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Phylogeography of Ticks (Acari: Ixodida)

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Acari, Ixodida, Ixodidae, ticks, phylogeography, evolution

Abstract

Improved understanding of tick phylogeny has allowed testing of some biogeographical patterns. On the basis of both literature data and a meta-analysis of available sequence data, there is strong support for a Gondwanan origin of Ixodidae, and probably Ixodida. A particularly strong pattern is observed for the genus *Amblyomma*, which appears to have originated in Antarctica/southern South America, with subsequent dispersal to Australia. The endemic Australian lineages of Ixodidae (no other continent has such a pattern) appear to result from separate dispersal events, probably from Antarctica. Minimum ages for a number of divergences are determined as part of an updated temporal framework for tick evolution. Alternative hypotheses for tick evolution, such as a very old Pangean group, a Northern hemisphere origin, or an Australian origin, fit less well with observed phylogeographic patterns.

1. INTRODUCTION

Phylogeography, a term first coined by Avise et al. (1) in 1987, initially simply referred to the fact that phylogenetic lineages often display distinct geographic patterns. Subsequently, Avise (2, 3) fine-tuned the concept as the “field of study concerned with the principles and processes governing the geographic distribution of genealogical lineages” [Reference 3, p. 3] a discipline based on a multidisciplinary approach involving the simultaneous study of the evolutionary history, phylogenetics, and spatial distribution of organisms. Since then, new methodologies and tools have greatly expanded on the original purpose of phylogeographic studies (4), but their goals are still most often associated with testing competing hypotheses about the mechanisms (often vicariance versus dispersal) accounting for the origin of spatially disjunct taxa.

Ticks (Acari: Ixodida) are large parasitiform mites characterized by mouthparts specialized for blood feeding (107). They have a worldwide distribution, have adapted to very diverse environmental niches, and can feed on almost all groups of terrestrial vertebrates. Ixodida have traditionally been subdivided in three families: Argasidae (~190 spp.), Ixodidae (~714 spp.), and Nuttalliellidae (1 sp.) (29, 40). A fourth family, the Deinocerotonidae, was recently erected based on fossil tick specimens found in 99 million-year-old Burmese amber deposits (82). The life cycles of ticks are slightly different, but all involve four stages: egg, larva, nymph (there are several nymphal stages in argasids), and adult. With some exceptions, each life stage requires a blood meal. Host specificity varies between species and, sometimes, between stages of a single species. An important part of tick biology is their longevity. Many ticks live several years, although feeding periods are generally short and span a maximum of 15–20 days. Therefore, most of a tick's life takes place in the environment away from its hosts. In their habitats, the main concerns of ticks are finding a host while avoiding dehydration, molting to the next life stage, and undergoing diapause. Aside from the periods spent questing for, or stalking, a host, ticks hide in secluded areas (leaf litter, crevices, caves, etc.) protected from unfavorable climatic conditions.

Ticks are characterized by relatively reduced autonomous vagility [for more information on tick dispersal and vagility, see Reference 108]. Argasidae are often associated with endophilic behavior and usually live in the close quarters of burrows, nests, or resting areas of their favorite vertebrate hosts, although they have been known to disperse at a small geographical scale in search of hosts. Ixodidae can be endophilic or exophilic, with some species stalking their prey and some questing on vegetation (waiting for hosts to come by). Without a doubt, long-distance dispersal of ticks depends on their hosts. Notably, among parasitiform mites, ticks are the only group of nonpermanent parasites that has repeatedly adapted to feeding on large mammals, which are more likely to move over large distances.

Given the importance of hosts for tick dispersal, is tick evolution driven by hosts? As with many obligately parasitic taxa, the idea that parasite and host evolution should mirror each other has been widely used in developing hypotheses on the origin of ticks and the radiation pattern of their main lineages. This concept was favored because tick–host relationships were considered to be mostly species specific (44, 45). This notion was first challenged by Klompen et al. (57), who analyzed a large amount of collection data and realized that host specificity was far from the rule. Analyzing a large amount of Neotropical data, Nava & Guglielmone (78) recently confirmed that ticks often will feed on hosts that are not taxonomically close to each other. Recently, a study of the closely related species of the *Amblyomma cajennense* group showed that speciation within the clade has been driven by allopatric adaptation to different environments and not by host associations (11). These sources of evidence indicate that, when taken as a whole, the evolution of ticks is more likely to be driven by habitat conditions than by host specificity, further justifying that vicariance may play a more important role than host specificity in explaining vicariance patterns. Nevertheless, in some cases, and at the local level or over short timescales, hosts might still play an important role.

Tick phylogeographical studies have so far been based on visual correlation between phylogenetic branching patterns and the biogeographical history of distribution ranges. With one exception (68), alternative hypotheses based on different node dating have never been applied to the study of the Ixodida, although data in the literature would be suited for such an exercise. Ideal requirements for accurate phylogeographical inferences include (a) a good knowledge of the studied group of species, in terms of morphology and classification; (b) accurate delimitations of geographic distributions of present-day and (where available) extinct taxa; (c) a well-resolved phylogenetic framework; and (d) calibration points derived from the fossil record or known paleogeographical events allowing for phylogenetic node dating. Herein, we will summarize earlier theories and conjectures, list facts that can be used for testing hypotheses, and attempt a critical meta-analysis of available data.

