilic» ticks, inhabit burrows, crevices, or other shelters to which a limited variety of vertebrates return periodically for nesting and/or resting. Multihost argasids may feed on unusual visitors to the shelter (humans or predators) but can seldom if ever complete their life cycle on atypical hosts in nature. A few argasids are more host-adaptable than most; these adaptable species thrive in man-made pigsties, stables, caranvansaries, and stone fences around pastures and feedlots. A few argasids *[Ornithodoros (Alectorobius) lahorensis, Otobius spp.]* adapted before the advent of man to survival with wandering herbivores utilizing an extensive home range away from shelters. In these exceptionally adaptable argasid species, the larva molts to a nymph on the host and the nymph undergoes several instars on the same host animal *[Ornithodoros (Alectorobius) lahorensis]* or the adults do not feed (Otobinae, Antricolinae, Nothoaspinae).

Three-host life cycle

In the family Ixodidae, about 600 of the ca. 650 species undergo a 3-host life cycle (Hoogstraal, 1978). The larval, nymphal, and adult stages each feed only once (Fig. 3). In «endophilic» species, in which each developmental stage inhabits

Stage (Phase)	Multihost	Remarks
EGG	all on ground	
LARVA (single feeding, usually long)	host 1	
	molt/ground	
NYMPH (several feedings, each short)	host 2	Generally 3-4 nymphal instars and hosts; may be more (5-8)
	molt/ground	
	host 3	
	molt/ground	
	host 4	
	molt/ground	
ADULT (several feedings, each short, and matings)	host 5	Adults feed and mate several times (3-5/6) (no molting)
	host 6	
	host 7	
(♀ oviposition) several (once after each bloodmeal) all on ground.		

Fig. 2: Argasid life cycle pattern (typical).
[For variations, see text and Hoogstraal (1978).]

a specific shelter, hosts of immatures and adults are generally the same, but not necessarily the same individual, and specificity is quite strict or quite limited. In species whose unfed adults emerge from the shelter entrance to become «exophilic» and seek a larger-sized wandering host, dichotomy is often extreme (Hoogstraal, 1956, 1978). In species that are nonsheltered (exophilic) in each developmental stage, stage-to-stage host preferences may be more or less alike or vastly different (especially between nymphal and adult stages). Three-host ixodids apparently co-evolved with large-sized Reptilia in the Paleozoic and/or Mesozoic and most species retain this primitive, conservative, hazardous life cycle pattern until today.

Two-host life cycle

The two-host pattern (Fig. 3), in which the larval and nymphal stages feed on one host and the adult stage on a second host, evolved in the Tertiary or afterward as an obligatory or occasionally facultative life cycle phenomenon among a few *Hyalomma* and *Rhipicephalus* parasites of wandering mammals in inclement environments (Hoogstraal, 1978).

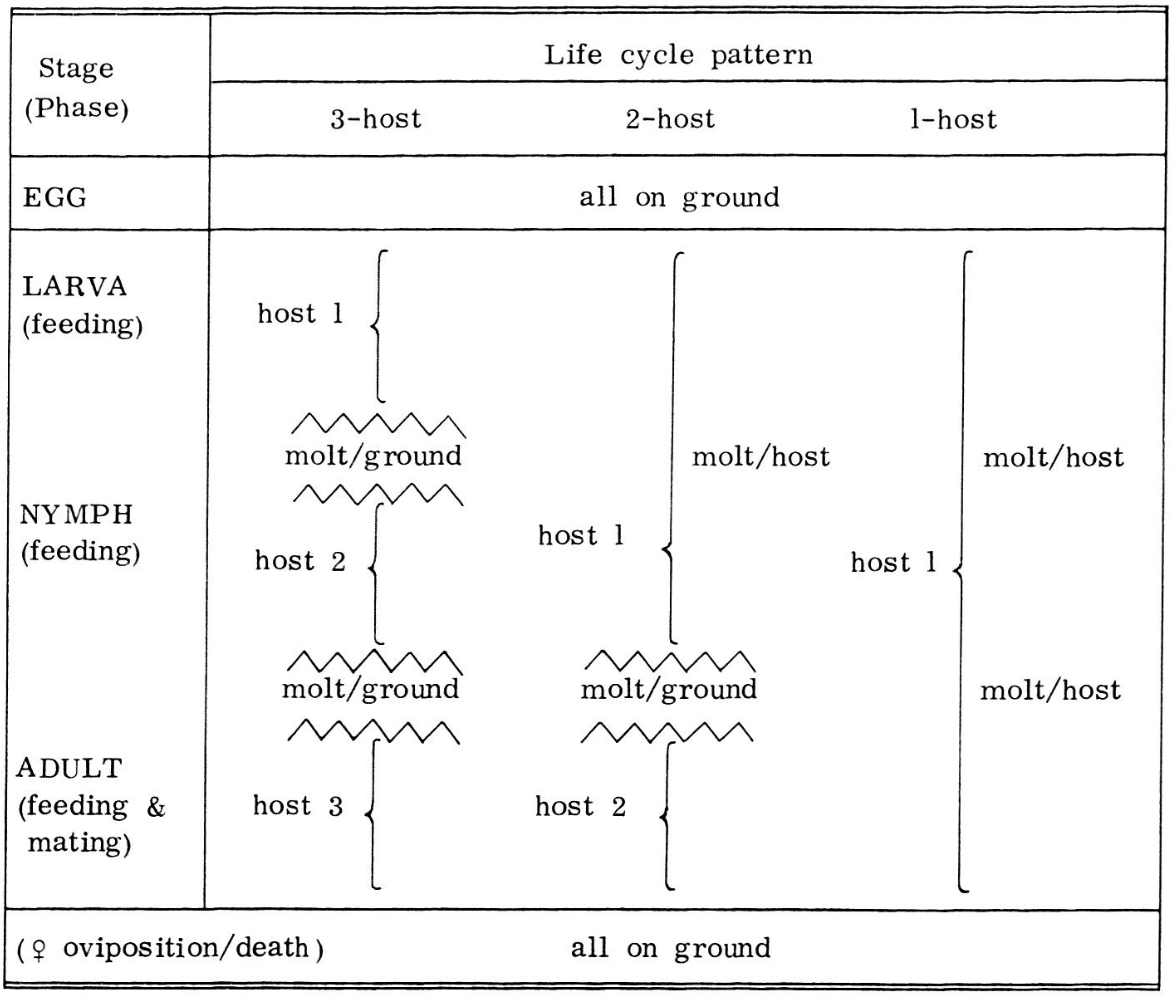

Fig. 3: Inoxid life cycle patterns

One-host life cycle

The 1-host cycle (Fig. 3) evolved rather recently in small-sized *Boophilus* and *Margaropus* (and in 2 or 3) *Dermacentor* species) parasitizing larger-sized herbivorous mammals (Perissodactyla and Artiodactyla) with extensive home ranges and secondarily, in some species of colder areas of temperate zones that parasitize wandering herbivorous mammals *(Dermacentor albipictus, Hyalomma scupense).*

Parthenogenesis

This phenomenon characteristically occurs only in northern populations of *Haemaphysalis (Kaiseriana) longicornis,* a temperate-zone outlier of a tropical, herbivore-parasitizing tick group, and in *Amblyomma rotundatum* and *A. cordiferum,* which parasitize Neotropical Amphibia (toads) and Oriental Reptilia (snakes), respectively.

Results of collaborative investigations between NAMRU-3 and South African scientists are suggestive of parthenogenesis (yet unproven) in *Nuttalliella namaqua* (Nuttalliellidae). The life cycle of this unique tick is unknown.

TICKS AND REPTILES

The basic biological, physiological, and structural properties of ticks appear to have been established during parasitic associations with Paleozoic-Mesozoic reptiles (HOOGSTRAAL, 1978). In the early Tertiary (70 million years ago), when bird and mammal lines exploded, the variety, numbers, and size of reptiles diminished. Tick-reptile associations became fewer and average tick size also diminished. Despite the few numbers of recent reptiles and of tick-reptile associations (Tables 1–4), many original biological, physiological, and structural properties persist among these biologically conservative parasites.

The question of parasitism on reptiles by the single species in the Family Nuttalliellidae is under study. Six of the ca. 155 species of the Family Argasidae are specific for reptiles (Table 1). In the Family Ixodidae, strict reptile-host specificity is dominant in the genus *Aponomma* (Table 2) and strong in *Amblyomma* (Table 3). The proliferation of *Aponomma* and *Amblyomma* species strictly specific for Australian tortoises and agamid, scincid, and varanid lizards is noteworthy. Equally notable are the six *Amblyomma* species on Galapagos reptiles, three on the giant tortoise and three on iguanid lizards. In *Haemaphysalis* (Table 4), more or less frequent parasitism of reptiles by immatures (virtually never by adults) is restricted to a few phylogenetically primitive or intermediate species. In *Hyalomma* (Table 4), only a single species (subgenus *Hyalommasta)* is reptile dependent; however, immatures of certain other species (subgenus *Hyalomma)* occasionally parasitize reptiles. Immatures of the subgenus *Hyalommina* are not known to infest reptiles. Immatures of fewer than 10 *Ixodes* species feed on reptiles, but also on birds and mammals. None of the ca. 115 species in the ixodid subfamily Rhipicephalinae parasitize reptiles. All ixodid parasites of reptiles, and the single *Amblyomma* species parasitizing Amphibia are, so far as we know, 3-host ticks. (The possibility that some species have 1-host pattern should be considered.) The fascinating subject of tick-reptile specificity and co-evolution will be reviewed in a more detailed report.

