

Amblyomma birmutum a new species of hard tick in Burmese amber

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(Received 24 March 2017; revised 4 May 2017; accepted 9 May 2017; first published online 6 June 2017)

SUMMARY

Amblyomma birmutum sp. nov. is formally described as a new record from 99 Ma old Burmese amber from Myanmar. This confirms the presence of the extant hard tick genus *Amblyomma* C.L. Koch, 1844 (Ixodida: Ixodidae) in the Late Cretaceous. This discovery is placed in its wider context and some reports of fossil hard ticks, such as a *Hyalomma* C.L. Koch, 1844 in Eocene Baltic amber, are misidentifications. The genus *Amblyomma* belongs to the clade Metastricata, a group which probably also accommodates two extinct genera, *Cornupalpatum* Poinar and Brown, 2003 and *Compluriscutata* Poinar and Buckley, 2008, also found in Burmese amber. All three fossils are thus only a little younger than published molecular divergence time estimates (ca. 124 ± 17 Ma) for the Metastricata lineage. *Amblyomma* has a largely Gondwanan distribution today. However, in some biogeographical scenarios, e.g. the Somafrica model, its predicted radiation time postdates the dissolution of the original Gondwana supercontinent raising questions about how its current distribution pattern was achieved.

Key words: Cretaceous, fossil, *Amblyomma*, Ixodidae, biogeography, Gondwana, Somafrica.

INTRODUCTION

Ticks (Arachnida: Parasitiformes: Ixodida) are a well-known group of haematophagous ectoparasites with about 900 living species (Guglielmone *et al.* 2014). Several are of considerable economic importance as vectors for viral and bacterial infections, affecting both humans and domestic animals. A summary of tick biology can be found in Sonenshine and Roe (2013) and a list of valid names in Guglielmone and Nava (2014). Given that ticks are parasitic on terrestrial vertebrates, there are interesting questions about when (and where) they first evolved and who their original hosts were; see e.g. Black and Piesman (1994) or de la Fuente (2003), as well as the Discussion section below. The tick fossil record is sparse. *Dermacentor reticulatus* (Fabricius, 1794) and *Ixodes sigelos* Keirans *et al.* 1976 are living species recorded as sub-fossils (Kulczyński *in* Schille, 1916; Sanchez *et al.* 2010). Records of *Amblyomma* Koch, 1844 which are almost indistinguishable from the living species *Amblyomma argentiniae* Neumann, 1905 and *Amblyomma dissimile* C. L. Koch, 1844 were found

in Miocene (ca. 16 Ma) Dominican Republic amber (Lane and Poinar, 1986; Keirans *et al.* 2002). The argasid tick *Ornithodoros antiquus* Poinar, 1995 also comes from Dominican amber. *Ixodes succineus* Weidner, 1964 from the Eocene (ca. 44–49 Ma) Baltic amber in northern Europe was re-described by Dunlop *et al.* (2016) and assigned to the modern *Ixodes* subgenus *Partipalpiger* Hoogstraal *et al.* 1973, whose members are geographically restricted to Asia nowadays. The argasid tick *Carios jerseyi* Klompen and Grimaldi, 2001 comes from Cretaceous (ca. 90–94 Ma) New Jersey amber from the USA. Finally, two tick species, *Cornupalpatum burmanicum* Poinar and Brown, 2003 and *Compluriscutata vetulum* Poinar and Buckley, 2008, were formally described in Burmese amber from Myanmar, representing the thus far oldest records from the Cretaceous (ca. 99 Ma). Both were assigned to extinct genera.

Burmese amber also hosts a provisional record of the genus *Amblyomma* by Klompen in Grimaldi *et al.* (2002). This is significant as it is the oldest putative example of a tick genus with species still living today. Here, we confirm the presence of an *Amblyomma* tick in Burmese amber based on a new specimen, which we formally describe as a new species and compare it to its living representatives and their patterns of distribution.

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MATERIALS AND METHODS

The type and only known specimen comes from the Jörg Wunderlich collection and bears the inventory number F24671BN/CJW. His material will probably later be deposited in the Senckenberg Museum Frankfurt/Main (J. Wunderlich, personal communication). Most Burmese amber comes from the Hukawng Valley in northern Myanmar. It is currently dated to the Late Cretaceous (lowermost Cenomanian) with an absolute age of ca. 99 Ma (Shi *et al.* 2012). In other words, it is very close to the boundary between the Early and Late Cretaceous.

