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Haemaphysalis cretacea a nymph of a new species of hard tick in Burmese amber

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Abstract

The first fossil potentially assignable to the extant hard tick genus *Haemaphysalis* CL Koch (1844) (Ixodida: Ixodidae) is described from the Late Cretaceous (ca. 99 Ma) Burmese amber of Myanmar. *Haemaphysalis* (*Alloceraea*) *cretacea* sp. nov. is the oldest and only fossil representative of this genus; living members of which predominantly feed on mammals. Their typical hosts are known since at least the Jurassic and the discovery of a mid-Cretaceous parasite, which might have fed on mammals raises again the question of to what extent ticks are coupled to their (modern) host groups. An inferred Triassic split of Argasidae (soft ticks) into the bird-preferring Argasinae and mammal-preferring Ornithodorinae dates to about the time when dinosaurs (later including birds) and mammaliaforms as potential hosts were emerging. Ixodidae may have split into Prostriata and Metastriata shortly after the end-Permian mass extinction, an event which fundamentally altered the terrestrial vertebrate fauna. Prostriata (the genus *Ixodes*) prefer birds and mammals today, and some may have used groups like cynodonts in the Triassic. Basal metastriate ticks (e.g. *Amblyomma*) prefer reptiles, but derived metastriates (including *Haemaphysalis*) again prefer mammals. Here, we may be looking at a younger (Cretaceous?) shift associated with more recent mammalian radiations.

Introduction

Ticks (Arachnida: Parasitiformes: Ixodida) are haematophagous ectoparasites found on a wide range of vertebrate hosts. For an overview of their biology and economic significance as disease vectors, see Sonenshine and Roe (2013). About 900 living species are known (Guglielmone *et al.* 2010), divided across three families and 18 extant genera (Table 1). Molecular data (Mans *et al.* 2012) suggest that the group may have originated during the Carboniferous, but their fossil record is sparse and restricted to deposits dating to the Late Cretaceous or younger. For recent summaries, see Dunlop *et al.* (2016), Chitimia-Dobler *et al.* (2017) and Peñalver *et al.* (2017). An extinct family and genus (Deinocrotonidae: *Deinocroton* Peñalver *et al.* 2017) – possibly related to Nuttalliellidae – was described recently. The oldest hard ticks (Ixodidae) are examples of the extant genus *Amblyomma* CL Koch (1844) and the extinct genera *Cornupalpatum* Poinar and Brown (2003) and *Compluriscutula* Poinar and Buckley (2008). All of these fossils come from the Late Cretaceous (ca. 99 Ma) Burmese amber outcropping in Myanmar.

Here we describe another Burmese amber tick (Figs 1–3): the first, and so far only, fossil potentially assignable to the extant genus *Haemaphysalis* CL Koch (1844). The new specimen is a well-preserved nymph that can probably be further placed in the subgenus *Alloceraea* Schulze (1919) and represents the fourth tick species found in this amber deposit. If this interpretation is correct, it draws another extant tick genus back into the Cretaceous, and is consistent with Mans *et al.* (2012) hypothesis that the so-called metastriate ticks, i.e. all hard ticks excluding *Ixodes* Latreille (1795) radiated in the Early Cretaceous. Modern species of *Haemaphysalis* usually parasitize birds and to a greater extent mammals (see ‘Discussion’ section). A Cretaceous record of this tick genus is thus of particular interest, given that both of their usual host groups would have been present (Brocklehurst *et al.* 2012; Williamson *et al.* 2014; see also ‘Discussion’ section), and may have been increasing in diversity towards the end of the Mesozoic. In this context, we also take the opportunity to review the tick fossil record compared with the fossil record of their (modern) host groups, together with molecular clock estimates for when both the parasites and their hosts are thought to have originated.