2. TICK SYSTEMATICS, PHYLOGENY, AND DISTRIBUTION BY TAXONOMIC GROUP

2.1. Position of Ixodida Relative to Other Parasitiformes

The mite superorder Parasitiformes includes four well-supported lineages, the (sub)orders Mesostigmata, Opilioacarida, Holothyrida, and Ixodida. Mesostigmata is highly diverse [$\sim 11,600$ described species; see Reference 111) with a cosmopolitan distribution. Many mesostigmatid mites retain the presumed ancestral life history of Arachnida, predation, but multiple lineages have switched to scavenging, parasitism, and even fungivory. The three remaining orders are relatively species poor: Opilioacarida (~ 40 spp.), Holothyrida (32 spp.), and Ixodida (~ 910 spp.) (111). Opilioacarida are free-living scavengers that are currently widely distributed in tropical and warm temperate regions of the world. Fossils have been found in Baltic and Burmese amber (26, 28). Holothyrida also appear to be free-living scavengers, but with a more particular distribution, largely limited to parts of the ancient supercontinent Gondwana (64). Holothyrida are also present on Haiti (59) and Cuba (specimens at Ohio State University), areas that were never part of Gondwana. Fossils of Holothyrida are currently absent.

Ideas on relationships among the four orders have evolved considerably over the past 30 years, with a consensus emerging on close relationships between Ixodida and Holothyrida (51, 66) and increasing evidence for relationships of that group to Opilioacarida (51, 77). This result raises an interesting problem: It suggests that Ixodida, obligate parasites of vertebrates, arose from ancestors that may have been scavengers. Also, it is significant that Holothyrida, the sister group of Ixodida, has a strong Gondwanan distribution. In addition, they, contrary to ticks, have never been found associated with any other organism, and their dispersal abilities are considered to be very limited.

2.2. Relationships Within Ixodida

While monophyly of the three families of living ticks, Ixodidae, Argasidae, and Nuttalliellidae, is generally accepted, the relationships among them have been unclear. Nuttalliellidae was initially described as an intermediate between Argasidae and Ixodidae (13), but full understanding of its position was long hampered by the limited availability of specimens. Major progress has recently been made with the discovery of considerable numbers of specimens of its single species, *Nuttalliella namaqua*, in South Africa (71). All instars have recently been redescribed (65), host associations studied (72), and extensive genomic analyses undertaken (69, 70). Although Burger et al. (18) supported a sister group relationship between Nuttalliellidae and Ixodidae on the basis of mitochondrial genome analysis, Mans et al. (69, 70), using more extensive data sets (full

mitochondria plus 18S and 28S nuclear rDNA), found fairly strong support for a position of Nuttalliellidae as a sister group to the assemblage of Argasidae plus Ixodidae. We will use this as a working hypothesis. *N. namaqua* has been recorded from Namibia, South Africa, and Tanzania. The species and family are also at the heart of the most recent hypothesis on the origin of Ixodida, focusing on a possible origin in the Karoo Basin in southern Africa in the mid-Carboniferous (68). Finally, the fossil family Deinocrotonidae also shares features in common with both Ixodidae and Argasidae. This new family has been placed as a sister lineage to Nuttalliellidae, although this classification might be premature (82).

2.3. Relationships and Distribution Records of Argasidae

The family Argasidae, the soft ticks, is moderately diverse [~190 described species; see Reference 30]. The history of Argasid classification has been chaotic but has been reviewed extensively elsewhere (30, 55, 88). Early phylogenetic analyses of relationships in Argasidae (50, 55) provided mixed support for two subfamilies, Argasinae and Ornithodorinae, with, respectively, one (*Argas*) and three (*Ornithodoros*, *Otobius*, *Carios*) genera. More recent analyses (18, 30) have shown that the concept of *Carios* may be paraphyletic, with the traditional subgenera *Carios* and *Chiropterargas* (*Carios* s.s.) separate from the remaining taxa in that lineage (a grouping for which the name *Alectorobius* is available). We use this modified arrangement as a working hypothesis. In terms of biogeographical distribution, the basal lineages of Argasinae have largely Old World distributions [only *Argas* (*Alveonassus*) *cooleyi* occurs in North America], while *Argas* (*Argas*) (associated with birds) is represented in all biogeographical regions. Within Ornithodorinae, *Otobius* is Nearctic (with *O. megnini* secondarily cosmopolitan as a parasite of cattle), and *Alectorobius* is mostly Neotropical [exceptions include a lineage of seabird-associated species (cosmopolitan) and a lineage of bat associates with an Old World distribution (55)]. *Carios* s.s. is strictly Old World and Australian. That leaves *Ornithodoros*, which, in its current composition, includes members from all biogeographical regions. Better resolution of these issues will require far better resolution of the species- and genus-level phylogeny within this family.

2.4. Relationships and Distribution Records of Ixodidae

The family Ixodidae, the hard ticks, includes five subfamilies and three species of uncertain affiliation. Most authors agree on a basal division in Prostriata (subfamily Ixodinae, genus *Ixodes*) and Metastriata (all other subfamilies). The speciose genus *Ixodes* has been subdivided in roughly 15 subgenera on the basis of morphology (21, 31), but monophyly of several of these subgenera has been challenged (79, 116). Some molecular studies have suggested that *Ixodes* might be polyphyletic, with endemic Australian taxa consistently clustering separately (35, 54, 56, 105). *Ixodes* as a genus is cosmopolitan, with many subgenera occurring in different continents (21, 32). Ixodinae are known to parasitize a wide range of host groups including reptiles, birds, and mammals. The Metastriata currently include four subfamilies: three monogeneric (Bothriocrotoninae, Amblyomminae, Haemaphysalinae) plus Rhipicephalinae, which contains eight genera (*Anomalohimalaya*, *Cosmiomma*, *Dermacentor*, *Hyalomma*, *Margaropus*, *Nosomma*, *Rhipicentor*, and *Rhipicephalus*) (40). Some recent changes relative to the traditional classifications (e.g., 43) include (a) the inclusion of Hyalomminae in the Rhipicephalinae (15, 56, 67, 76), (b) the synonymy of *Boophilus* with *Rhipicephalus* (75), and (c) the dissolution of *Aponomma* (52). *Aponomma* has been subdivided into multiple groups. The Australian endemics (48) have been placed in the genus *Bothriocroton*, while most other species have been subsumed in *Amblyomma* (52). Three species, *A. sphenodonti*, *A. elaphense*, and *A. transversale*, are currently *incertae sedis*. The phylogenetic

position of these three species varies depending on data used in the analysis, but they are always basal in Metastriata. *Aponomma sphenodonti* and *A. elaphenese* have recently been placed in new genera, respectively, *Archaeocroton* and *Robertsicus* (8). Support for Bothriocrotoninae, Amblyomminae, and Rhipicephalinae is generally strong, but primitive *Haemaphysalis* do not consistently group with the advanced ones (terminology following Hoogstraal & Kim; see Reference 45).