Imaging

The images for focus stacking were taken using a Leica Z16 APO, driven and controlled by a Cognisys Stackshot macro rail system. The lighting system used was a 12 channel light-emitting diode (LED) system developed by one of the authors (Bruno Cancian de Araujo) and composed of 300 super bright LEDs. The system works with direct light diffused by a central tube made with a photographic filter (Lee filters, model 129). The stack images were combined using the software Helicon Focus 6.7.1. A Keyence VHX-5000 Digital Microscope with a tiltable stand and a combination of upper light and transmitted light for focus stacking was used. We partly used polarized light for more details.

Micro CT

For X-ray microCT scanning the piece of amber containing the specimen was fixed on a glass stub with a clamp formed of Styrofoam. Scanning was performed with a Phoenix Nanotome m (GE Measurement and Control, phoenix|x-ray, Wunstorf, Germany). The 1440 projections (3 averaged, 1 skipped, total duration 48 min) were taken at a current of 100 kV and 100 mA using a molybdenum target. Voxel resolution of the resulting dataset was $3.42472\ \mu\text{m}$. Initially, the dataset was cropped and converted to 8 bit (by adjustment of the histogram) with the help of the software VG Studio Max 2.3 (volume Graphics, Heidelberg, Germany). The noise was reduced with VG Studio Max or Amira 6.0.1 (FEI, Hillsboro, OR, USA). The data were visualized by volume rendering with VG Studio Max (Phong Volume renderer), Drishti 2.6.2 (Limaye, 2012, <https://github.com/nci/drishti>).

SYSTEMATIC PALAEOLOGY

Ixodida Leach, 1815

Amblyomma C.L. Koch, 1844

Amblyomma birmitum sp. nov.

Etymology: From Burmite, the original name of this fossil resin used in the first description by Helm (1894).

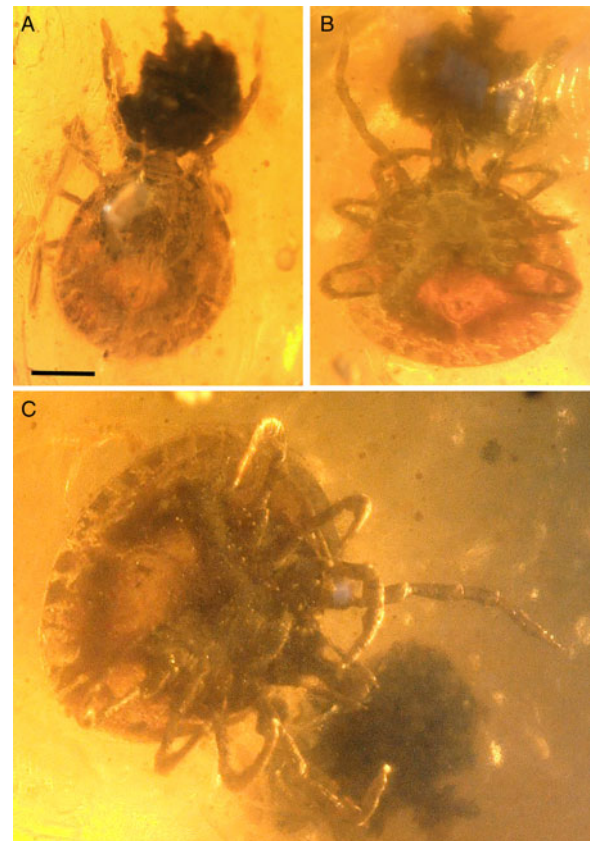


Fig. 1. Holotype of *Amblyomma birmitum* sp. nov., Jörg Wunderlich collection no. F24671BN/CJW, from Late Cretaceous (ca. 99 Ma) Burmese amber from Myanmar. Overview in (A) dorsal, (B) ventral and (C) ventral-oblique view.

Material: Holotype and only known specimen, Jörg Wunderlich collection no. F24671BN/CJW, Burmese amber, Myanmar, Late Cretaceous (Cenomanian).

Diagnosis: Body subcircular, scutum heart-shaped, the second article of palps is at least twice as long as third article, 11 festoons, eyes present, spiracle plates comma-shaped, coxae I–IV with no obvious spurs.