Material and methods

The type and only known specimen comes from the collection of Mr Patrick Müller and bears the inventory number BUB990. Burmese amber mostly comes from deposits in the Hukawng Valley of northern Myanmar and has been dated to the Late Cretaceous (earliest Cenomanian), or about 98.79 ± 0.62 Ma (Shi *et al.* 2012). Further details about the history of discovery and the geological setting can be found in Grimaldi *et al.* (2002) and Ross *et al.* (2010); see also Selden and Ren (2017) for a recent review focused on the arachnids. A complete online list

Table 1. Summary of the 18 extant (and three extinct) tick genera based on Guglielmone and Nava (2014) and Guglielmone *et al.* (2014), indicating the oldest fossil record of each genus, molecular divergence estimates based on Mans *et al.* (2012), their typical modern hosts, the oldest potential fossil of a host taxon used by living members of this genus, plus suggested origination dates for these hosts based on molecular clock techniques

Tick genus	Oldest fossils of the tick (Ma)	Estimated divergence dates (Ma)	Host(s) of the living tick species	Oldest fossils of a (living) host taxon (Ma)	Estimated date of origin for this host (Ma)
Ticks first appear? Ticks diversify?	— —	350 ± 23 319 ± 25	Tetrapods? Land tetrapods? Amniotes?	365 330–345 311	408–419 — 323–326
NUTTALLIELLIDAE					
1. *Nuttalliella*	No fossils (0)	319 ± 25	Lizards, birds and mammals	170 (lizards) 160–208 (mam.) 150 (birds)	238–250 161–217 > 139
DEINOCROTONIDAE[a]					
2. *Deinocroton*[a]	Cretaceous (99)	—	Feathered dinosaurs?	200?	—
Argasids/ixodids	—	290 ± 23			
ARGASIDAE					
Argasinae		234 ± 25			
3. *Argas*	No fossils (0)		Birds and bats	150 (birds) 52 (bats)	>139 64
Ornithodorinae		234 ± 25			
4. *Ornithodoros*	Cretaceous (94) (as *Carios*)	158	Mammals, birds and reptiles	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 139
5. *Otobius*	No fossils (0)	—	Placental mammals; adults do not feed	65	72–108
6. *Antricola*	No fossils (0)		Mammals (bats)	52	64
7. *Nothoaspis*	No fossils (0)		Mammals (bats)	52	64
Argasids/ixodids		290 ± 23			
IXODIDAE					
PROSTRIATA		249 ± 23			
8. *Ixodes*	Eocene (49)	217 ± 24	Mammals, occasionally birds and reptiles	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 >139
METASTRIATA		249 ± 23			
Modern metastriates		124 ± 17			
Bothriocrotoninae					
9. *Bothriocroton*	No fossils (0)	—	Reptiles and mammals	311 (reptiles) 160–208 (mam.)	323–326 161–217
Amblyomminae					
10. *Amblyomma*	Cretaceous (99)	78 ± 20	Reptiles and mammals, rarely birds	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 >139
11. *Cornupalpatum*[a]	Cretaceous (99)	—	Dinosaurs (Pennaraptora) and/or birds?	160 (Pennarap.) 150 (birds)	n/a >139
12. *Compluriscutula*[a]	Cretaceous (99)	—	Unknown	n/a	n/a
Haemaphysalinae					
13. *Haemaphysalis*	Cretaceous (99)		Mammals and birds, rarely amphibians and reptiles	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 >139
Rhipicephalinae					

(*Continued*)

Table 1. (*Continued.*)

Tick genus	Oldest fossils of the tick (Ma)	Estimated divergence dates (Ma)	Host(s) of the living tick species	Oldest fossils of a (living) host taxon (Ma)	Estimated date of origin for this host (Ma)
14. *Cosmiomma*	No fossils (0)	—	Hippos and rhinos (adults)	38–42 (rhinos) 16 (hippos)	50 (rhinos)
15. *Dermacentor*	Pleistocene (1)	—	Mammals incl. lagomorphs	160–208	161–217
16. *Rhipicentor*	No fossils (0)	—	Mammals	160–208	161–217
17. *Nosomma*	No fossils (0)	60 ± 17	Buffalo (adults), rodents (juv.)	18 (bovids)	23 (bovids)
18. *Hyalomma*	No fossils (0)	36 ± 3	Mammals, birds and reptiles	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 >139
19. *Anomalohimalaya*	No fossils (0)	—	Mammals	160–208 (mam.)	160–208
20. *Rhipicephalus*	No fossils (0)	—	Mammals, rarely on birds and reptiles as immature	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 >139
21. *Margaropus*	No fossils (0)	—	Mammals, exceptionally birds and reptiles	311 (reptiles) 160–208 (mam.) 150 (birds)	323–326 161–217 >139