TYPES OF TICK-HOST SPECIFICITY

Some diversification of reptile-host specificity may have occurred during the Mesozoic but evidence pointing to early adaptations to different hosts is clouded by the essential conservativeness of tick structure, physiology, behavior, and bionomics, as well as by the extreme reduction in size, variety, and numbers of post-Mesozoic reptiles. Host-related structural, physiological and biological variations seen today reflect adaptations associated with parasitizing the birds and mammals that evolved during the Tertiary. Thus, it is logical to outline tick-host specificity types at this stage in our discussion. In elaborating this outline, we can progress toward answering the questions raised by MAYR (1957) (quoted in our introductory paragraph).

TABLE 1. TICKS AND REPTILES (1). STRICT - TOTAL SPECIFICITY: *ARGASIDAE*

Genus Argas[*]

NEOTROPICAL: Argas (Microargas) transversus[+]*:* Galapagos giant tortoise.

MALAGASY: Argas (Secretargas) hoogstraali: Opulurus lizards (3 spp.).

PALEARCTIC: Argas (subgenus & species undescribed): Afghan lizard.

Genus Ornithodoros[x]

NEOTROPICAL: Ornithodoros (Alectorobius) darwini & O. (A.) galapagensis: Galapagos land and marine iguanid lizards & larva lizard.

ETHIOPIAN: Ornithodoros (O.) compactus: tortoise.

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[*] Among the 55 species of *Argas, A. (Secretargas) transgariepinus* and *A. (Ogadenus) brumpti* sometimes feed on reptiles. All other *Argas* are specific for birds (40 spp.), bats (10 spp.) or mammals (2 spp.).

[+] *A. (M.) transversus* is the only tick species known to oviposit on the host (i. e., even the egg stage is host-specific).

[x] Among the ca. 100 species of *Ornithodoros,* ca. 15 other species more or less frequently feed on reptiles entering shelters where the ticks await their usual mammal or bird hosts.

TABLE 2. TICKS AND REPTILES (2). STRICT - TOTAL SPECIFICITY: *IXODIDAE (1)*

Genus Aponomma

22 of the 24 *Aponomma* species are Strict-Total parasites of large snakes and/or varanid lizards (not iguanid lizards or tortoises). [The 2 other species parasitize Australian mammals (echidna & wombat).] There are virtually no atypical host records of *Aponomma* ticks. Distribution: Australian (including 1 sp. on the New Zealand tuatara) and Oriental (44 spp.), Ethiopian (4 spp.), Neotropical and Nearctic (1 sp. each). Palearctic (0). Malagasy (0).

TABLE 3. TICKS AND REPTILES (3). STRICT - TOTAL SPECIFICITY: *IXODIDAE (2)*

Genus Amblyomma

(37 of the 102 *Amblyomma* species are specific for Reptiles; all specificity is Strict-Total unless otherwise stated in footnotes.)
AUSTRALIAN [tortoises, snakes, lizards (Varanidae, Scincidae, Agamidae)]: *A. albolimbatum, A. calabyi, A. limbatum, A. moreliae.*

ORIENTAL (tortoises, snakes, varanid lizards): *A. clypeolatum, A. cordiferum, A. geomydae*[*+], *A. helvolum*[+], *A. nitidum* (sea snakes), *A. robinsoni* (Komodo lizard), *A. squamosum.*

MALAGASY (tortoise): *A. chabaudi.*

ETHIOPIAN (tortoises, snakes, varanid lizards): *A. marmoreum, A. falsomarmoreum, A. nuttalli*[*], *A. sparsum*[*+], *A. sylvaticum*[*].

NEOTROPICAL (tortoises, snakes, iguanid lizards): *A. albopictum, A. antillorum, A. boneti, A. crassum, A. cruciferum, A. dissimili*[x], *A. fulvum, A. fuscum, A. rotundatum*[x], *A. scutatum, A. subanerae, A. testudinis, A. torrei.* [Galapagos (giant tortoise): *A. macfarlandi, A. pilosum, A. usingeri;* (iguanid lizards): *A. boulengeri, A. darwini, A. williamsi.]*

NEARCTIC (gopher tortoise): *A. tuberculatum*[*].

PALEARCTIC: None.

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[*] Immature stages also parasitize birds and mammals.
[+] Some adults also parasitize pigs, pangolins, or rhinoceros, etc.
[x] Also parasitize Amphibia *(Bufo).*

TABLE 4. TICKS AND REPTILES (4). *IXODIDAE (3)*

Other Genera

Ixodes: Immatures of several Nonparticular species, especially the *I. (I.) ricinus* group (Nearctic, Neotropical, Palearctic), accept available reptiles. *I. (I.) asanumai* may parasitize chiefly lizards in southern Japan (Palearctic).

Haemaphysalis: Immatures of 12 primitive/intermediate Oriental and Palearctic species more or less frequently feed on reptiles; one *[H. (Herpetobia) kashmirensis]* depends on lizards for population survival.

Hyalomma: H. (Hyalommasta) aegyptium (Palearctic) depends on the tortoise *(Testudo)* for survival; immatures also infest lizards, snakes, birds and mammals. Adults of no other *Hyalomma* species parasitize reptiles. Immatures of several subgenus *Hyalomma* species (Palearctic) occasionally feed on reptiles. Immatures of the subgenus *Hyalommina* are not known to feed on reptiles.

RHIPICEPHALINAE (8 genera, 114 spp.): Never or virtually Never feed on reptiles.

The types of tick-host specificity are outlined in Table 5.

The fact that ticks are obligate parasites of reptiles, birds, or mammals causes vertebrate animal kinds and ethological patterns to be the dominant factors relating to tick host-specificity in any form. The fact that most tick species spend much of their lifetime off the host («free-living») causes various ecological-environmental characteristics to be more or less important secondary factors relating to tick host selection, distribution, behavior, life cycle extension (diapause), seasonal dynamics, etc.

TICKS AND BIRDS

The number and variety of tick-bird associations is greater than is generally realized (Table 6).

Family Nuttalliellidae. The single species of this family is circumstantially associated with mud nests constructed on rocks by swallows, but the actual hosts are unknown.

Family Argasidae. Strict-Total specificity for certain birds nesting or resting in trees or in rocky situations characterizes 38 of the 55 *Argas* species and 13 of the 100 *Ornithodoros* species. The specificity for birds of about 10 argasid species is Moderate-Total.

Family Ixodidae. Bird-parasitizing ixodid ticks characteristically lack the well-developed spurs of the coxae, palpi, and basis capituli, and also the marginal concavities or acute angles of parts of the capitulum, that characteristically serve as hair-hooking and grasping devices among smaller-sized adult ixodid parasites of mammals.

Among the 212 *Ixodes* species, 40 are Strict-Total for birds *[Scaphixodes* (6), *Multidentatus* (12), *Ceratixodes* (2), other subgenera (18)]. The hosts are marine birds with fixed nesting or resting sites and others nesting in tree holes or in tunnels in river banks or cliffsides. Ground-feeding birds are more or less prominent among hosts recorded for 16 species in the genus *Ixodes* (8 Nonparticular, 8 Moderate).

Among the 102 *Amblyomma* species, immatures of about 20 in the last two categories of host specificity (M and NP) fairly frequently or often parasitize ground-feeding birds. One, *A. loculosum,* is a Strict-Total parasite of marine birds nesting in the southern oceans. [Historically, reptiles (lizards and tortoises) may also have been important hosts of *A. loculosum.]* The Neotropical *A. longirostre* is in the Strict-Stage group, with adults infesting chiefly the porcupine *(Coendou)* and immatures feeding mostly on various birds.