Description: Unengorged female (Fig. 1A–C). Idiosoma: Ornamentation indistinct; body subcircular; length (excluding capitulum) $1569\ \mu\text{m}$, greatest width $1591\ \mu\text{m}$; scutum $849\ \mu\text{m}$ (measured in the middle of the scutum, and $732\ \mu\text{m}$ from the scapula to the edge) in length; maximum width $1026\ \mu\text{m}$, heart-shaped, punctuations rare, deep and medium-sized, distributed irregularly, sides are straight and posterior angle broad; scapulae rounded and short; cervical grooves short and deep; eyes small and distinctly convex located around level of leg II; eleven festoons ranging in basal width from 153 to $156\ \mu\text{m}$ and 144 to $149\ \mu\text{m}$ length (Fig. 1B and C); anus located $456\ \mu\text{m}$ from posterior border; anal groove Y-shaped with lateral branches reaching upper margin of anus and the

Y-tail extending to the sixth festoon; genital aperture subcircular in form, situated between coxa III–IV; spiracle plates comma-shaped, medial and lateral margins parallel, posterior margin slightly convex, dorsal prolongation long, broad, perpendicular to the anterior–posterior axis, macula, round, situated subterminally.

Capitulum: Length from apices to the posterior margin of basis 671 μm ; basis capituli subtriangular posterior margin almost straight, lateral margins round, cornua absent, ventrally posterior margin straight, length from palpal insertion to posterior margin of basis 428 μm , width 228 μm ; palps cylindrical, with length of four segments as follows; segment 1, 46 μm ; segment 2, 266 μm ; segment 3, 139 μm ; segment 4, 56 μm ; visible dorsally and ventrally and no setae observed; hypostome length 537 μm , width at base 177 μm ; columns of teeth on hypostome are 2 + 2 blunt-tipped teeth on the anterior half; apical corona not observed; porose areas oval, diameter of one area 122 μm length, 62 μm width, slightly depressed, length in horizontal position.

Legs: Coxae I–IV with no obvious spurs; tarsus I tapering distally, length 455 μm , clear, oval area on the dorsum of tarsi I is Haller's organ; claws paired, slender, simple, slightly curved; with distinct pulvillus on all legs. Chaetotaxy: Marginal setae observed. On the ventral side, small setae and two setae on each leg joint were observed.

DISCUSSION

The presence of eyes in the new fossil (Fig. 2A and B) excludes the previously described Burmese amber tick species. Both *C. burmanicum* and *C. vetulum* were described as eyeless (or at least eyes were not detected). Additionally, *C. burmanicum* differs from our new fossil in that it does not have an elongate second pedipalp article and has a unique extra claw on the penultimate (third) pedipalp article (Poinar and Brown, 2003: Figs 3 and 4). The pedipalp of *C. vetulum* is closer to that seen in our new fossil, but this species has 13 festoons along the posterior margin of the idiosoma (Poinar and Buckley, 2008: Fig. 3). Our new specimen (and *C. burmanicum*) has only 11 festoons (Fig. 2A and B). We are therefore confident that at least three distinct species of hard tick were present in the Burmese amber forest.

In the new fossil, the hypostome tooth columns have a 2/2 arrangement, albeit only in the anterior half (Fig. 2E). The hypostome teeth are not easy to resolve, but can be recognized as a total of four rows of sharp, triangular and backwards-pointing projections emerging along the length of the hypostome. All modern Asian, African and Neotropical *Amblyomma* adults have a 3/3 or 4/4 tooth arrangement, or even 5/5 in *Amblyomma clypeolatum* Neumann, 1899 females (Voltz et al., 2007).

In this respect, our new fossil resembles the Recent Australian species *Bothriocroton auruginans* (Schulze, 1936), although here the 2/2 teeth are distributed along the whole length of the hypostome. The new fossil differs from other *Amblyomma* species coming from the former Gondwana region in that the genital aperture is located between coxa III–IV (Fig. 1C). In the other species it is located between coxae II and III or between coxae II (Voltz et al., 2002, 2003), except in three Neotropical *Amblyomma* species which have the genital aperture between coxae III – namely *Amblyomma cruciferum* Neumann, 1901, *Amblyomma darwini* Hirst and Hirst, 1910 and *Amblyomma humerale* C.L. Koch, 1844 (Voltz et al., 2007) – and no coxal spurs. The position of the eyes is close to the condition seen in, e.g. *Amblyomma variegatum* Fabricius, 1794 or *Amblyomma pomposum* Dönitz, 1909. We should also note that the fourth segment of the palps is very long (Fig. 1B and C) compared with recent *Amblyomma* species and, in this sense, it is similar to the condition in one of the other amber species *C. vetulum*. Adults of most *Amblyomma* species are medium- or large-sized ticks in which the second article of the palp is at least twice as long as the third article. The scutum is usually ornamented with varying-colour iridescent patterns. Eyes are present and in most species are not positioned in sockets (Nicholson et al., 2009).