Bothriocrotoninae are restricted to the Australian region (10); Amblyomminae are widespread in South America, Africa, and Australia, with smaller numbers of species in southern Asia and North America; Haemaphysalinae are highly diverse in Southeast Asia and Africa and quite rare (only three species) in the New World; and Rhipicephalinae are concentrated in Africa and southern Asia, with only a few species in the New World and Australia. Metastriata are most often associated with mammals and birds, and only rarely with reptiles and amphibians (mostly *Amblyomma* species). *Archaeocroton sphenodonti* is found exclusively on the tuatara in New Zealand, *Robertsicus elaphensis* is exclusive to the Trans-Pecos rat snake in North America, and *A. transversale* is restricted to pythonid snakes in Africa (48).

2.5. Fossil Record

The tick fossil record is sparse and, with few exceptions, is made up of relatively recent samples (Miocene to Holocene) that are very similar to extant taxa (25, 39, 49, 64, 80, 84, 92, 97, 101, 113). The oldest records date back to the mid-late Cretaceous and were found in New Jersey (53) and Burmese amber deposits (20, 82, 83, 85). While the New Jersey tick was recognizable as a member of the genus *Carios* s.l. (now *Alectorobius*), the study of Burmese deposits revealed specimens assigned to the newly established family Deinocrotonidae (82), adults of *Amblyomma* (20), and larvae assigned to two new genera in the family Ixodidae, *Compluriscutala* and *Cornupalpatum* (83, 85). Notably, these two new genera were referred to as *Amblyomma* by Grimaldi et al. (39).

3. EVALUATION OF EXISTING BIOGEOGRAPHICAL AND PHYLOGEOGRAPHICAL HYPOTHESES

The various hypotheses developed in the past can be divided into three main categories based on the type of data they emphasize: (a) specificity of tick–vertebrate host associations, (b) plate tectonics and biogeographical vicariance, and (c) a combination of modern cladistic and phylogenetic analysis with known biogeographical vicariance events (Table 1).

3.1. Vertebrate Hosts

During the first half of the twentieth century, various tick taxonomists proposed somewhat contrasting hypotheses about the origin of ticks coinciding with the evolution of their hosts. These hypotheses were all based on the assumption that ticks coevolved with their vertebrate hosts. Sassuchin (94) and Pomerantsev (86) opted for a coevolutionary origin of ticks and mammals on the basis of the observation that primitive mammals are the hosts of the most primitive subgenera of *Ixodes* (itself assumed to be more primitive than the Metastriata). In their view, all associations with birds, reptiles, and amphibians were secondary. Pomerantsev (86) proposed an origin of Ixodidae in the late Mesozoic or early Cenozoic, matching the divergence of monotremes and placental mammals. Schulze (98, 99), using the same reasoning, preferred an origin of ticks on reptiles in the Carboniferous, on the basis of a hypothesis of close relationships between ticks and Trilobita. Clearly inspired by Schulze's (98, 99) and Zumpt's (120) work, Hoogstraal (43) and Hoogstraal & Kim (45) proposed that ticks evolved as obligate parasites of reptiles. Once again

Table 1 Hypotheses on the origin of the Ixodida

Citation	Geological era	Geological period	Approximate date range
Oliver 1989 (81)	Paleozoic	Devonian	350–400 Mya
Dobson & Barker 1999 (24)	Paleozoic	Devonian	350–400 Mya
Mans et al. 2011, 2016 (71, 68)	Paleozoic	Carboniferous	319 Mya
Jeyaprakash & Hoy 2009 (47)	Paleozoic	Carboniferous	300 Mya
Schulze 1936 (98, 99) and Zumpt 1951 (120)	Paleozoic	Permian	250–290 Mya
Hoogstraal et al. 1978, 1982, 1985 (43–45)	Paleozoic	Permian	200–250 Mya
Morel 1969 (73)	Early Mesozoic	Triassic	200–250 Mya
Pomerantsev 1948 (86), Ixodidae only	Mesozoic	Jurassic	150–200 Mya
This review	Mesozoic	Late Triassic/Early Jurassic	180–220 Mya
Balashov 1994 (6)	Mesozoic	Jurassic	150–200 Mya
Klompen et al. 1996, 2000 (56, 57), Ixodidae only	Mesozoic	Middle-to-Late Cretaceous	65–120 Mya
Filippova 1977 (31), <i>Ixodes</i> only	Mesozoic	Late Cretaceous	65–95 Mya

assuming an origin of Ixodidae that coincides with that of their hosts, this implied an origin of the three main tick families at the end of the Paleozoic or early Mesozoic. The main problem with these hypotheses is that they depend on a considerable level of host specificity. As noted above, this assumption is rejected in more detailed analyses of host associations, which often reveal a closer association with off-host habitat and relatively low host specificity (5, 57, 78).