Among the 155 *Haemaphysalis* species, eight are Strict-Total on ground-feeding birds (7 spp.) or tree-hole nesting birds (1 sp.). About 25 other Moderate-Specific haemaphysalines frequently infest birds: almost exclusively and in each stage *(H. wellingtoni)* or mostly as immatures whose adults are Moderate-Stage-Specific for mammals; two are Nonparticular. *Haemaphysalis* in the Moderate category are usually associated with large-leaved plants or dense clumps of vegetation where certain birds typically rest and predatory mammals search for food or other mammals (such as leporids) come either as transient visitors or to rest or breed. Among the well known species in this category are immatures of *H. leporispalustris, H. concinna, H. punctata, H. kutchensis,* and *H. bispinosa.*

TABLE 5. TYPES OF TICK-HOST SPECIFICITY

1. STRICT-TOTAL (ST): Both adults and immatures (nymphs & larvae are strictly specific for the same limited host group («monotropic»). *ARGASIDAE* (all genera) & *IXODIDAE* (chiefly *Aponomma, Boophilus, Margaropus,* and a few species in other major genera).
2. MODERATE-TOTAL (MT): As above, but the host group is somewhat less limited (the available data in this category are often imprecise) (chiefly *Ornithodoros, Ixodes, Amblyomma, Rhipicephalus).*
3. STRICT-STAGE-STAGE (SSS): Adults and immatures are each strictly specific for different limited host groups («tritropic»). *IXODIDAE* (chiefly *Ixodes, Amblyomma, Hyalomma, Dermacentor, Nosomma, Rhipicephalus).*
4. STRICT/MODERATE-STAGE-STAGE (SMSS): *IXODIDAE*
   A. Adults are strictly specific for a host group; immatures are moderately specific for a different group («ditropic-A»).
   B. Immatures are strictly specific for a host group, adults are moderately specific for a different group («ditropic-B»).
5. MODERATE-STAGE-STAGE (MSS): Adult and immature specificity for host groups are moderately limited («telotropic-moderate»). *IXODIDAE.*
6. NONPARTICULAR (NP): Adults and immatures are both catholic in host acceptability («telotropic»). *IXODIDAE.*

TABLE 6. TICKS AND BIRDS

ARGASIDAE

STRICT-TOTAL SPECIFICITY: *Argas:* subgenera *Argas* (all 21 spp., each Region except Malagasy) and *Persicargas* (all 17 spp., each Region) [see HOOGSTRAAL *et al.* (1979) for details]. *Ornithodoros:* subgenera *Proknekalia* (all 3 spp., Palearctic and Ethiopian). *Alectorobius capensis* group with marine birds (6 spp.) and others nesting on rocks (3 spp.) [each Region (except Malagasy)] and *Pavlovskyella* (1 sp., Australian tree holes).

MODERATE-TOTAL SPECIFICITY: About 15 species in different subgenera of *Ornithodoros.*

IXODIDAE

STRICT-TOTAL SPECIFICITY: *Ixodes* (±40 spp.), *Haemaphysalis* (8 spp.), *Amblyomma* (1 sp.).

STRICT-STAGE (IMMATURES) SPECIFICITY: *Amblyomma (Haemalastor) longirostre* (Neotropical).

MODERATE (IMMATURES) SPECIFICITY: *Ixodes* (±8 spp.), *Haemaphysalis* (±25 spp.), *Amblyomma* (±17 spp.), *Hyalomma* (6 spp.).

NONPARTICULAR (CHIEFLY IMMATURES) SPECIFICITY: *Ixodes* (±8 spp.), *Haemaphysalis* (2 spp.), *Amblyomma* (±8 spp.).

It is important to record that no *Aponomma* (24 spp.) feed on birds and that no *Hyalomma* (30 spp.) are specific parasites of birds; however, immatures of six *Hyalomma* frequently feed on birds (as well as on mammals; some also on reptiles). No Rhipicephalinae (114 spp.) characteristically feed on birds. A few adult and/or immature *Rhipicephalus* occasionally infest large-sized ground-feeding birds. Immature *Dermacentor* rarely parasitize birds; adults never do so. The almost exclusive limitation of bird-ixodid relationships to subfamilies other than Rhipicephalinae appears to have considerable phylogenetic and evolutionary significance.

The burgeoning basic knowledge of tick and bird interrelationships appears in a relatively small group of recent, easily available publications. Thus, owing to space and time limitations, we do not review this subject in detail here.

TICKS AND MAMMALS

Monotremata (Table 7). Strict-Total parasites are *Ixodes ornithorhynchi* of the platypus and *Amblyomma echidnae* and *Aponomma concolor* of the echidna. Moderate (4 spp.) and Nonparticular (3 spp.) *Amblyomma* (4 spp.), *Ixodes* (2 spp.) and *Haemaphysalis* (1 sp.) parasitize the echidna.

TABLE 7. TICKS AND MAMMALS (1). MONOTREMATA AND MARSUPIALIA* (AUSTRALIA-NEW GUINEA)

Monotremata

STRICT-TOTAL SPECIFICITY (4 spp.): *Ixodes (-) ornithorhynchi* (platypus). *Ornithodoros (Pavlovskyella)* sp. undescribed, *Amblyomma (Adenopleura) echidnae, Aponomma concolor* (echidna).

MODERATE SPECIFICITY: *Amblyomma* (3 spp.), *Haemaphysalis* (1 sp.).

NONPARTICULAR SPECIFICITY: *Amblyomma* (1 sp.), *Ixodes* (2 spp.).

Marsupialia

STRICT-TOTAL SPECIFICITY (12 spp.): *Ornithodoros (Pavlovskyella) gurneyi* & sp. undescribed (wallaby & kangaroo). *Ixodes (Endopalpiger) victoriensis* (wombat), *I. (Exopalpiger) antechini* (dasyurids), *I. (E.) vestitus* (marsupial anteater), *I. (Sternalixodes) trichosauri* (bandicoots), *I. (S.) cordifer* (cuscus), *I. (Exopalpiger) fecialis* (various). *Haemaphysalis (Ornithophysalis) petrogalis* (wallaby). *Amblyomma (-) postoculatum* (wallaby), *A. (-) macropi* (kangaroo). *Aponomma auruginosus* (wombat).

MODERATE SPECIFICITY (8 spp.): *Ixodes* (6 spp.), *Haemaphysalis* (2 spp.).

NONPARTICULAR SPECIFICITY (3 spp.): *Ixodes* (2 spp.), *Haemaphysalis* (1 sp.).

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*Neotropical opossums (Marsupialia: Didelphidae) are parasitized by *Ixodes (I.) loricatus* (Strict-Total) and adult *I. (I.) luciae* (immatures chiefly on rodents). Moderately specific and Nonparticular ticks also parasitize Neotropical and Nearctic opossums.

Marsupialia (Table 7). *Ornithodoros (Pavlovskyella) gurneyi* and a related undescribed species are Strict-Total parasites in shaded resting places of certain wallabys and kangaroos. Strict-Total ixodid parasites of Australian-New Guinean marsupials are *Ixodes* (6 spp.), *Amblyomma* (2 spp.), *Aponomma* (1 sp.), and *Haemaphysalis* (1 sp.). Moderately specific and Nonparticular ixodids are *Ixodes* (6 and 2 spp.) and *Haemaphysalis* (2 and 1 spp.). The chief *Haemaphysalis* parasites of marsupials have the facies of bird-associated haemaphysalines.

The paucity of tick species specific for contemporary Australian marsupials may result from a combination of factors including harsh environment and low population densities of many marsupial species together with extensive home ranges and solitary habits.

The specificity of two of the 24 *Aponomma* species for a monotreme and a marsupial host, while the 22 other species of this genus parasitize only reptiles, probably reflects an ancient changeover in host preference.

Neotropical marsupials have only two strict (Strict-Total and Strict-Stage) *Ixodes* parasites. Neotropical and Nearctic Didelphidae are parasitized by several *Ixodes* and *Amblyomma* species with Moderate or Nonparticular specificity but seldom by other ixodid genera.

Insectivora (Table 8). The Strict-Total specificity of eight species *[Argas* (1), *Ixodes* (1), *Haemaphysalis* (6)] on Madagascar tenrecs is noteworthy. About an equal number of *Ixodes* and *Haemaphysalis* are Strict-Total parasites of Insectivora in other Regions (in the Nearctic only *I. soricis;* in the Neotropical, none). Some adults and numerous immatures of tick species with Moderate and Nonparticular specificity infest insectivores.

Chiroptera (Table 9). The 55 Strict-Total tick species parasitizing bats (24 in the Old World, 31 in the New World) are listed by subgenus or species in Table 9. The large colonies of bats in caves and other structures sheltering both the bats and the ticks in a limited area provide for an optimum host-parasite relationship.

TABLE 8. TICKS AND MAMMALS (2). INSECTIVORA

STRICT-TOTAL SPECIFICITY: *(MALAGASY* tenrecs) (8 spp.): *Argas (Secretargas) echinops, Ixodes (I.) lunatus, Haemaphysalis (Ornithophysalis) simplex, H. (O.) simplicima, H. (Elongiphysalis) elongata, H. (E.) subelongata, H. (E.) tiptoni, H. (Sharifiella) theilerae.* [Ixodid parasites of tenrecs also infest *Rattus rattus,* which was recently introduced into Madagascar and has spread extraordinarily widely there, but these ticks seldom feed on endemic Malagasy rodents (Nesomyidae).]

STRICT-TOTAL SPECIFICITY: *(ETHIOPIAN):* Examples: *Ixodes (Afrixodes) dawsi* (Potamogalidae), *Haemaphysalis (Rhipistoma)* sp. undescribed (Erinaceidae).

OTHER CATEGORIES: Examples of ticks that commonly infest insectivores but are not totally dependent on them are *Ixodes (Pholeoixodes) soricis* (Nearctic, Soricidae), *I. (P.) hexagonus* and *H. (R.) erinacei* subspp. (Ethiopian, Erinaceidae), and *I. (Afrixodes) bedfordi* and *I. (Exopalpiger) alluaudi* (Ethiopian, Soricidae). Other families of Insectivora are not known to be parasitized by host-specific ticks.