Biology of *Amblyomma*

Following Klompen et al. (2002) the genus *Aponomma* Neumann, 1899 is now considered a synonym of *Amblyomma*, which is represented today by 132 valid, extant species (Guglielmone and Nava, 2014). In detail, Klompen et al. (2002) transferred some of the *Aponomma* species from the indigenous Australian *Aponomma* to *Bothriocroton* Keirans et al., 1994 and the remaining *Aponomma* species to *Amblyomma*. The genus *Amblyomma* is thus currently distributed in all six zoogeographic regions (Guglielmone et al., 2014), although we should stress that 98% of them occur exclusively or non-exclusively in territories that originally constituted Gondwana. By contrast, only three species are exclusively found in the Neartic region (Guglielmone et al., 2014), which was originally part of Laurasia. Typical hosts of *Amblyomma* today include lizards and snakes (Squamata) as well as tortoises (Testudines) which form the principal host for several species. In fact, *Amblyomma* as a group utilizes a wide range of hosts, which is different from the situation in other genera of Ixodidae (Guglielmone et al., 2014). Our new taxon in Burmese amber confirms the presence (see also Grimaldi et al., 2002) of *Amblyomma* in the Cretaceous of Southeast Asia. It is only the third

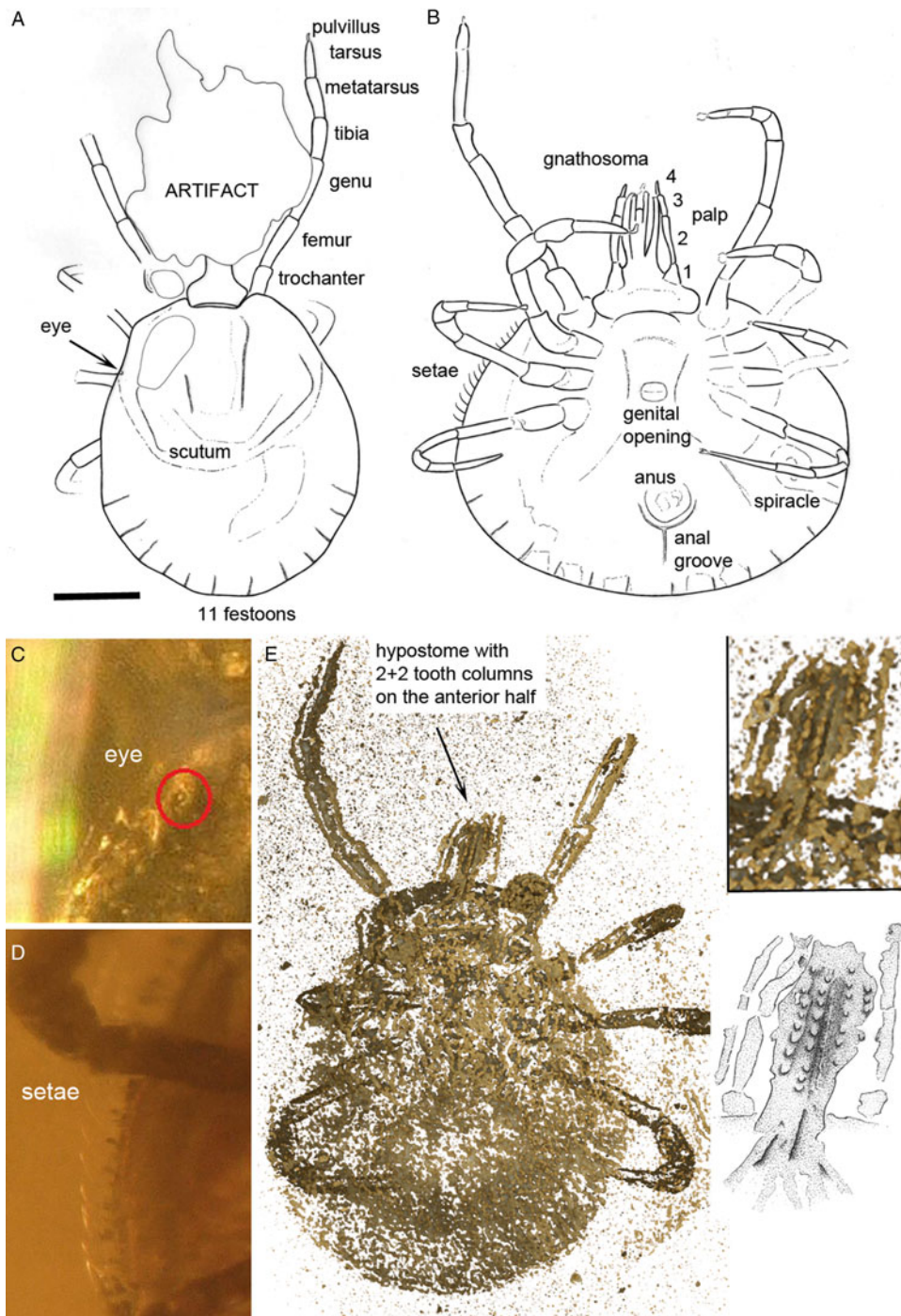


Fig. 2. Holotype of *Amblyomma birmitum* sp. nov., Jörg Wunderlich collection no. F24671BN/CJW, from Late Cretaceous (ca. 99 Ma) Burmese amber from Myanmar. (A) Drawing of the dorsal face showing the leg segments, eye, scutum and festoons. (B) Drawing of the ventral face showing gnathosoma with the palp segments, coxae, genital aperture, stigma, setae and anal groove. (C) Detail of eye (photos with Keyence 5000 Digital Microscope). (D) Focus on setae on the idiosoma side (photos with Keyence 5000 Digital Microscope). (E) Hypostome tooth columns (2 + 2 arrangement), μ CT Drishti 2.6.2; including insets showing close up and interpretative drawing of the hypostome.

tick species to be described from this deposit and the first to be formally placed in an extant genus. *Amblyomma* can thus be traced back approximately 99 million years. Together with an opilioacarid mite from the same amber deposit (Dunlop and de Bernardi, 2014), these Cretaceous ticks also represent the oldest records of parasitiform acarids in general.

Phylogeny and divergence times

With respect to the phylogenetic position of *Amblyomma*, there is a basic division of hard ticks into the Prostriata group, restricted to the genus *Ixodes*, and the Metastriata group containing all the other genera (e.g. Black and Piesman, 1994). In