3.2. Biogeography

One of the earliest efforts at explaining tick evolution using biogeographical data was by Balashov (6). Although Balashov did not include a (quantitative) analysis, his hypotheses were based on good distributional data and led to the conclusion that the Ixodidae arose about 180–190 Mya in the mid-Mesozoic. Unfortunately, this effort was significantly hampered by his now outdated understanding of systematics. For example, he assumed monophyly of *Amblyomma*, *Aponomma*, and *Exopalpiger* (a subgenus of *Ixodes* with members in Australia, Africa, South America, and Europe), and did not consider relationships within genera. Therefore, he hypothesized that the genera *Ixodes*, *Amblyomma*, and *Aponomma* originated before the breakup of Pangaea (middle Jurassic) because species assigned to those genera currently occur in most faunal regions. Within *Ixodes*, he did consider the Australian endemics as basally diverging, but the logical follow-up, stressing the importance of Australia, is absent, probably in part because he assumed the monophyly of *Exopalpiger*. Overall, Balashov's hypotheses were innovative and well grounded for the time. They have unfortunately mostly been overturned by newer data.

3.3. Phylogeny and Biogeography

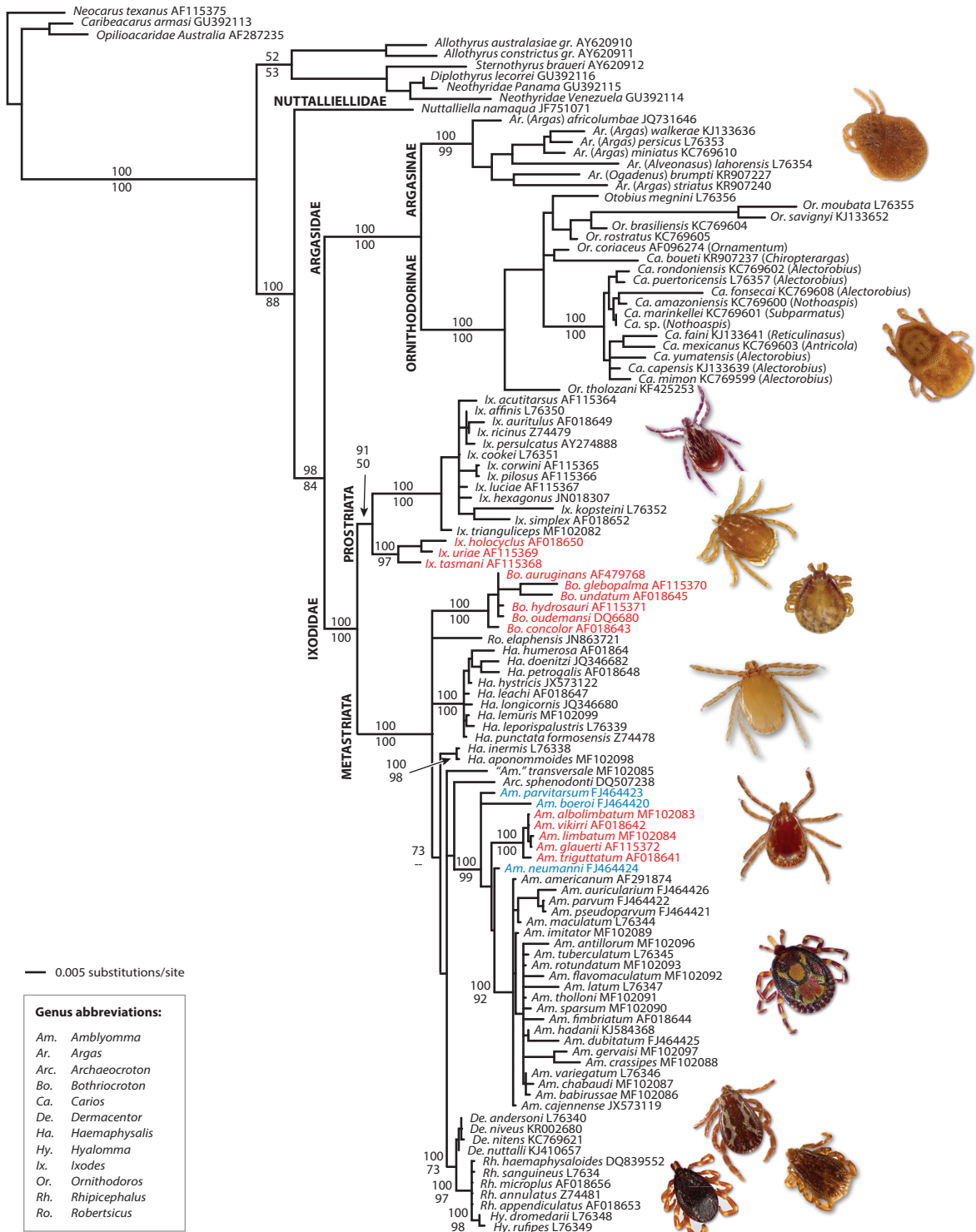
One of the earliest applications of phylogenetic data to tick evolution was by Oliver (81). Using data for the earliest mite fossils (Devonian, 370 Mya), he proposed that ticks should have a Devonian origin as well. After all, if ticks are the sister group to Acariformes (the lineage to which the fossils belong), they should be of the same age as Acariformes. Given that, he proposed a primitive association with amphibians, the predominant terrestrial vertebrate group in the Devonian. Problems with this hypothesis derive from two incorrect assumptions. First, Acari may not be monophyletic (23), which would mean that data for the superorder Acariformes have little bearing