Phylogenetic sequence based on Barker and Murrell (2002, 2004). See text for details.
[a]An extinct genus.

of Burmese amber inclusions can be found in Ross (2017). For photography, stack images were combined using the software Helicon Focus 6.7.1. A Keyence VHX-6000 Digital Microscope with a tiltable stand and a combination of upper light and transmitted light for focus stacking was used (with 100× to 1000× magnification). We partly used polarized light for more details. Drawings were prepared using a M205 C Leica stereomicroscope with a *camera lucida* attachment.

Fig. 1. Holotype of *Haemaphysalis* (*Alloceraea*) *cretacea* sp. nov., P. Müller collection no. BUB990, from Late Cretaceous (ca. 99 Ma) Burmese amber from Myanmar. Overview of dorsal surface. Scale bar equals 200 μm.

Systematic palaeontology

Ixodida Leach (1815)
Haemaphysalis CL Koch (1844)
Alloceraea Schulze (1919)
Haemaphysalis (*Alloceraea*) *cretacea* sp. nov.

Etymology: From the Cretaceous age of the fossil.

Material: Holotype and only known specimen, BUB990 (coll. P. Müller). Burmese amber, Myanmar, Late Cretaceous (Cenomanian).

Diagnosis: Body oval-elongate, scutum broader than long with margins broadly rounded, palpi elongate and clavate, 11 festoons, eyes absent, spiracle plates oval–elongate, coxae I–IV with small spurs, trochanter spurs lacking.

Description: Unengorged nymph (Fig. 1). Idiosoma: Ornamentation indistinct; body integument leathery; body oval–elongate; length (excluding capitulum) 1489 μm, greatest width 884 μm; scutum width 684.1 μm (measured in the middle of the scutum) and 539.6 μm (from the scapula to the edge); margins broadly rounded, no evidence for punctuations; scapulae acute-angled, resembling elongate, sharp prongs, cervical grooves deep, linear anteriorly and diverging posteriorly, can be traced along whole length of the scutum (Fig. 2); eyes absent (Figs 2A and 3A); 11 festoons ranging from 87 to 110 μm in basal width and 73 to 87 μm in length (Figs 2 and 3B); stigma oval–elongate with a narrower part dorsally and rounded macula located on the antero-inferior side (Fig. 2B); anus and anal groove not visible (Fig. 3B).

Capitulum: (Figs 3C, D): Length from apices to posterior margin of basis 406.6 μm; basis capituli slightly wider (240 μm) than long (216 μm), posterior margin straight, lateral margins straight, cornua absent, ventrally posterior margin straight, length from palpal insertion to posterior margin of basis 83.7 μm, width 239.6 μm; palpi elongated and clavate, with length of four articles as follows:

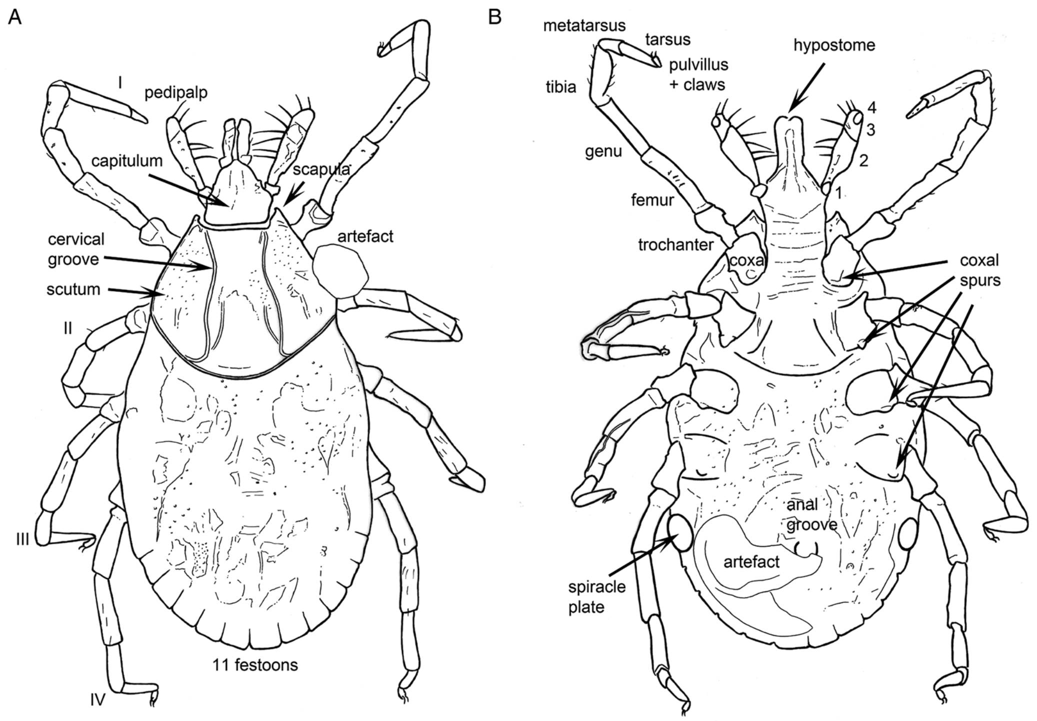

Fig. 2. *Camera lucida* drawing of the specimen shown in Fig. 1. (A) Dorsal view. (B) Ventral view.