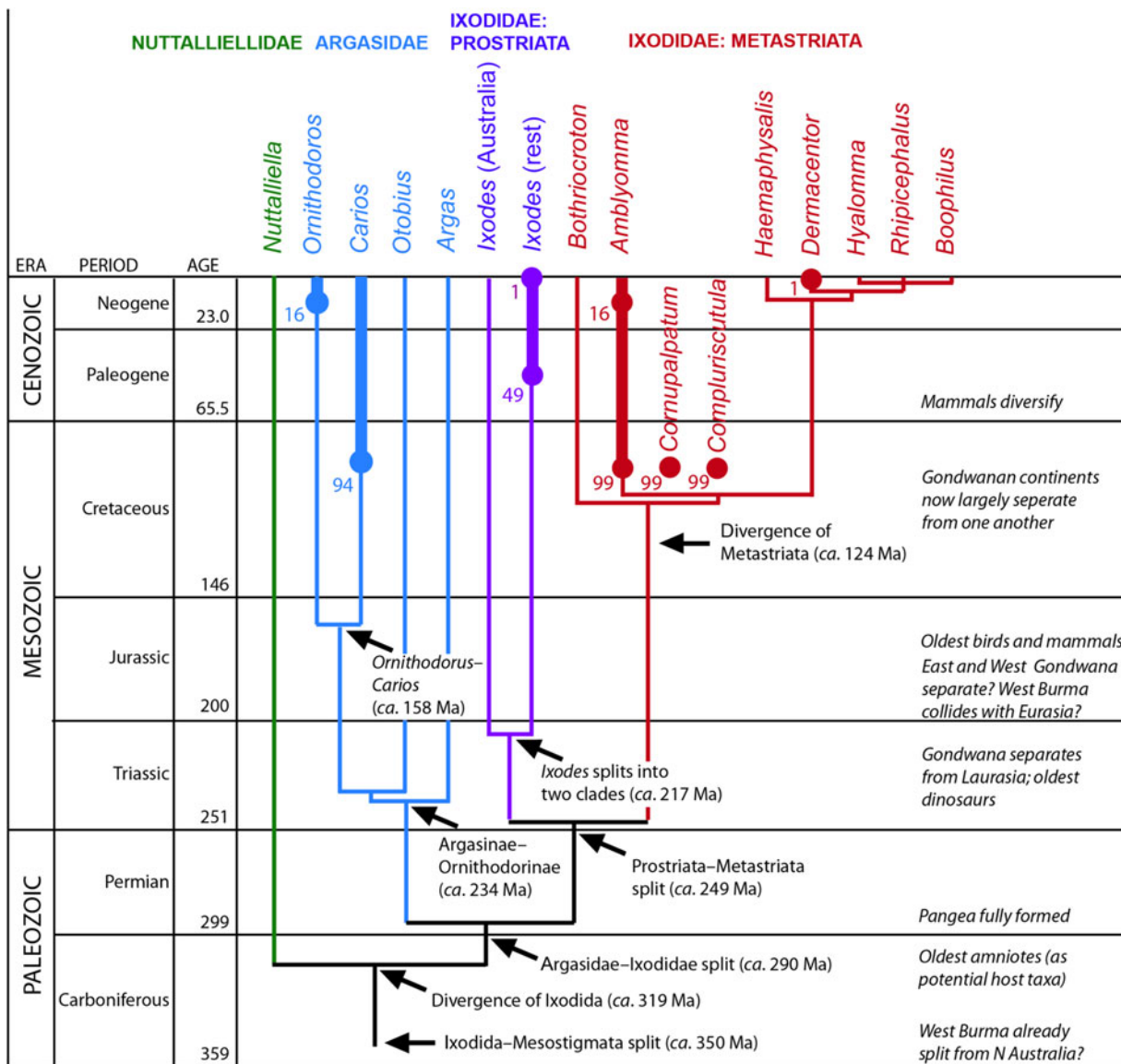


Fig. 3. Phylogenetic tree largely based on Mans *et al.* (2012) with the fossil record of the main genera superimposed. Circles indicate the known fossil occurrences with their estimated dates in millions of years. The inferred origination dates of the major clades are based on Mans *et al.* although we should caution that all of them had error bars of about ± 20 million years. Colour scheme: green (Nuttalliellidae), blue (Argasidae), purple (Ixodidae: Prostriata), red (Ixodidae: Metastriata). Poinar’s extinct genera are assumed to be metastriates too, possibly close to *Amblyomma* (see text for details).

Prostriata the anal groove extends anterior to the anus, while in Metastriata the anal groove is located posterior to the anus (Beati and Keirans, 2001; Nicholson *et al.* 2009). We should note that for the genus *Ixodes* most authors now recognize a split between the Australian and non-Australian species, or have even questioned the monophyly of the genus (e.g. Klompen *et al.* 2000). In overview, Barker and Murrell (2004, Fig. 1) proposed a working hypothesis for hard ticks of the form [*Ixodes* (*Bothriocroton* (*Amblyomma* (*Haemaphysalis* + *Rhipicephalinae* and *Hyalommine* genera)))]]. This reflects the older, non-cladistic, scheme of Hoogstraal and Aeschlimann (1982) and the same basic pattern was also recovered in the molecular phylogeny of Mans *et al.* (2012, Fig. 2) using 18S

rDNA; although other genes gave slightly different results (see their Fig. 3) such as the non-monophyly of *Amblyomma*.