on Parasitiformes. Second, Ixodida do not appear to form an early branch within Parasitiformes, and thus inferences on the age of the superorder cannot be transferred directly to Ixodida (or Ixodidae) (54). In 1996, Klompen et al. (57) examined tick evolution based on the first available molecular phylogenetic data (14) and opted for an origin of Ixodidae (or at least the basal division within Ixodidae) close to Australia about 120 Mya in the mid-Cretaceous. This hypothesis had its basis in two distributional observations: (a) The sister group of the Ixodida, Holothyrida, has a clear Gondwanan distribution (suggesting a Gondwanan origin for the Ixodida), and (b) two very basal lineages in the Ixodida, the Australian *Ixodes* (basal within Prostriata) and *Bothriocroton* (basal within Metastratiata), are exclusively Australian (9). Dobson et al. (24) supported a similar idea but hypothesized a much greater age: an origin of the entire Ixodida in the Devonian (~390 Mya) in what is now Australia and with labyrinthodont amphibians as initial hosts. A key issue in the Dobson et al. hypothesis is the idea that climate and the peripheral position of Australia in both Pangaea and Gondwana provided continuous isolation of Australia, resulting in a distinct fauna. There is some evidence for this, such as the continued dominance of amphibians throughout the early Mesozoic, while various reptile lineages dominated most other terrestrial systems (24, 89). Even so, continued isolation over a period of ~250 My is a strong assumption. In an added complication, none of the recent phylogenetic treatments of the Ixodidae indicate that the three endemic Australian lineages (Australian *Ixodes*, *Bothriocroton*, and Australian *Amblyomma*) originated at the same time (15, 56, 71), rejecting the hypothesis that Australian versus non-Australian lineages resulted from a single vicariance event. By analyzing complete mitochondrial genomes of different Chelicerata, Jeyaprakash & Hoy (47) inferred that the Ixodida originated in the Permian (300 Mya) on amphibians (the only available terrestrial vertebrates at that time), while the Argasidae originated 214 Mya and the Ixodidae 241 Mya. However, mitochondrial sequences are known to evolve rapidly and are sometimes plagued by introgression issues. Resulting artifacts due to sequence saturation can be overcome by dense sampling, but that was not the case in this study (27). Mans et al. (71) succeeded in obtaining *N. namaqua* DNA and included for the first time a member of this family in a molecular phylogenetic analysis. Because *N. namaqua* was revealed to be the most basal lineage of the Ixodida, the authors argued for an origin of ticks approximately 300 Mya in southern Africa on therapsid hosts, followed by an accelerated diversification immediately succeeding the global mass extinction event which occurred at the Permian–Triassic boundary (250 Mya). Naturally, hypotheses on the origin of organisms are often drawn from the common understanding that basally diverging lineages in a phylogeny should better correspond to the geographical origin of the taxonomic group under study than crown lineages. Appealing as this way of thinking might be, it completely omits from consideration the possibility that early branches went extinct without leaving traces of their existence in different areas. Given the very limited fossil record in ticks, it is difficult to establish whether or not some of the lineages now confined to a single geographical zone might have actually existed in other areas. As a case in point, the finding of *Amblyomma* and *Amblyomma*-like species in Burmese amber (20, 83, 85), far away from what we believe is the original distribution of the Metastratiata, is surprising.

4. PHYLOGENETIC META-ANALYSIS AND NODE DATING

4.1. Phylogeny

In order to develop alternative phylogeographical scenarios for the origin of Ixodida, we generated Bayesian (90) and Maximum Parsimony (109) phylogenetic meta-analyses of 113 Ixodida taxa based on available 18S rDNA sequences obtained from GenBank accessions and from sequences generated in our laboratories (102). Overall, the two reconstructions are congruent (**Figure 1**)



(Caption appears on following page)

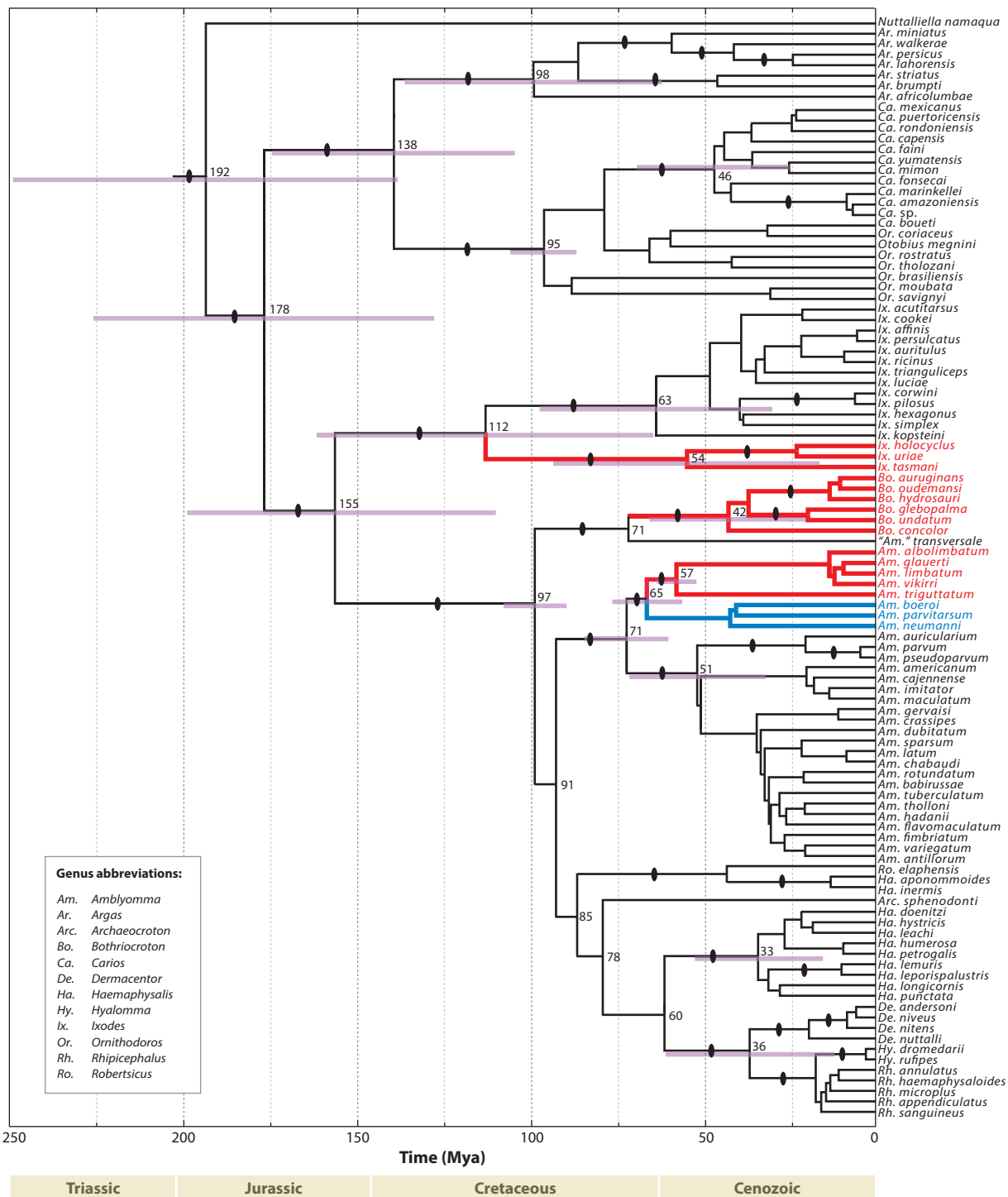
Figure 1 (Figure appears on preceding page)