Wide seasonal movements and migrations of bat hosts have permitted the extraordinarily extensive distribution of certain tick species. *Argas (Chiropterargas) boueti* occurs through much of Africa eastward to Malaysia, *A. (Carios) vespertilionis* in Africa, Europe, and southwestern Asia to India, *Ixodes (Echatocephalus) simplex* and *I. (E.) vespertilionis* in Africa, Europe and southern Asia; the former is also present in Australia. *Argas (Secretargas) transgariepinus* ranges from southern Africa to middle Europe. However, other bat-parasitizing species are much more restricted in distribution. Notably, the Old World and the New World share no subgenera of argasid or ixodid parasites of bats.

The presence of *Ixodes (Lepidixodes) kopsteini* (with its unique type of egg-larva production - see Table 9) in southern Asia (Malay peninsula, Java, Sulawesi), Australia, New Guinea, and Central and East Africa possibly represents historical Gondwanaland relationships. If this were true, one wonders whether *I. (L.) kopsteini* remains to be discovered in Borneo and Madagascar.

Primates (Table 10). Two *Ixodes* species are Strict-Total parasites of African *Colobus* and *Cercopithecus* monkeys (and occasionally also *Galago* bushbabies). One *Ixodes* and one *Haemaphysalis* are Strict-Total parasites of Malagasy lemurs.

TABLE 9. TICKS AND MAMMALS (3). CHIROPTERA

ARGASIDAE

STRICT-TOTAL SPECIFICITY (52 spp.). *PALEARCTIC, ETHIOPIAN, ORIENTAL, MALAGASY, AUSTRALIAN: Argas (Carios)* (all 6 spp.), *A. (Chiropterargas)* (all 4 spp.), *Ornithodoros (Reticulinasus)* (all 11 spp.). *NEARCTIC-NEOTROPICAL: O. (Alectorobius)* (20 spp.). *O. (Subparmatus)* (all 3 spp.). *Antricola* (all 7 spp.). *Nothoaspis* (monotypic).

MODERATE SPECIFICITY (1 sp.). *ETHIOPIAN, PALEARCTIC: Argas (Secretargas) transgariepinus.*

IXODIDAE

STRICT-TOTAL SPECIFICITY (3 spp.). *PALEARCTIC, ETHIOPIAN, ORIENTAL, AUSTRALIAN: Ixodes (Eschatocephalus) simplex, I. (E.) vespertilionis, I. (Lepidixodes) kopsteini*. NEARCTIC-NEOTROPICAL:* none.

**I. (L.) kopsteini* is the only tick species in which embryogenesis and larval hatching occur inside the dead female exoskeleton.

TABLE 10. TICKS AND MAMMALS (4). PRIMATES*

STRICT-TOTAL SPECIFICITY (4 spp.). *ETHIOPIAN (Colobus* and *Cercopithecus* monkeys): *Ixodes (Afrixodes) schillingsi, I. (A.) rageaui. MALAGASY* (Lemurs): *I. (A.) lemuris, Haemaphysalis lemuris.*

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*Adults and/or immatures of other *Ixodes, Amblyomma, Haemaphysalis, Dermacentor* and *Rhipicephalus* species more or less frequently feed on monkeys and other primates and may be important in the epidemiology of infections of wildlife and humans.

Adults and/or immatures of other *Ixodes, Amblyomma, Haemaphysalis, Dermacentor* and *Rhipicephalus* species incidentally infest primates in the Ethiopian, Oriental, and Neotropical Regions. Immature *Haemaphysalis (Kaiseriana) spinigera* feeding on monkeys or humans are primary vectors of Kyasanur Forest disease virus (Bunyaviridae, *Flavivirus)* in Karnataka, India, but numerous other tick species participate in the enzootic circulation of this virus.

Edentata (Table 11). Five *Amblyomma* (subgenus *Amblyomma)* species are Strict parasites of Neotropical Edentata (two Strict-Total, three Strict-Stage). In the same subgenus, two other species are moderately specific for armadillos and several others also infest various edentates. The limited proliferation of ticks associated with Edentata is noteworthy.

Pholidota (Table 11). Two *Amblyomma* (subgenus *Adenopleura)* species, one Oriental and one Ethiopian, are Strict-Total parasites practically wherever pangolins or scaly anteaters occur. Notably, other *Adenopleura* species are specific for reptiles [except *A. (A.) loculosum,* recorded mostly from nesting marine birds]. Few other ticks parasitize pangolins in nature.

Lagomorpha (Table 12). Pikas (Ochotonidae) are incidentally parasitized by a variety of Moderate Specificity ticks in the Nearctic and Palearctic. They are hosts of two Strict-Total *Ixodes* species in the Himalaya (Palearctic-Oriental marginal area) and of the Moderate-Total *Ixodes (Pholeoixodes) ochotonae* in the Nearctic. More intensive search, or more exact reporting, should reveal additional tick species associated chiefly with the pika.

Rabbits and hares (Leporidae) are exceptionally attractive hosts for numerous immatures and some adults of tick species with various types of Moderate

TABLE 11. TICKS AND MAMMALS (5). EDENTATA AND PHOLIDOTA

Edentata *(NEOTROPICAL)**

Anteaters *(MYRMECOPHAGIDAE)*

STRICT-TOTAL SPECIFICITY: *Amblyomma (A.) calcaratum.* STRICT-STAGE (ADULT) SPECIFICITY: *A. (A.) nodosum, A. (A.) pictum.*

Sloths *(BRADYPODIDAE)*

STRICT-TOTAL SPECIFICITY: *A. (A.) perpunctatum (= geayi).* STRICT-STAGE (ADULT) SPECIFICITY: *A. (A.) varium.*

Armadillos *(DASYPODIDAE)*

MODERATE SPECIFICITY: *A. (A.) auricularium, A. (A.) pseudoconcolor.*

Pholidota *(MANIDAE)*

STRICT-TOTAL SPECIFICITY: *ORIENTAL: Amblyomma (Adenopleura) javanense. ETHIOPIAN: A. (A.) compressum* (Ethiopian). (Other ticks seldom infest Manidae in nature.)

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*Adults of 5 or more other *Amblyomma* species occasionally infest Edentata; ticks of other genera rarely do so in nature.

Specificity. [See CLIFFORD *et al.* (1976) for ticks infesting hares in Kenya and HOOGSTRAAL (1979) for biologically and epidemiologically important relationships between certain ixodid ticks and hares in Eurasia and Africa.] Perhaps severe competition from numerous Moderate Specificity ixodids accounts for the few ticks with Strict Specificity for leporids. Each strictly specific species is confined to a certain leporid host either having a relatively limited geographic range *[Ixodes (I.) sachelinensis, Haemaphysalis (H.) pentalagi, H. (Rhipistoma) hispanica]* or inhabiting an ecological zone providing little occasion for competition from other ticks *[Otobius lagophilus, Dermacentor (D.) parumapterus, Ixodes (Pholeoixodes) pomerantzevi]. Rhipicephalus (R.) arnoldi* and *R. (R.) deltoideus,* known only from a few Ethiopian leporids, are poorly documented.

Leporids are parasitized by two «remarkable» ticks. *Otobius lagophilus* [adapted to hares (jack rabbits) in arid zones of western North America] has an exceptional life cycle. *Haemaphysalis (Gonixodes) leporispalustris* is distributed from Alaska into Argentina. Notably, the genus *Otobius* contains only two species, both inhabiting similar environments in the Nearctic and having similar unique nonfeeding adult stages. The American continents hold only five of the world's 155 *Haemaphysalis* species, but *H. (G.) leporispalustris* is unique in its extraordi-

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TABLE 12. TICKS AND MAMMALS (6). LAGOMORPHA

Ochotonidae

STRICT-TOTAL SPECIFICITY. *PALEARCTIC: Ixodes (I.) hyatti, I. (-) shahi.*

MODERATE-TOTAL SPECIFICITY. *NEARCTIC: I. (Pholeoixodes) ochotonae.*

OTHER CATEGORIES: Pikas in the Nearctic are also parasitized by immatures of several *Ixodes* and *Dermacentor* species and in the Palearctic-Oriental by occasional immatures of these 2 genera and immatures and adults of several *Haemaphysalis* and *Rhipicephalus* species.