There are numerous proposals, summarized by de la Fuente (2003, Fig. 8), for when ticks – or specifically hard ticks – are thought to have originated. Most were derived, in part, from the fossil record of their typical modern host species. For example, Hoogstraal (1985) inferred late Palaeozoic or early Mesozoic origins for argasid-like ticks in general, with amblyommid ticks present on reptile hosts as early as the Permian and hyalommine and rhipicephaline tick lineages evolving later on mammalian hosts in the Cretaceous and Cenozoic, respectively. In fact, published inferences on tick origins range from as old as the Devonian (Oliver, 1989; Dobson

and Barker, 1999), with amphibians as putative hosts, to as young as the Cretaceous (Black and Piesman, 1994; Nava *et al.* 2009): a difference of almost 300 million years! Klompen *et al.* (1996) also criticized the assumption that tick phylogeny is determined by the phylogeny of their hosts; i.e. that the early derivative ticks must be those that live on reptiles today. Mans *et al.* (2012: Table 2) estimated divergence times directly using molecular clock methods. Their results include origins for the entire Ixodida in the late Carboniferous (319 ± 23 Ma), the family Ixodidae around the Permian–Triassic boundary (249 ± 23 Ma), and the Metastriata radiating in the Early Cretaceous (124 ± 17 Ma). Thus the Late Cretaceous Burmese amber records of *Amblyomma* are not much younger than Mans *et al.*'s estimated divergence time for metastriate ticks in general. Fossils also constrain the split between *Amblyomma* and its putative sister-group (i.e. *Haemaphysalis* + rhipicephalines + hyalommines) to at least 99 Ma.