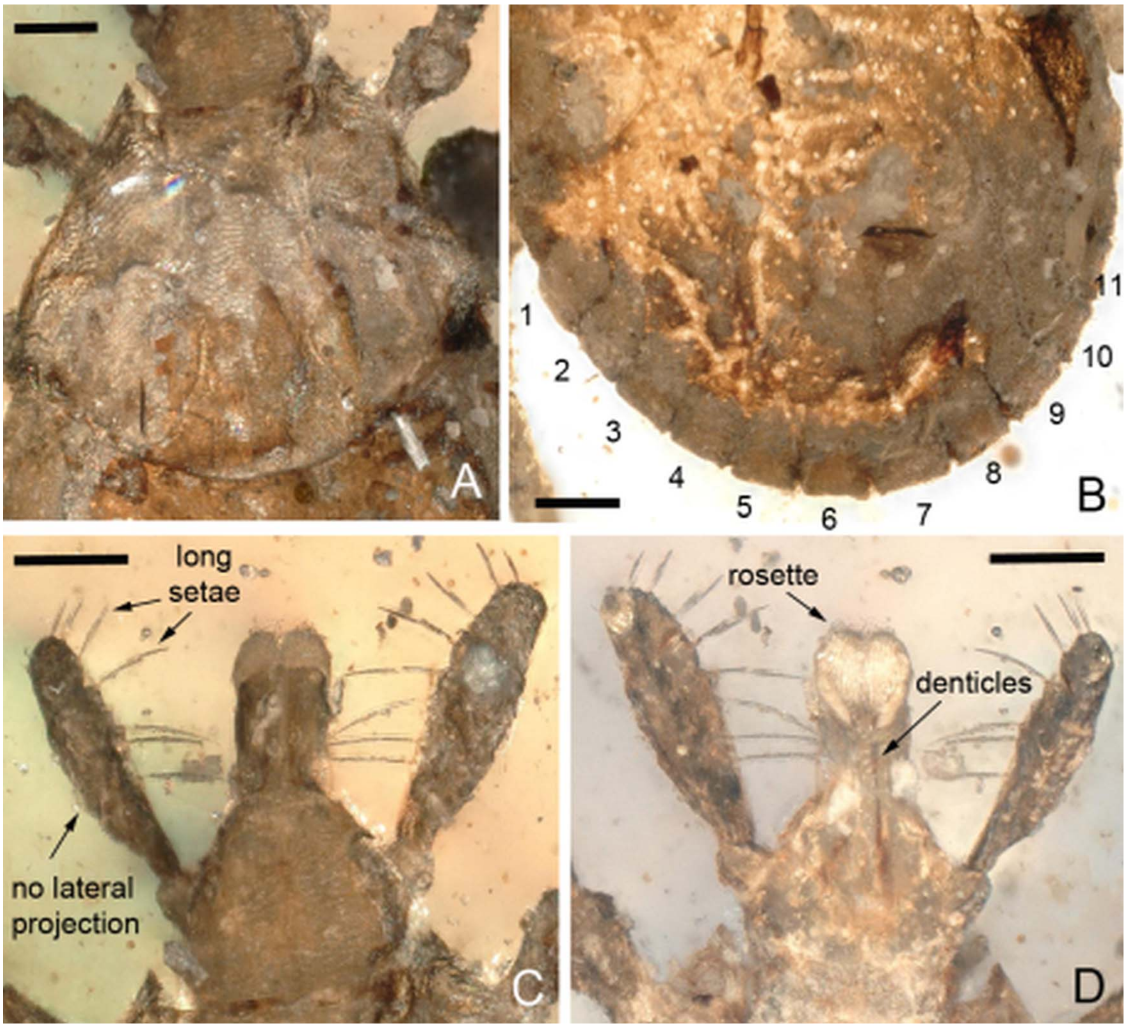

Fig. 3. Morphological details. (A) Dorsal scutum; note the absence of eyes. (B) Ventral idiosoma revealing 11 festoons. (C–D) Details of capitulum including basis capituli, palps and hypostome in dorsal (C) and ventral (D) views. Scale bars equal 100 μm.

article 1, 49.8 μM; article 2, 170 μM – with external proximal side concave, while distal end of article 2 is noticeably wider, 1.6 times longer as the third article (but appears shorter in the figures due to the angle of view) – article 3, 106 μM, without external spur; article 4 is in apical pit, visible ventrally; hypostome almost as long as palpi, length 182 μM, width at base 97.7 μM; dental formula equivocal, but with numerous denticles (almost 8–10 in a single file), distally a rosette is visible (Fig. 3B); porose areas absent (Fig. 3A). Legs: Short and robust (Figs 1 and 2). Coxae I with very small, short, widely triangular spur, located in the middle (Fig. 2B); coxae II with sub-basal triangular spur, located in the middle; coxae III and IV with small basal ridge spur, located externally; tarsus I tapering distally, length 378 μM, clear, oval area on dorsum of tarsi I is Haller's organ; claws paired, slender, simple, slightly curved; with distinct pulvillus on all legs (Fig. 2). *Chaetotaxy*: Eight long setae on palpi (Fig. 3C), four on the article 2 and four on the article 3 (the left article 2 has only three setae, probably one was broken). Small and tiny hairs can be observed on the legs.

Discussion

The presence in the new fossil of marginal festoons (Figs 1 and 2) rules out affinities with the recently described Burmese amber tick *Deinocroton draculi* Peñalver *et al.* (2017). The absence of eyes in our fossil (Fig. 3A) also excludes the Burmese amber species *Amblyomma birmitum* Chitimia-Dobler *et al.* (2017). The absence of eyes matches the condition in the extinct Burmese amber species *Compluriscutula vetulum* Poinar and Buckley (2008). However, the pedipalps of *C. vetulum* are different from those in our new fossil; in *C. vetulum*, the fourth segment of the pedipalp is long and ends with elongate terminal setae and there are also 13 festoons on the body (not 11, cf. our Fig. 3B) (Poinar and Buckley, 2008: Fig. 3). The other extinct Burmese amber tick, *Cornupalpatum burmanicum* Poinar and Brown (2003), differs from our new fossil in that it has a unique extra claw on the penultimate (third) pedipalp article (Poinar and Brown, 2003: Figs 3 and 4).