Bayesian phylogeny of the Ixodida based on the analysis of 18S rDNA gene sequences. Numbers above branches indicate Bayesian posterior probability values; numbers below branches indicate maximum parsimony bootstrap values. Endemic Australian lineages are shown in red; endemic taxa from the southern cone of South America are shown in blue. GenBank sequence accession numbers are placed after scientific names. For further discussion, see Section 4.

and support a monophyletic Ixodida with *N. namaqua* as sister lineage to all other ticks. Ixodidae and Argasidae are monophyletic. Within Argasidae, the Argasinae and the Ornithodorinae [sensu Klompen & Oliver (55)] are well-supported sister clades, while the genus *Ornithodoros* is paraphyletic. Most *Carios* cluster in a strongly supported group (*Alectorobius* s. nov.), excluding *C. boueti*. Within hard ticks, the Prostriata are monophyletic, with two identified sister lineages, the Australian endemics and a clade including all other *Ixodes*. Australian Prostriata appear to have undergone less molecular evolution than their sister lineage, at least in 18S rDNA. Notably, the only *Exopalgiger* available, *I. trianguliceps*, is sister to all remaining (non-Australian) *Ixodes* taxa. Considering the worldwide distribution of *Exopalgiger*, sequences from other species are needed to verify both the monophyly of the subgenus and its phylogenetic position. The resolution within Metastratiata is weak, with a basal polytomy that involves a monophyletic *Bothriocroton* and a polyphyletic *Haemaphysalis* separated into two entities, one including two of the so-called primitive *Haemaphysalis*, *H. inermis* and *H. aponommoides*, and one including nonprimitive Haemaphysalinae. This result suggests that Hoogstraal & Kim (45) correctly identified an important taxonomic split within the subfamily. Rhipicephalinae (including a strongly supported *Dermacentor*) is monophyletic, as is Amblyomminae. The three former *Amblyomma* of unresolved classification did not cluster within Amblyomminae. While two of them have recently been assigned to two new genera (8), the third, *A. transversale*, would also need to be assigned to a new genus [*Neumaniella*, proposed by Lahille (63), is a preoccupied name]. Perhaps the most surprising result concerns the monophyletic group encompassing the remaining *Amblyomma*. All stem lineages involve Australian endemics or species presently restricted to the southernmost cone of South America (*A. boeroi*, *A. parvitarsum*, and *A. neumanni*), while the other taxa, represented by a large polytomy, appear to have evolved later and very rapidly. This suggests an origin in southern South America (or western Antarctica) with subsequent dispersal to Australia and the rest of the world.

4.2. Node Dating

Tentative estimates of divergence times were performed by following previously applied methods (11, 62) and by using a relaxed molecular clock. Monophyly was constrained for all well-supported clades in the Bayesian reconstruction and for the Australian/southern South American cluster. Node calibrations were derived from the scant fossil record and one known and relatively recent vicariance event. By applying the date of a given fossil record to a node, we are choosing to calibrate it with the latest possible date (the most conservative option), as the taxa certainly existed for an unknown amount of years before then. Extinct *Alectorobius* and *Amblyomma*-like extinct genera have been reported from Cretaceous amber deposits in New Jersey and Burma, respectively. Therefore, we placed the node separating the *Alectorobius* lineage from the other Ornithodorinae and the origin of Metastratiata at 95 ± 5 Mya. We added a 60 ± 3 Mya calibration at the split between the Australian *Amblyomma* and the southern South American taxa (date of the beginning of the separation of Australia from eastern Antarctica). Based on this very conservative calibration, the origin of Ixodida would date back to at least 195 Mya, and the Ixodidae would have separated from Argasidae 178 Mya, Prostriata from Metastratiata 153 Mya, and Ornithodorinae from Argasinae 138 Mya (Figure 2). Within the genus *Ixodes*, the Australian endemics and non-Australian



(Caption appears on following page)

Figure 2 (Figure appears on preceding page)

Node dating with BEAST. Tentative dates of radiation are indicated near nodes; nodes supported by >90% posterior probability are indicated by black ovals. Purple bars on nodes correspond to confidence intervals. Endemic Australian lineages are shown in red; endemic taxa from the southern cone of South America are shown in blue.

taxa split at least 112 Mya. As for the Metastriata, the basal branches are not well resolved, with many clades originating from a large polytomy including (a) the genus *Bothriocroton*, which clusters, in this case, with *A. transversale*, although their split is deep (71 Mya); (b) the two structurally primitive *Haemaphysalis* [subgenus *Alloceraea* and *A. elaphense* constitute a monophyletic group, with *A. elaphense* diverging 42 Mya and the two remaining taxa radiating more recently (12 Mya)]; (c) other *Haemaphysalis* diverging around 33 Mya; (d) the monophyletic Rhipicephalinae, showing a split between the genus *Dermacentor* and the *Rhipicephalus*–*Hyalomma* clade at approximately 36 Mya; and (e) the monophyletic genus *Amblyomma* s.s. Within *Amblyomma*, the close relationship between Australian and southern South American taxa is confirmed by high posterior probability values (>90%). The remaining *Amblyomma* form a monophyletic group that includes unranked lineages from tropical and subtropical South America, North America, Africa, and Asia that started diverging from each other around 51 Mya. Age confidence intervals (95% highest posterior density) (shown in **Figure 2**) are, however, fairly large, particularly for early-branching lineages.