The extinct Burmese amber genera have not been formally integrated into the phylogeny of living taxa. The position of the anal groove is unhelpful here as both *C. burmanicum* and *C. vetulum* were described without an anal groove (Poinar and Brown, 2003; Poinar and Buckley, 2008); or at least none could be resolved in the material available. A better guide is the presence of marginal festoons in these Cretaceous fossils. These structures are absent in the prostriate *Ixodes* and strongly suggest that the two extinct Burmese genera are also metastriate ticks such as *Amblyomma*. We should also mention de la Fuente's (2003) observation that *C. burmanicum* resembles *Aponomma* (= either *Bothriocroton* or *Amblyomma*) and comments in Mans *et al.* (2012) that these extinct species are probably close to *Amblyomma*. Transposing the (albeit limited) fossil record of the ticks onto the current phylogenetic hypothesis (Fig. 3, see also Mans *et al.* Fig. 4) yields a framework evolutionary scenario. Nuttalliellidae lacks a fossil record. Argasidae is known since the Cretaceous but is estimated to have split from Ixodidae in the Permian. *Ixodes* is known from the Eocene but is predicted to have split from the metastriate lineage in the early Triassic. The modern metastriate genera are inferred to have radiated in the Cretaceous.

Corrections to the tick fossil record

Origins of the most recently diverged hard tick genera – namely *Haemaphysalis*, *Dermacentor*, *Hyalomma*, *Rhipicephalus* and *Boophilus* – were previously constrained to an Eocene divergence date of at least 49 Ma by de la Fuente's (2003: Fig. 6) report of a *Hyalomma* sp. from Baltic amber. However, during the preparation of the present manuscript, it was pointed out to us (Ekaterina Sidorchuk, personal communication) that de la Fuente's amber fossil is

not a tick. In fact, it is a rake-legged mite (Acariformes: Caeculidae), a fact clearly indicated by the large inward-facing spines on the forelegs which are very typical for this group of predatory mites and not seen in *Hyalomma* or any other tick genus. de la Fuente's (2003) paper contains a further misidentification (Ekaterina Sidorchuk, personal communication). The soft ticks figured from Miocene Dominican amber (Fig. 7) are large parasitengonids. It may also be necessary to further check the identity of the larval *Ixodes* from Baltic amber (de la Fuente, 2003: Fig. 1) and larval ticks from Miocene Dominican amber (his Fig. 4), but this is difficult from the photographs and would require restudy of the original material. Removal of the amber *Hyalomma* record means that the oldest fossil constraint for the five derived metastriate tick genera listed above is the subfossil *D. reticulatus* mentioned by Kulczyński in Schille (1916) from the ear of an extinct rhinoceros. Its ca. 1 Ma age is clearly much too young for realistically dating when the genus evolved and means that we must currently rely on molecular clock methods to estimate cladogenesis dates for *Haemaphysalis*, *Dermacentor*, *Hyalomma*, *Rhipicephalus* and *Boophilus*.

Palaeobiogeography

A last point of interest is the fact that Southeast Asia has a complex geological history (e.g. Heine and Müller, 2005; Metcalfe, 2011, 2013; Seton *et al.* 2012). The region containing modern Myanmar was originally interpreted as having been part of the so-called Sibumasu terrane, which is thought to have rifted from the northern (i.e. Australian) part of Gondwana in the late Palaeozoic/early Mesozoic and collided with the Indochina plate by the Late Cretaceous. This led to a hypothesis that Burmese amber arthropods could have arrived in Asia by rafting across the Sibumasu terrane from Australia; see e.g. Dunlop and de Bernardi (2014) for a scenario along these lines involving an opilioacarid mite. A challenge to this hypothesis is the fact that back when the Sibumasu terrane is thought to have rifted from Gondwana (creating the Mesotethys Ocean), the landmass may actually have been covered by shallow seas. Also, much of Australia at this time was thought to have been covered in ice, and Sibumasu was still linked to Gondwana via the Lhasa block, Argoland and South West Borneo blocks (see e.g. Metcalfe, 2011). If this model is correct, the survival of terrestrial arthropods on the Sibumasu terrane after separation from Australia seems unlikely.

More recently, the area containing the source of Burmese amber has been interpreted as having been on the West Burma terrane instead; see Broly *et al.* (2015: Fig. 1) for a map of how the various elements may have accreted together to form modern

Myanmar. As discussed for a Burmese amber spider by Selden *et al.* (2016), one hypothesis is that the West Burma terrane rifted from northern Australia in the Late Jurassic at ca. 156 Ma, and collided with the Sibumasu terrain the Late Cretaceous at about 80 Ma. In this scenario, at the time of amber deposition (ca. 99 Ma) the fauna would have been on an island which had been separated from Australia for about 75 million years. However, Metcalfe (2013) provided evidence for a much earlier (Devonian) separation from Australia and an earlier (Jurassic) collision of the West Burma terrane with Eurasia. In this model the Burmese amber fauna could potentially have arrived from Eurasia at some time between the Jurassic and the mid-Cretaceous.