Lagomorpha

STRICT-TOTAL SPECIFICITY: *PALEARCTIC: Haemaphysalis (H.) pentalagi, H. (Rhipistoma) hispanica. NEARCTIC: Otobius lagophilus, Dermacentor (D.) parumapterus. NEOTROPICAL: I. (I.) pomerantzevi, I. (-) ventalloi.*

STRICT-MODERATE STAGE SPECIFICITY. *NEARCTIC-NEOTROPICAL: Haemaphysalis (Gonixodes) leporispalustris. NEOTROPICAL: Amblyomma (-) philipi. NEARCTIC: I. (I.) dentatus. PALEARCTIC: I. (I.) sachalinensis, Rhipicephalus (R.) leporis, R. (R.) pumilio. ORIENTAL: H. (-) kutchensis. ETHIOPIAN: Rhipicephalus (R.) arnoldi, R. (R.) deltoideus.*

OTHER CATEGORIES: Immatures (chiefly) and adults of numerous Nonparticular or Moderate-Specificity species infest lagomorphs, which are often exceptionally attractive hosts to otherwise narrowly discriminating tick species [especially in *Haemaphysalis, Hyalomma,* and *Rhipicephalus* (worldwide except Nearctic and Neotropical), and *Dermacentor* (worldwide temperate zones); relatively few in *Ixodes* and *Amblyomma].*

TABLE 13. TICKS AND MAMMALS (7). RODENTIA (1): STRICT-TOTAL SPECIFICITY*

Neotropical Region

SCIURIDAE: Ixodes (I.) guatamalensis, I. (I.) tamaulipas, I. (I.) tiptoni. GEOMYIDAE: I. (I.) tecpanensis, I. (Pholeoixodes) dampfi. HETEROMYIDAE: I. (I.) sinaloa. CRICETIDAE: Ornithodoros (Alectorobius) casebeeri, O. (A.) puertoricensis, O. (-) aragaoi, O. (-) davisi, I. (I.) galapagoensis, I. (I.) nectomys, I. (I.) tancitarius, I. (I.) tropicalis, I. (Exopalpiger) andinus, I. (E.) jonesae, I. (Haemixodes) uruguayensis. DASYPROCTIDAE: I. (I.) lasallei, Amblyomma (A.) pacae. CHINCHILLIDAE: I. (P.) nuttalli. CAPROMYIDAE: I. (Alloixodes) capromydis. ECHIMYIDAE: O. (A.) echimys. VARIOUS RODENT FAMILIES: I. (-) sigelos.

Nearctic Region

SCIURIDAE: Ornithodoros (Pavlovskyella) hermsi^{+}*, Ixodes (Pholeoixodes) hearlei, I. (P.) marmotae*$^{+}$*, I. (P.) marxi*$^{+}$*, I. (P.) sculptus. GEOMYIDAE: I. (P.) holdenreidi. HETEROMYIDAE: I. (I.) jellisoni. CASTORIDAE: I. (P.) banksi. CRICETIDAE: O. (O.) eremicus, O. (P.) sparnus, I. (I.) peromysci, I. (P.) woodi. VARIOUS RODENT FAMILIES: I. (I.) eadsi, I. (I.) minor, I. (I.) neotomae, I. (P.) angustus, I. (P.) kingi, I. (P.) marmotae.*

Palearctic Region

SCIURIDAE: Argas (-) bureschi, Ixodes (Pholeoixodes) crenulatus^{+}*, Haemaphysalis (H.) verticalis*$^{+}$*. CRICETIDAE: Anomalohimalaya lama*$^{+}$*, A. lotozkyi. MURIDAE: I. (I.) apronophorus*$^{+}$*, I. (I.) nipponensis, I. (I.) occultus, I. (I.) redikorzevi*$^{+}$*, I. (P.) angustus*$^{+}$*, I. (P.) pomerantzevi*$^{+}$*. CTENODACTYLIDAE: Rhipicephalus (Pterygodes) fulvus. MISCELLANEOUS RODENT FAMILIES: I. (I.) laguri.*

Ethiopian Region

SCIURIDAE: Haemaphysalis (Rhipistoma) calcarata, H. (R.) houyi. MURIDAE: Ornithodoros (Pavlovskyella) zumpti, Ixodes (Afrixodes) bedfordi, I. (A.) elongatus^{+}*, I. (A.) minutae, I. (A.) myotomys, I. (A.) rhabdomysae, I. (A.) transvaalensis. HYSTRICIDAE: O. (Alveonasus) eboris, H. (Ornithophysalis) tauffliebi*$^{+}$*. THYRONOMYIDAE: Rhipicephalus (R.) simpsoni.*

Malagasy Region

NESOMYIDAE: Ornithodoros (P.) grenieri, Ixodes (Afrixodes) albignaci, I. (A.) nesomys, I. (A.) randrianasoloi, Haemaphysalis (Dermaphysalis) nesomys, H. (-) anoplos.

Oriental Region

SCIURIDAE: Ixodes (I.) kuntzi, I. (I.) petauristae, Haemaphysalis (H.) verticalis, H. (Ornithophysalis) sciuri, H. (Rhipistoma) bartelsi. CRICETIDAE: Rhipicephalus (R.) ramachandrai. MURIDAE: I. (I.) granulatus, I. (I.) himalayensis, I. (I.) werneri, I. (Afrixodes) radfordi, H. (O.) bandicota, H. (O.) kadarsani. HYSTRICIDAE: H. (Aborphysalis) atherurus, H. (A.) kyasanurensis^{+}*.*

Australian Region

MURIDAE: Ixodes (Endopalpiger) hydromydis, Haemaphysalis (Ornithophysalis) ratti[+].

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[*] This listing is close to complete but not complete.

[+] May also infest other ground-dwelling, small-sized mammals (however, data from carnivores re believed generally to be associated with predation on infested rodents).

narily extensive distribution (which does not result from human activity). It is closely related only to *H. (G.) juxtakochi,* a parasite of Neotropical deer. Immature *H. (G.) leporispalustris* and *H. (-) kutchensis* infest both ground-feeding birds and leporids but adults are strictly specific parasites of leporids.

On each continent where leporids occur, they have major roles in the survival of populations of a variety of tick species [among them *Ixodes (I.) dentatus* and *I. (I.) spinipalpis* in the Nearctic]. However, the biologically and epidemiologically important subject of utilization of leporid and different hosts by numerous tick species remains to be investigated more precisely in many areas of the world.

Rodentia (Tables 13, 14). Accurate appraisal of the complex topic of tick-rodent specificity is, in many areas, bedeviled by lack of investigation, scanty data, or ambiguous reporting in literature. Here we can present merely a brief introduction to the subject and point to the need for more intensive investigations of rodent-tick specificity at many levels.

Strict-Total specificity. Most Rodentia parasitized by Strict-Total ticks shelter in burrows or rock ledges, many of which have been insufficiently investigated for the purpose of this overview. Known Strict-Total tick species of Rodentia in the Neotropical and Nearctic number 23 and 18, respectively (Table 13). These 41 species are limited to three widely distributed subgenera of *Ornithodoros,* three widely distributed and two monotypic Neotropical subgenera of *Ixodes,* and one Neotropical subgenus of *Amblyomma.* (The subgenera of three Neotropical *Ornithodoros* and *Ixodes* species are uncertain.)

TABLE 14. TICKS AND MAMMALS (8). RODENTIA (2): OTHER SPECIFICITY CATEGORIES

Moderate-Total Specificity: Several species in each genus listed in Table 13 (each Region except MALAGASY).

Strict- and Moderate-Stage-Stage Specificity: See text on Rodentia and sections and tables for Lagomorphs, Carnivora, Proboscoidea, Perissodactyla, and Artiodactyla, which are often hosts of adults whose immatures feed exclusively or frequently on Rodentia. Chiefly *Ixodes, Amblyomma, Haemaphysalis, Hyalomma, Dermacentor, Rhipicephalus* (each Region except Australian and Malagasy). Adults of some species *[Hyalomma (Hyalommina) hystricis (ORIENTAL)]* are specific for larger-sized rodents (Hystricidae) but their immatures apparently also infest smaller rodents.

In the Palearctic, known Strict-Total ticks of Rodentia are fewer (12 species). They include eight *Ixodes* in the same «widely distributed» subgenera recorded in the Neotropical and Nearctic; single, unique species of *Argas* and *Rhipicephalus,* both in need of more intensive investigation; and both species of *Anomalohimalaya.* Rather many other Palearctic *Ornithodoros* and *Ixodes* species are at the «upper level» of Moderate specificity (close to Strict-Total) but are difficult to categorize because of imprecise data recording.

Twelve Strict-Total species are listed for Ethiopian Rodentia; the actual number is probably greater. Each of the six *Ixodes* species is a member of the Ethiopian subgenus *Afrixodes.*

Fourteen species are listed for the Oriental; the actual number is probably also greater. Five Oriental *Ixodes* species are in the subgenus *Ixodes,* which is also included in the Neotropical, Nearctic, and Palearctic listings but not elsewhere. The sixth *Ixodes* species is in the subgenus *Afrixodes.*

Malagasy Nesomyidae, with six Strict-Total *Ornithodoros, Ixodes,* and *Haemaphysalis* species, illustrate the extensive radiation of a few vertebrate and parasitic groups characterizing the fauna of Madagascar. Notably, the three *Ixodes* species are members of the subgenus *Afrixodes*... which needs explanation in view of the close relationship between Nesomyidae and Cricetidae, a family poorly represented in the contemporary Ethiopian fauna. Both *Haemaphysalis* species are structurally unusual *[H. (-) anoplos]* or unique *[H. (D.) nesomys]* but poorly known owing to difficult access to their habitats. The wholesale deforestation of Madagascar in recent times has probably wiped out other Strict-Total tick parasites of Nesomyidae.

The few species and low population densities of Australian Rodentia in harsh environments probably account for the fact that only two tick species are Strict-Total here.

Other categories of specificity (Table 14). Rodents are important hosts of many *Ornithodoros* species and of some ixodid species in the Moderate-Total category. Rodents are also important hosts of immature stages of some 300 of the ca. 600 ixodid species with a three-host life cycle pattern. Numerous examples based on reasonably extensive data and intensive investigations could be cited. However, the overall picture is blurred by lack of data or scanty or imprecise data for many species whose immature stages parasitize rodents and also shrews, hedgehogs, rabbits, hares, certain small-sized carnivores, etc. It is futile, at this stage, to try to classify most of these tick species in rigid types of specificity.