5. DISCUSSION

The phylogenetic analyses (**Figures 1 and 2**) do not differ in any major way, at least not where consistently supported groups are involved. They also correspond to results reported in other analyses based on 18S rDNA (15, 54, 57, 69). We are aware that conclusions that can be drawn from our analyses are somewhat limited because we used a single gene, the geographical representation of some taxonomic groups is sometimes insufficient, fossil taxa cannot be included in a molecular analysis, our knowledge of the systematics of some genera is still fragmentary, valid fossil calibration points are scarce, and the paleogeographical history of some areas of the World has yet to be fully understood. Nevertheless, these reconstructions are based on the best available data and can provide an updated framework for further testing of specific hypotheses.

5.1. The Argasidae

The Argasidae and Ixodidae are sister groups. Diversification of extant lineages is hypothesized at about the same time, with the hard ticks preceding the soft ticks by about 20 My. It is most likely that both groups evolved in a similar area, the Southern Hemisphere. Nevertheless, currently available data do not allow us to discern a clear phylogeographical pattern among argasids. A better taxonomic and geographic representation of all soft tick groups is needed before even the simplest hypothesis can be formulated.

5.2. The Ixodidae and Support for a Gondwanan Origin for Ticks

The evolutionary history of the extant Ixodidae retains a strong Gondwanan vicariance signature. The temporal sequence of the breakup of Gondwana therefore becomes critical in interpreting patterns. The traditional view proposes a separation between eastern (Australia, India, Madagascar, and Antarctica) and western (South America and Africa) Gondwana (approximately 140 Mya)

(95, 100), with a subsequent reconnection of southern South America and Antarctica (93); a second hypothesis depicts Africa separated from everything else before the end of the Cretaceous (60); and a third reconstruction suggests a connection between all Gondwanan elements until the end of the Early Cretaceous, followed by a rapid sequence of splitting in the Late Cretaceous (103). Extensive fossil evidence supports the idea that the southern landmasses were connected and provided a continuous land bridge for terrestrial vertebrates and plants up to the Early Tertiary (37, 60, 91, 93, 106, 114). In addition, the South America–Antarctica–Australia bridge persisted until the end of the Eocene (approximately 35 Mya). The tropical to temperate Antarctic climate that persisted from the Late Cretaceous to the Early Eocene supported land dispersal for plants and animals for 70–95 My after Africa drifted away (33). However, the decreasing temperatures associated with the progressive opening of the Drake passage (41 Mya), might have limited faunal dispersal to relatively cold-tolerant species (19, 87, 118). The traditional views on continental drift also hypothesize that India–Madagascar–Seychelles drifted apart from Africa in the Early Cretaceous (121 Mya) and from Antarctica–Australia approximately 135 Mya (93, 96), while Africa remained connected to northern South America until about 100 Mya (93, 96). The exact sequence of these events is, however, the object of much debate. For example, the long isolation of India conflicts with the bioconnectivity exhibited by India with other landmasses. Explanations are somewhat contradictory, but they often evoke the presence of nonsubmerged volcanic islands playing stepping stones between India and Australia up to 90–95 Mya or a northward trajectory of India grazing the African coast, with frequent faunal interchange between the two landmasses (16).

With these biogeographical scenarios in mind and on the basis of our data, we hypothesize that the Ixodida and Ixodidae are of Gondwanan origin. The basal split in the Ixodidae (155 Mya) involves the well-supported Prostriata and Metastriata clades. By the Late Jurassic, North America had separated from Gondwana, but all Gondwanan elements were still fully connected. In terms of climate, the large continents were mostly arid from latitude 40°N to 40°S (119). In this period, dinosaurs dominated the arid areas of the planet, but other vertebrate species and in particular small mammals had started to diversify. Gondwana, however, had moved into temperate zones characterized by important biological diversity (119). It is reasonable to believe that the ancestors of the Ixodidae, particularly of the genus *Ixodes*, which favors more humid conditions, were more likely to evolve in such a habitat than anywhere else. The extant Prostriata diversified first (112 Mya), with one lineage probably reaching eastern Gondwana (Australian *Ixodes*), while the other occupied most of the continent. Better resolution within the non-Australian *Ixodes* and better geographical and taxonomic representation are needed to explore alternative phylogeographical scenarios. This group of ticks, which currently occurs in all modern continents, may have reached Laurasia through South America, Africa, or both. The radiation of the Australian *Ixodes* (54 Mya) started while Australia was progressively drifting away from eastern Antarctica. As the two landmasses did not sever until 30 Mya, we can consider the clade to be of eastern Antarctic–Australian origin. Unlike for the Prostriata, the basal topology of the metastriate clade is not well resolved, for lack of informative characters but also because this group of taxa might really have radiated very rapidly. The polytomy gives rise to a number of well-supported monophyletic groups and three solitary branches corresponding to the previously mentioned species with unclear affinities. *A. transversale* is a sub-Saharan species associated with Pythonidae. A convincing African origin for pythons, closely related to Gondwanan Boidae, has recently been proposed (38). In the BEAST analysis, *A. transversale* clusters with *Bothriocroton*, but the branching of the two lineages is very deep. *Arc. sphenodonti* appears to have split from the other metastriate ticks approximately 75 Mya, which corresponds roughly with the separation of Zealandia from Gondwana (80 Mya). Its unique host, the tuatara, is a likely Gondwanan endemic (110). If the ancestor of the tuatara was a good

swimmer, as extant tuataras are, survival in a largely (but not completely) submerged Oligocene New Zealand (58, 112) is conceivable. The genus *Haemaphysalis* is not monophyletic: The two structurally primitive species *H. aponommoides* and *H. inermis* constitute a separate clade which (BEAST analysis only) clusters with *R. elaphensis*. The North American distribution of *R. elaphensis* (and of an additional structurally primitive tick, *H. chordeilis*) and the Eurasian distribution of the two primitive *Haemaphysalis* taxa could suggest a dispersal route through the Americas and later through Beringia. Among the other metastriate groups, the other *Haemaphysalis* lineage and the Rhipicephalinae seem to have radiated at least 85 Mya.