With respect to ticks, Klompen *et al.* (1996) argued that basal taxa among both prostriate and metastriate ticks predominantly come from Australia today, which could imply that at least the Ixodidae have their origins here. Given that modern *Amblyomma* are strongly associated with a Gondwanan distribution (see above) it would be instructive to compare estimated dates of cladogenesis with some of these dates for major events in palaeobiogeography (see also Mans *et al.* 2012: Fig. 4). Caution is needed in dating ancient geographical splits between continents, and complete physical separation of landmasses may postdate the start of a split by a considerable period of time. Upchurch (2008) reviewed several competing models for Gondwana – albeit with a focus on fossil vertebrates – and recognized four potential scenarios. In the Samafra model, West Gondwana (South America + Africa) separated from East Gondwana (Antarctica, Australia and Indo-Madagascar) during the mid-Jurassic (perhaps ca. 180 Ma). This seems to be the most widely accepted scenario; see also Gibbons *et al.* (2013) for example. In the Africa-first model, Africa separated from the rest of Gondwana during the Cretaceous while South America was still in contact with East Gondwana until the Late Cretaceous. In the multistage scenario elements of the previous hypotheses are combined, and in the Pan-Gondwana hypothesis the southern continents were still connected, at least at their southern tips, until the Late Cretaceous; perhaps as late as 80 Ma.

If the Samafra model is correct, current molecular estimates for the Cretaceous radiation of the metastriate ticks (Fig. 3) postdate the Jurassic dissolution of Gondwana into an eastern and western province. Genera such as *Amblyomma* may show a Gondwanan distribution today, but current estimates of their origination dates correspond to a time in which Gondwana may have already separated into what would become the modern continents. In this hypothesis, either the molecular dates are too young, or modern patterns of biogeography have to be explained by alternative mechanisms. Furthermore, we still have to explain

the presence of *Amblyomma* in the Cretaceous of Southeast-Asia. If its origins are Gondwanan, then the northern route was potentially closed by the breakup of Pangaea and the separation of Gondwana from Laurasia as early as ca. 220 Ma. If its ancestors rafted from Australia on the West Burma terrane, then in Metcalfe's (2013) model the rafting lineage must have separated from the Australian tick fauna around 360–420 million years ago. This seems highly unlikely as it would require these animals to have radiated into modern genera back in the Devonian, which significantly predates the Late Carboniferous molecular estimates (see above) of tick origins.

A final possibility is that *Amblyomma* actually originated in Eurasia – again perhaps during the Cretaceous as part of this metastriate radiation – and arrived (and was fossilized) in the West Burma region *via* a northern route long after it had collided with Asia. As noted above, Upchurch's (2008) scenarios for the dissolution of Gondwana are largely based on fossil vertebrate data. However, there are numerous examples of plants and animals distributed both in former Gondwanan regions and (often as fossils) in the northern hemisphere. Examples include palpimanoid spiders (Wood *et al.* 2013, and references therein), ants (Zryanin, 2015), hemipterans (Szwedo *et al.* 2015), neuropterans (Wedmann and Makarkin, 2007) and branchiopod crustaceans (Korovchinsky, 2006; Van Damme and Sinev, 2013). The implication here is that these groups were once globally distributed across both the northern and southern continents, but at some stage (perhaps in response to glaciation) either became extinct in the north and/or migrated south. This has been referred to as the ousted relicts (Eskov and Golovatch, 1986) or ejected relicts (Korovchinsky, 2006) hypothesis. Such a scenario should also be borne in mind when considering how *Amblyomma* came to be so widespread in the former Gondwana region today: did it really originate here, or is it a relict of a once much wider distribution? A final thought is that several species of *Amblyomma* parasitize birds today, in which case trans-oceanic dispersal through flight remains a possibility.

ACKNOWLEDGEMENTS

We thank Jörg Wunderlich (Hirschberg) for making this material available for study, Lorenza Beati Ziegler (Georgia Southern University) for initial comments on the specimen, Ekaterina Sidorchuk (Borissiak Paleontological Institute) for drawing our attention to misidentifications in the literature and Martin Pfeffer and two anonymous reviewers for helpful comments on the manuscript.

FINANCIAL SUPPORT

This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

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