Biological questions relating to tick specificity for rodent hosts appear to arise not so much from lack of specificity as from paucity of proper investigation and data reporting in relation to the extent of the subject.

Carnivora (Table 15). The primary parasites of Carnivora are adults of certain species of *Haemaphysalis* and *Rhipicephalus.* Adults of both *Rhipicentor* species feed chiefly on carnivores. Adults of a few *Ixodes* and *Dermacentor* species are specific or moderately specific parasites of carnivores. Some *Hyalomma* species occasionally infest these animals but *Amblyomma* uncommonly do so. *Argas (Ogadenus) brumpti* and a few *Ornithodoros* species parasitize burrow- and den-dwelling carnivores. A certain number of species listed as moderately specific for Perissodactyla and Artiodactyla also more or less frequently parasitize Carnivora.

Hosts of immature stages of primary and secondary parasites of carnivores may be rodents, hares, rabbits, hedgehogs or shrews (depending on species) but rarely birds.

TABLE 15. TICKS AND MAMMALS (9). CARNIVORA*

Strict-Total Specificity. *ALL REGIONS* (domestic dogs; see text): *Rhipicephalus (R.) sanguineus. NEOTROPICAL: Ixodes (I.) diversifossus?. NEARCTIC: I. (Pholeoixodes) rugosus. PALEARCTIC: Haemaphysalis (Rhipistoma) adleri. ORIENTAL: H. (R.) heinrichi, H. (R.) lagrangei. MALAGASY: H. (R.) obtusa.*

Strict- and Moderate-Stage (Adult) Specificity. *NEOTROPICAL: I. (I.) monotoyensis, Amblyomma (Anastosiella) tigrinum. NEARCTIC: Dermacentor (D.) variabilis*$^{+}$. *PALEARCTIC: I. (I.) tanuki, I. (P.) cornuatus*$^{+}$, *I. (P.) crenulatus, I. (P.) hexagonus*$^{+}$, *I. (P.) kaiseri, H. (H.) campanulata*$^{+}$, *H. (H.) flava*$^{+}$, *H. (R.) erinacei* subspp.$^{+}$. *ETHIOPIAN: I. (Afrixodes) oldi*$^{+}$, *H. (R.) leachi, H. (R.) moreli, H. (R.) punctaleachi, H. (R.) spinulosa, H. (R.) zumpti*$^{+}$, *Rhipicephalus* (ca. 15 spp.**), *Rhipicentor bicornis, R. nuttalli*$^{+}$. *MALAGASY: H. (R.) eupleres, H. (R.) fossae. ORIENTAL: I. (I.) spinicoxalis, H. (R.) asiatica, H. (R.) canestrinii, H. (R.) indica, H. (R.) koningsbergeri, H. (-) hoogstraali, H. (-) palawanensis, H. (-) silvafelis, H. (-) vidua.*

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* Footnotes as for Table 13.

** Revision of the genus *Rhipicephalus* (Clifford and colleagues) is not yet finished.

Most strict and moderately strict tick parasites of carnivores are tropical species. Most are associated with smaller-sized hosts in the family Viverridae, some with Mustelidae, Procyonidae, Felidae, Canidae, Hyaenidae, and Ursidae. In nature, healthy large-size carnivores (lion, leopard, tiger, jaguar, bear, etc.) characteristically carry few and only a limited variety of ticks.

The African *Rhipicephalus (R.) sanguineus* has been transported far and wide with domestic dogs and thrives in heated homes and kennels in temperate zones, where it is almost invariably Strict-Total in host specificity. However, in tropical Africa, adult *R. sanguineus* infest a wider variety of carnivores and other larger-sized mammals and birds (such as the ostrich) and immature stages feed on smaller-sized mammals.

Tubulidentata (Table 16). We have no data to show tick specificity for the aardvark which, however, is parasitized by several species associated with Artiodactyla, as mentioned in Table 16.

Proboscidea (Table 17). Adults of two species are Strict-Stage parasites of Ethiopian elephants. Notably, of these *[Dermacentor (D.) circumguttatus]* is one of the only two *Dermacentor* species in the Ethiopian Region. There is no evidence that Oriental elephants have or have had specific tick parasites; however, this picture may be marred by lack of proper study or by extinction of specific species in recent times. Elephants in both Regions are infested by ticks associated with artiodactyls and perissodactyls. Healthy wild elephants seldom carry heavy tick loads.

Hyracoidea (Table 18). The sheltered dens inhabited by rock hyraxes *(Procavia* and *Heterohyrax)* are optimum microhabitats in which six East and South African ticks [four in the *Haemaphysalis (Rhipistoma) orientalis* group, one *Ixodes* and one *Rhipicephalus]* and one West African *Rhipicephalus* species have evolved as Strict-Total parasites. This specificity is additionally interesting in that tree hyraxes *(Dendrohyrax)* are sometimes infested by the same tick species, which practically never feed on other vertebrates (we have no authentic data for other hosts). The apparent absence of hyrax-parasitizing *Haemaphysalis* species in West Africa remains to be explained. The rock hyrax-parasitizing argasid *Ornithodoros (O.) procaviae* isolated (so far as known) in the Negev desert (Palearctic) is a remarkable enigma in view of the great geologic age and limited distribution of hyraxes in Africa, southwestern Asia, and southeastern Europe. The lack of biological study of this unique tick in southwestern Asia is sad.

Perissodactyla (Table 19). The status of tick specificity for perissodactyls is obscured by the results of human plundering of the earth's environments.

Equidae. Among ticks parasitizing horses, zebras, and asses, the only contemporary Strict-Total species is the South African *Margaropus winthemi,* probably originally specific for the mountain zebra but now best known as a wintertime parasite of domestic horses and also of domestic artiodactyls. Certain *Rhipicephalus* ticks may possibly best be categorized as chiefly parasitizing zebras but the host-parasite data for these species are imprecise. *Dermacentor* and *Hyalomma* species, and possibly *Boophilus annulatus,* were probably closely associated with wild Palearctic equines.

Rhinocerotidae. One *Dermacentor* and two *Amblyomma* species are Strict-State (adult) parasites of Ethiopian rhinoceroses (see also these genera under Ethiopian elephants and Table 17). Exceedingly little is known about the Oriental *A. (-) crenatum;* like its rhinoceros host, this tick may be close to extinction.

Tapiridae. The six species (one *Ixodes,* one *Dermacentor,* four *Amblyomma* subgenus *Amblyomma)* appearing to be Strict-Stage (adult) parasites of Neotropical tapirs are poorly documented. The few ticks *(Amblyomma, Haemaphysalis, Dermacentor)* recorded from Oriental tapirs are those also collected from artiodactyls.

Artiodactyla (Table 20). Artiodactyla are the chief hosts of adults of at least 190 ixodid species (none are *Aponomma, Anomalohimalaya,* or *Rhipicentor;*

TABLE 16. TICKS AND MAMMALS (10). TUBULIDENTATA

All active stages of *Argas (Ogadenus) brumpti* and of certain forms of the *Ornithodoros (O.) moubata* complex parasitize aardvarks *(Orycteropus)* in their burrows *(ETHIOPIAN).* Adults of ca. 10 *Rhipicephalus* species also frequently feed on these animals, as well as adults of a few *Amblyomma* and *Hyalomma* species. Most if not all of these species are Moderate-specific parasites of large- and medium-sized African Artiodactyla. The burrow habitat is a delimiting factor only for the 2 argasid species.

TABLE 17. TICKS AND MAMMALS (11). PROBOSCIDEA

STRICT-STAGE (ADULT) SPECIFICITY (2 spp.). *ETHIOPIAN: Amblyomma (Theileriella) tholloni, Dermacentor (D.) circumguttatus.* (Immatures of both species parasitize small-sized mammals and ground-feeding birds.)

MODERATE OR NONPARTICULAR SPECIFICITY. *ETHIOPIAN & ORIENTAL:* Numerous *Amblyomma, Hyalomma,* and *Rhipicephalus* spp. (adults only).

TABLE 18. TICKS AND MAMMALS (12). HYRACOIDEA

STRICT-TOTAL SPECIFICITY (8 spp.). *ETHIOPIAN: Ixodes (Afrixodes) procaviae, Haemaphysalis (Rhipistoma) bequaerti, H. (R.) cooleyi, H. (R.) hyracophila, H. (R.) orientalis, Rhipicephalus (R.) distinctus, R. (R.) boueti. PALEARCTIC: Ornithodoros (O.) procaviae.*

MODERATE AND/OR NONPARTICULAR SPECIFICITY: *ETHIOPIAN: Argas (Ogadenus) brumpti* frequently infests rock hyrax dens but also feeds on other shelter-seeking vertebrates. *Nuttalliella namaqua* possibly also frequently parasitizes rock hyraxes.

TABLE 19. TICKS AND MAMMALS (13). PERISSODACTYLA

EQUIDAE

STRICT-TOTAL SPECIFICITY. *ETHIOPIAN: Margaropus winthemi*$^+$.