These clades (with few exceptions) have strong African and Eurasian affinities. If the timing of our dating is correct, by the time these lineages radiated from the metastriate backbone, Africa and India had already split from Gondwana. Given the dating uncertainty in the basal topology of the tree, and the conservative choice in the calibration strategy, the most parsimonious explanation is that both the Ixodida and the Metastriata radiations happened 30–40 My earlier and that the modern *Haemaphysalis* and the Rhipicephalinae moved with the African landmass and later into Eurasia. The lack of resolution within *Haemaphysalis* does not tell us whether Asian species arise from African lineages or the other way around, thus precluding any speculation about the possible role of India–Madagascar in ferrying *Haemaphysalis* ticks toward Asia and from there into Europe and Africa. The presence of two structurally advanced *Haemaphysalis* species associated with mammals in South and North America can probably be attributed to a southward migratory route from Asia to North America and to South America during the Great American Biotic Interchange. Finally, the radiation pattern within the genus *Amblyomma* has a strong Antarctica signature, with basal lineages having an Australian–southern South American distribution. The genus *Amblyomma* sensu stricto, like many other organisms [Marsupialia (12, 115), terrestrial Aves (17, 22, 36), Chelidae (34, 61), Hylidae (117), and Salticidae (42)], appears to have exploited the South America–Antarctica–Australia land bridge. The African and Asian lineages all seem to have evolved from a paraphyletic South and North American cluster at least 51 Mya. The migration from South America to Africa–Asia in the Eocene is hard to explain but has been observed in other organisms (7, 46, 74).

The various fossil *Amblyomma* and *Amblyomma*-like species from the Late Cretaceous Burmese amber (20, 83, 85) do not, by themselves, invalidate this chain of events, although they definitely complicate it. The presence of *Amblyomma* in Myanmar is certainly not predicted in the above scenario. However, as was comprehensively discussed by Chitimia-Dobler et al. (20), the geographical origin of the Burmese amber deposits is still being disputed. The northward rifting of the Sibumasu terrane from the northern Australia part of Gondwana at the Permian–Triassic boundary cannot be considered a likely source for any of the Burmese tick fossils because it started when climatic conditions in northeastern Gondwana were unsuitably cold and arid (119) and because most of the Sibumasu terrane traveled northward under shallow waters. A Late Jurassic northward rifting of the northwestern Australian shelf (41, 104) would fit better, albeit in a loose way. It would require a roughly 30–40 My shift backward for the dates generated in BEAST, an acceptable possibility given our confidence intervals. Notably, under this hypothesis, the Burmese fossils should be most closely related to Australian *Amblyomma*. As an alternative, a Middle-to-Late Cretaceous migratory route for the Burmese lineages along the African east coast into the Eurasian archipelago has yet to be considered. Although climatically the African inland is supposed to have been very arid in this period, the coast around the Tethys Sea presumably maintained more humid conditions that could have provided an appropriate migratory corridor for both ticks and their vertebrate hosts. In general, most of the crown groups appear to have radiated after the combined Cretaceous–Tertiary/Deccan trap extinction events (60–50 Mya), indicating that (a) several tick lineages survived these extreme geological events and (b) the subsequent diversification of

vertebrate hosts, particularly mammalian hosts, also resulted in increased tick diversification rates. The alternative hypotheses, placing tick origins in the Devonian and Early Permian in Pangaea (68, 71, 81), are unrealistic because ice-house and arid climatic conditions were not conducive to tick survival (119). A Northern Hemisphere origin, mentioned by Chitimia-Dobler et al. (20), followed by migration to the South would imply, like the Pangaeian hypothesis, massive selective extinction of basically all northern lineages. Such a catastrophic scenario does not fit with the adaptive skills ticks have demonstrated over their evolutionary history. In addition, these scenarios cannot explain the existence of endemic Australian lineages or the diversification pattern of *Amblyomma*, as noted in **Figure 1**. Finally, the only material that appears to be yielding good morphologically informative tick fossils is amber and, so far, all amber tick fossil records have been reported from the Northern Hemisphere; hence there may be a bias toward a northern tick origin hypothesis. Unfortunately, similar findings from the southern Hemisphere, which might clarify the problem, have yet to be made and might even be hidden under the Antarctic ice sheet.

SUMMARY POINTS

1. Early Ixodida, like its sister group Holothyrida, appear to have had a Gondwanan distribution.
2. A reanalysis of available molecular data supports an origin of Ixodidae in the Southern Hemisphere, as all basal splits involve southern landmasses.
3. The out-of-Australia scenarios may have to be replaced with hypotheses where the remarkable endemic Australian fauna results from multiple, independent dispersal events to Australia, perhaps from Antarctica.
4. The presence of fossil *Amblyomma* taxa in Burmese amber can be reconciled with the out-of-Gondwana hypothesis, provided the dates generated in our reanalysis are shifted back roughly 40 My, which is within the 95% highest posterior density limits of our tree.
5. Alternative hypotheses placing the origin of ticks much earlier or in the Northern Hemisphere are considered less likely because they require massive, selective extinction and cannot explain the diversification pattern shown in the phylogenetic trees.

DISCLOSURE STATEMENT

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