Excluding Amblyomma *(including* Aponomma*) and* Bothricroton

The absence of eyes is also characteristic for species that used to be placed in the genus *Aponomma* Neumann (1899) and that are now included either in *Amblyomma* or *Bothriocroton* Keirans, King and Sharrad (1994) (e.g. Klompen *et al.* 2002; Guglielmone *et al.* 2014). There are currently 14 extant *Amblyomma* species without eyes (Madder *et al.* 2010; Schachat *et al.* 2018). However, unlike our fossil, species belonging to *Amblyomma* (either with or without eyes) invariably have a more circular body, a striated integument texture, straight lateral margins on the basis capitulum and unequal paired spurs on coxae 1. Kaufman (1972) described what used to be called the 'indigenous Australian *Aponomma*' ticks with the following character combination: a single subterminal spur on the trochanter (absent in all other *Aponomma*) and lateral grooves on the scutum of the male being partial or complete. These grooves are absent in 'typical *Aponomma*', *A. elaphense* Price (1959) and *A. glebopalma*, but present in *Amblyomma sphenodonti* Dumbleton (1943). These seem to be reliable phylogenetic markers. Other characters that may support 'indigenous Australian *Aponomma*' are a hypostomal dentition of 3/3 or 2/2; it is 3/3 or more in 'typical *Aponomma*', 2/2 in *A. transversale* Lucas (1845), 2/2 in *A. elaphense* and 3/3 but with the internal row almost gone in *A. sphenodonti*. Large wax glands laterally near setae s6 [Md3 of Clifford *et al.* (1961)] and anterior to the first festoons (Klompen *et al.* 1996) found in the larvae are probably the most promising diagnostic characters for the 'indigenous Australian *Aponomma*'. Overall, although the new fossil shares a similar palpal morphology with modern members of the subgenus *Aponomma*, it cannot be easily matched to any of these living ticks in which the body of all life stages is almost circular and never elongated like our amber example.

The absence of eyes and elongate palps are also characteristic for living *Bothriocroton* species. On the other hand, a subpentagonal basis capituli – it is subtriangular in *Bothriocroton oudemansi* nymphs (Beati *et al.* 2008) – coxae with two spurs in all instars and trochanters with a single subterminal ventral spur (absent in *Bothriocroton glebopalma*, cf. Klompen *et al.* 2002) exclude the possibility that the new fossil belongs to *Bothriocroton*. It can be further excluded from *Bothriocroton* (in other words the Australian species placed in *Aponomma*; see above) as these ticks are generally large animals with a subcircular body and long mouthparts. Iridescent ornamentation on the scutum can be absent or present and the hypostomal dentition in *Bothriocroton* adults is 2/2 or 3/3. The coxae generally have two spurs in all instars and the trochanters have a single subterminal ventral spur. However, we should note that none of these characters is unique for 'indigenous Australian *Aponomma*' (Keirans *et al.* 1994; Klompen *et al.* 2002; Beati *et al.* 2008).

Excluding Anomalohimalaya

Like our new fossil, living members of the genus *Anomalohimalaya* Hoogstraal, Kaiser and Mitchell (1970) have an elongate body, but the basis capituli is peculiar, the palps are shorter and there are many punctations on the scutum (Filippova, 1997), which make them quite different from our amber specimen. Filippova and Bardzimashvily (1992) discussed morphological differences between the nymphs of *Anomalohimalaya*. The *Anomalohimalaya cricetuli* nymph has a smooth, nitidous scutum with closely positioned lateral and cervical grooves, forming a narrow deep and short furrow, while in the other two species, the scutum is dull, the furrow between the lateral and cervical grooves is short and nearly reaches the posterolateral margins of the scutum. The shape and location of the lateral projections of the gnathosoma basis correspond to those of females. Filippova and Panova (1978) concluded that *Anomalohimalaya* combines characters of *Haemaphysalis* and *Rhipicephalus* Koch (1844), and is thus potentially significant for a more precise definition of the phylogeny of the subfamily Amblyomminae; however, it does not appear to be relevant of the affinities of the new fossil.

Assignment to Haemaphysalis

We are confident that our new fossil belongs to a previously unrecognized species in Burmese amber, and that at least five distinct species of tick (four hard ticks, plus the extinct *Deinocroton*) were present in the original amber forest. Three apparently belonged to the extinct genera and, as we will argue here, the other two belonged to the living genera (*Amblyomma* and *Haemaphysalis*). A re-evaluation of relationships in the Metastriata by Klompen *et al.* (1997) clearly showed that morphological analysis of the genus *Haemaphysalis* is complicated by the presence of plesiomorphic, so-called 'structurally primitive' species (see below). Their final conclusion was that *A. sphenodonti* and *A. elaphense* lack any of the characters unique to the derived *Haemaphysalis* species: e.g. the 'blade-like dorsal retrograde process' on trochanter I, palps projecting laterally over the basis capitulum or the presence of large wax glands mid-dorsal on segment XI in the larvae (Klompen *et al.* 1997).