MODERATE-STAGE (ADULT) SPECIFICITY. *PALEARCTIC, ORIENTAL & ETHIOPIAN:* Numerous *Amblyomma, Hyalomma, Rhipicephalus, Dermacentor,* and *Boophilus* species [Moderate-Specific (adult) parasites of Artiodactyla] also parasitize equines in these and other Regions where horses and asses have been introduced.

RHINOCEROTIDAE

STRICT-STAGE (ADULT) SPECIFICITY. *ETHIOPIAN: Amblyomma (Theileriella) rhinocerotis, A. (T.) personatum, Dermacentor (D.) rhinocerinus. ORIENTAL: A. (-) crenatum.*

MODERATE-STAGE (ADULT) SPECIFICITY. *ETHIOPIAN & ORIENTAL:* Numerous *Amblyomma* and *Rhipicephalus* (and 2 *Hyalomma)* species [Moderate-Specific (adult) parasites of Artiodactyla] also parasitize rhinoceroses in both Regions. Adult *A. (T.) testudinarium* infest Oriental Rhinocerotidae and Tapiridae.

TAPIRIDAE

STRICT-STAGE (ADULT) SPECIFICITY. *NEOTROPICAL: Ixodes (I.) tapirus, A. (A.) coelebs*$^+$*, A. (A.) incisum, A. (A.) scalpturatum*$^+$*, A. (A.) tapirellum*$^+$*, Dermacentor (D.) latus.*

$^+$ May also infest Artiodactyla.

relatively few are *Ixodes).* Only six argasid species (five *Ornithodoros,* one *Otobius)* are associated with artiodactyls. There is apparently no association between Nuttalliellidae and Artiodactyla.

The Suidae, before the advent of human civilization, undoubtedly had a greater role in tick speciation and population survival than is generally realized. Recent contacts between Cervidae and domestic artiodactyls, and worldwide

TABLE 20. TICKS AND MAMMALS (14). ARTIODACTYLA*

The specificity of all species listed is Strict-Stage (adult) except that those printed in **bold face type** are Strict-Total.

Pigs and hogs *(SUIDAE)*

ETHIOPIAN: **Ornithodoros (O.) porcinus,** *Amblyomma (Theileriella) paulopunctatum*$^+$. *Rhipicephalus (R.) complanatus*$^+$, *R. (R.) cuspidatus*$^+$.

ORIENTAL: Haemaphysalis (Kaiseriana) papuana$^+$, *H. (H.) susphilippensis, Dermacentor (Indocentor) atrosignatus*$^+$, *D. (I.) auratus*$^+$, *D. (I.) compactus, D. (I.) taiwanensis.*

Peccaries *(TAYASSUIDAE)*

NEOTROPICAL: Amblyomma (A.) naponense$^+$, *D. (D.) halli.*

Hippopotamus *(HIPPOPOTAMIDAE)*

ETHIOPIAN: Cosmiomma hippopotomense?

Camels *(CAMELIDAE)*

PALEARCTIC: Hyalomma (H.) asiaticum asiaticum, H. (H.) asiaticum caucasicum, H. (H.) asiaticum kozlovi, H. (H.) dromedarii, H. (H.) schulzei, Dermacentor (D.) nuttalli, Rhipicephalus (R.) schulzei$^+$.

NEOTROPICAL: Amblyomma (Anastosiella) parvitarsum.

Mouse deer and chevrotains *(TRAGULIDAE)*

ORIENTAL: **Haemaphysalis (-) traguli.** *ETHIOPIAN:* None?

Deer, muntjac, pudu, caribou *(CERVIDAE)*

NEOTROPICAL: Ixodes (Pholeoixodes) taglei, Haemaphysalis (Gonixodes) juxtackochi$^+$, **Dermacentor (Anocentor) nitens**$^+$, (possibly also some *Amblyomma* spp. but taxonomy confusing and data poor).

NEARCTIC: **Ornithodoros (Ornamentum) coriaceus**$^+$, *Ixodes (I.) dammini*$^+$, *Dermacentor (D.) albipictus*$^+$ (also commonly infested by *Amblyomma* and *Dermacentor* species with Moderate or Nonparticular specificity).

PALEARCTIC: Haemaphysalis (Alloceraea) inermis$^+$, *H. (A.) kitaokai*$^+$, *H. (H.) concinna*$^+$, *H. (H.) filippovae*$^+$, *H. (H.) fujisana*$^+$, *H. (H.) japonica japonica*$^+$, *H. (H.) japonica douglasi*$^+$, *H. (H.) megaspinosa*$^+$, *H. (Kaiseriana) longicornis.*

ORIENTAL: **Ornithodoros (O.) indica?,** *Ixodes (I.) moschiferi,* **Haemaphysalis (H.) birmaniae**$^+$, *H. (H.) darjeeling*$^+$, *H. (H.) roubaudi*$^+$, *H. (H.) traubi, H. (-) calvus, H. (-) mjoebergi, H. (-) rusae, H. (Kaiseriana) borneata, H. (K.) celebensis*$^+$, *H. (K.) cornigera*$^+$, *H. (K.) davisi*$^+$, *H. (K.) lagrangei*$^+$, *H. (K.) luzonensis*$^+$, *H. (K.) ramachandrai*$^+$, *H. (K.) renschi*$^+$, *H. (K.) sambar, H. (K.) shimoga*$^+$, *H. (K.) yeni*$^+$, *H. (Segalia) sumatraensis*$^+$, *R. (-) scalpturatus?*

Giraffe, okapi *(GIRAFFIDAE)*

ETHIOPIAN: **Margaropus reidi**[+], **M. wileyi**[+], *Ixodes (Afrixodes) okapiae*[+], *Rhipicephalus (R.) camelopardalis*[+].

Pronghorn *(ANTILOCAPRIDAE)*

NEARCTIC: **Otobius megnini**[+].

Buffaloes, bison, antelopes, gazelles, cattle, goats, sheep *(BOVIDAE)*

NEARCTIC: Dermacentor (D.) albipictus[+], *D. (D.) andersoni*[+], *D. (D.) hunteri*[+], *D. (D.) occidentalis*[+].

PALEARCTIC: **Ornithodoros (Alveonasus) lahorensis**[+], **O. (Pavlovskyella) tholozani**[+], *Ixodes (I.) gibbosus, Haemaphysalis (Allophysalis) kopetdaghica, H. (A.) tebetensis, H. (A.) pospelovashtromae, H. (Aboimisalis) punctata, H. (Herpetobia) sulcata, H. (Segalia) parva, Hyalomma (Hyalommina) rhipicephaloides, H. (H.)* sp. n., *H. (Hyalomma) anatolicum anatolicum, H. (H.) anatolicum excavatum*[+], *H. (H.) detritum, H. (H.) franchinii, H. (H.) lusitanicum, H. (H.) marginatum marginatum*[+], *H. (H.) marginatum turanicum*[+], *H. (H.) sinai*[+], **H. (H.) scupense**, *Dermacentor (D.) daghestanicus, D. (D.) everestianus*[+], *D. (D.) marginatus*[+], *D. (D.) niveus*[+], *D. (D.) raskemensis*[+], *D. (D.) reticulatus*[+], *Rhipicephalus (Digineus) bursa*[+], *R. (R.) guilhoni, R. (R.) turanicus*[+], **Boophilus annulatus**[+], **B. kohlsi.**

ORIENTAL: Haemaphysalis (Alloceraea) aponommoides[+], *H. (A.) vietnamensis?, H. (Allophysalis) danieli, H. (A.) garhwalensis, H. (A.) warburtoni, H. (A.) xinjiangensis, H. (Aboimisalis) cornupunctata, H. (Herpetobia) kashmirensis, H. (H.) quinghaiensis, H. (H.) moschisuga, H. (H.) nepalensis, H. (H.) sundrai, H. (Haemaphysalis) campanulata*[+], *H. (H.) indoflava, H. (H.) goral, H. (Kaiseriana) aculeata, H. (K.) bispinosa*[+], *H. (K.) capricornis, H. (K.) semermis*[+], *H. (K.) spinigera*[+], *H. (Segalia) montgomeryi*[+], *Hyalomma (Hyalommina) brevipunctata, H. (H.) hussaini, H. (H.) kumari, H. (Hyalomma) marginatum isaaci*[+], *Rhipicephalus (R.) haemaphysaloides*[+], *R. (R.) pilans, Boophilus microplus*[+].

ETHIOPIAN: Ixodes (Afrixodes) cavipalpus[+], *I. (A.) drakensbergensis, I. (A.) evansi, I. (A.) lewisi, I. (A.) moreli*[+], *I. (A.) muniensis*[+], *I. (A.) neitzi, I. (A.) pilosus*[+], *I. (A.) pseudorasus*[+], *I. (A.) rubicundus*[+], *Amblyomma (Theileriella) astrion*[+], *A. (T.) cohaerens*[+], *A. (T.) eburneum*[+], *A. (T.) gemma*[+], *A. (T.) hebraeum*[+], *A. (T.) lepidum*[+], *A. (T.) pomposum*[+], *A. (T.) splendidum*[+], *A. (T.) variegatum*[+], *Haemaphysalis (H.) silacea, H. (Kaiseriana) aciculifer, H. (K.) parmata, H. (K.) rugosus, Hyalomma (Hyalommina) punt, H. (Hyalomma) albiparmatum*[+], *H. (H.) erythraeum*[+], *H. (H.) impressum, H. (H.) marginatum rufipes*[+], *H. (H.) nitidum*[+], *H. (H.) truncatum*[+], *Rhipicephalus appendiculatus*[+], *R. bergeoni, R. capensis*[+], *R. complanatus*[+], *R. compositus*[+], *R. cuspidatus*[+], *R. duttoni, R. dux*[+], *R. evertsi evertsi*[+], *R. evertsi mimeticus*[+], *R. falcatus*[+], *R. glabroscutatum, R. humeralis*[+], *R. hurti, R. kochi*[+], *R. longiceps*[+], *R. longicoxatus, R. longus*[+], *R. lunulatus*[+], *R. maculatus*[+], *R. masseyi*[+], *R. muehlensi*[+], *R. oculatus*[+], *R. pravus*[+], *R. pulchellus*[+], *R. reichenowi*[+], *R. sculptus*[+], *R. senegalensis*[+], *R. sulcatus*[+], *R. tricuspis*[+], *R. ziemani*[+], **Boophilus decoloratus**[+], **B. geigyi.**

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[*] This listing is close to complete but not complete.

[+] May also infest other artiodactyls, occasionally perissodactyls and carnivores, infrequently other mammals.

introduction of herds of domestic artiodactyls infested by ticks which originally were strictly or moderately specific for certain wild Bovidae and/or Cervidae, bring some of these parasites to considerable medical and economic attention. Contemporary environmental modification, as for perissodactyls, is obliterating many clues to ixodid-artiodactyl interrelationships. Much of this section is based on precise unpublished data from «remote» areas of the world. However, we do not pretend to present final conclusions regarding relative roles of certain Cervidae and Bovidae (and Antilopcapridae in western North America) as specific hosts of adults of several species, which we tentatively «lumped» under parasites of Bovidae. These relationships need further investigation.

Suidae. The postulated importance of pigs and hogs as specific hosts of certain tick species and groups, mentioned above, is based on considerable unpublished data from numerous collections from the Oriental, Palearctic, and Ethiopian Regions. However, data from Central and West Africa are particularly unsatisfactory in regard to host specificity of Suidae and other artiodactyls. Species listed in Table 20 are one Ethiopian Strict-Total *Ornithodoros* parasitizing chiefly burrowing warthogs and eight ixodid species with Strict-Stage (adult) specificity for forest-dwelling pigs and hogs. Three of these are Ethiopian (one *Amblyomma,* two *Rhipicephalus)* and five are Oriental [one *Haemaphysalis,* four *Dermacentor (Indocenter)].* This list is incomplete.

Numerous ticks with Moderate specificity for Perissodactyla and Artiodactyla parasitize pigs and hogs; these are chiefly *Amblyomma, Dermacentor,* and *Rhipicephalus,* also some *Ornithodoros, Haemaphysalis,* and *Ixodes.* The Nonparticular adults of *Ixodes (I.) ricinus* are included in most of numerous collections of ticks from wild pigs from northern Iran (unpublished).

Tayassuridae. Neotropical peccaries have two Specific-Stage (adult) parasites *(Amblyomma* and *Dermacentor)* and are also infested by several *Amblyomma* species with Moderate specificity for different Artiodactyla. One or two of these species may in fact be most closely associated with peccaries.

Hippopotamidae. The lone record of *Cosmiomma hippopotomense* from the hippopotamus dates from 1844. This almost-extinct tick is otherwise recorded only from a few specimens taken on vegetation in East Africa and on domestic goats in Namibia. Adults of several *Amblyomma* and *Rhipicephalus* parasites of other artiodactyls also infest the hippopotamus (attaching chiefly to the ears). Available data provide clues to no tick species that is more closely associated with the hippopotamus than with other artiodactyls.

Camelidae. Palearctic camels (the dromedary and bactrian) are parasitized by six Strict-Stage (adult) ticks (five *Hyalomma* and one *Dermacentor).* These parasites apparently survive only or chiefly where camels are present though they also infest other artiodactyls and perissodactyls. *Ornithodoros (O.) savignyi,* listed under Bovidae, might more properly be included under Camelidae. Our numerous records of adult *Dermacentor (D.) nuttalli* and *Rhipicephalus (R.) schulzei* from camels suggest a high level of specificity between these ticks and camels. Practically all tick species common to domestic artiodactyls and perissodactyls parasitize camels where their contemporary ranges are confluent.

Neotropical Camelidae (lamas and allies) are specific hosts of adults of the exceptionally interesting *Amblyomma (Anastosiella) parvitarsum.* Few other ticks feed on these animals.

Tragulidae. The Oriental mouse deer is generally parasitized by *Haemaphysalis traguli.* As true of a number of tick species confined to medium-sized wandering hosts, *H. traguli* is a Strict-Total rather than a Strict-Stage parasite. Other ixodids occasionally infest the mouse deer. We know of no ticks specific for Ethiopian chevrotains *(Hyemoschus).*

Cervidae. As suggested in the paragraph introducing the Artiodactyla, mingling of deer and domestic artiodactyls, generalized reporting of host data, and lack of proper study make it difficult to sort out specificity data for some Nearctic and Palearctic tick species. However, our voluminous data for the Oriental Region (mostly unpublished) are quite precise for a number of tick and cervid species.

Ticks specific for Cervidae are mostly *Haemaphysalis* (Neotropical, Palearctic, and Oriental). The Strict-Total specificity of the Neotropical one-host *Dermacentor (A.) nitens* for wandering, small-sized deer that do not form large herds is noteworthy (this tick also infests introduced domestic horses and cattle). Several other species should undoubtedly be added to the list of ticks specific for Cervidae.

Giraffidae. Giraffes are infested by a variety of ticks common to the numerous artiodactyls and perissodactyls in their Ethiopian savanna habitat. The giraffe has three specific tick species, two of which *(Margaropus reidi* and *M. wileyi)* are exceptionally specialized one-host parasites. The secretive forest-dwelling okapi and its parasites have not been well studied.

Antilocapridae. The one-host *Otobius megnini* is specially adapted to survival with wandering pronghorns in Nearctic deserts and open grasslands. This unusual biological phenomenon is expanded to include the ability to develop on introduced horses and cattle and to survive in other biotopes (Neotropical, Oriental, Malagasy, Ethiopian) into which *O. megnini* has been transported in the ears of these domestic hosts.

Bovidae. The list of bovid-specific ticks (Table 20), including ca. 140 species, points to the extensiveness of this host-parasite association but is probably only ca. 85–90 percent complete. Despite the stated problems in categorizing certain ticks closely associated with Bovidae, quite specific interrelationships characterize numerous ixodids and bovine subfamilies, as well as some bovid genera and species. These specific ticks are chiefly adults of *Haemaphysalis, Dermacentor,* and *Rhipicephalus,* some adults of *Amblyomma,* all immatures and adults of the five *Boophilus* species, but relatively few *Ixodes* species. In the Argasidae, very few *Ornithodoros* species parasitize or are specific for Bovidae. Owing to space and time constraints here, the roles of bovine subfamilies, genera, and species as hosts of specific ticks are treated in forthcoming reports.

NONPARTICULAR SPECIFICITY

Nonparticular specificity (Table 21) is a category that should be assigned and employed with caution. A relatively small number of ticks associated chiefly with Rodentia, Perissodactyla, and Artiodactyla are in fact more or less indiscrimate in host selection. Other ticks are easily dumped into this category («out of sight, out of mind») because of poor data regarding tick-host preferences and/or lack of investigation. The examples included in Table 21 appear to be truly Nonparticular in both the immature and adult stages. However, it is biologically and epidemiologically important to record that in different biotopes of the geographical range of these generally widely distributed species some vertebrate species stand out as much more commonly infested than others in the same biotope. The complex evolutionary, ecological, ethological, faunistic, and physiological factors involved

TABLE 21. NONPARTICULAR SPECIFICITY (EXAMPLES)

NEOTROPICAL-NEARCTIC: Amblyomma (A.) americanum, A. (A.) cajennense, A. (A.) imitator. NEOTROPICAL: A. (Anastosiella) ovale. PALEARCTIC: Ixodes (I.) acutitarsus (also Oriental), *I. (I.) persulcatus, I. (I.) ricinus. ORIENTAL: A. (Theileriella) testudinarium. AUSTRALIAN: I. (Exopalpiger) fecialis, I. (Sternalixodes) holocyclus, I. (Endopalpiger) tasmani.*

in actual and assumed Nonparticular specificity in most cases require more intensive investigation than they have received.

CONCLUSION

This presentation, as stated in the Introduction, is intended only to provide data and models which should help to answer the questions of MAYR (1957). Some of our Tables are quite complete, others are somewhat less so. We trust, however, that this effort will be a serviceable preliminary contribution for constructing a clear picture of tick-host specificity and evolutionary, biological-ecological-physiological factors determining this specificity.

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