We entertained the possibility of creating a new (extinct) genus for our fossil, but on balance we feel that it is better to assign the inclusion to the extant genus *Haemaphysalis* based primarily on a combination of: (1) an elongated body, (2) the absence of eyes, (3) the presence of festoons, (4) a dental formula with 8–10 denticles in a file, (5) lack of cornua, (6) the absence of trochanter spurs and (7) segment III of palps lacking a ventral spur and segment IV being an apical pit. *Haemaphysalis* ticks are generally small, inornate animals with short mouthparts: the brevirostra condition. The genus *Haemaphysalis* is further defined by specific morphological features, which we cannot resolve in the fossil like the presence of a prominent 'blade-like' dorsal retrograde process on trochanter I (Nuttall and Warburton, 1915).

Assignment to the subgenus Alloceraea

Most members of *Haemaphysalis* can also be recognized by the second palpal article being expanded and projecting laterally beyond the basis capitulum (Geevarghese and Mishra, 2011). Hoogstraal and Kim (1985) studied *Haemaphysalis* and proposed a trend in the evolution of morphology within and among the subgenera from atypical and 'primitive' *Amblyomma*-like forms, such as the subgenus *Alloceraea* Schulze (1919) (Geevarghese and Mishra, 2011), to the more typical *Haemaphysalis*-like forms. Hoogstraal and Kim (1985) thus graded the subgenera of *Haemaphysalis* into three groups: (1) the structurally primitive, (2) structurally intermediate and (3) structurally advanced species. In several species belonging to the 'structurally primitive' group, the expanded and laterally projecting second palpal article is not seen. This includes *Haemaphysalis* (*Alloceraea*) *inermis* Birula (1895) [also known as *Allocerea inermis* Birula (1895), *A. inermis inermis* Birula (1895), *A. inermis aponomoides* Warburton (1913)], *H. ambigua* Neumann (1901) and *H. ibrikliensis* Ozkan (1978) (Feider, 1965; Guglielmone and Nava, 2014).

Other structurally primitive species are *H.* (*A.*) *aponommoides* Warburton (1913), *H.* (*Allophysalis*) *garhwalensis* Dhanda and Bhat (1968), *H.* (*A.*) *kitaokai* Hoogstraal (1969), *H.* (*A.*) *vietnamensis* Hoogstraal and Wilson (1966) – currently known as *H. colasbelcouri* Santos Dias (1958) (Guglielmone and Nava, 2014) – *H. verticalis* Itagaki, Noda and Yamaguchi (1944) and *H.* (*A.*) *primitiva* Teng (1982). Further details about these taxa can be found in, e.g. Feider (1965), Hoogstraal and Kim (1985), Filippova (1997), Geevarghese and Mishra (2011) and Guglielmone *et al.* (2014). Our new fossil tick also lacks an expanded and laterally projecting second palpal article (Fig. 3C and D). Its palps are elongate and clavate and the external proximal side of the second article is concave, while the distal end is noticeably wider. This is similar to the condition seen in the structurally primitive taxa mentioned above and implies that the fossil could be a structurally primitive *Haemaphysalis* sensu Hoogstraal and Kim (1985), and may be further related to this particular *Alloceraea* group of living species.

Haemaphysalis *biology and systematics*

Haemaphysalis is the second largest tick genus, currently including 167 species. It occurs in all six zoogeographic regions, with the greatest diversity in south-eastern Asia and poorly represented in the Nearctic and the Neotropics (Kolonin, 2009; Guglielmone *et al.* 2014). The best represented area for *Haemaphysalis* is the Oriental region (with 64 species) – which is of course geographically consistent with Burmese amber – followed by the Afrotropical region with 38 species (Guglielmone *et al.* 2014). One hundred and forty-six species are distributed exclusively (118 species) and non-exclusively on continents derived from Gondwana, and 20 species are established in areas derived from Laurasia (Guglielmone *et al.* 2014).

Haemaphysalis is currently divided into 11 subgenera (Hoogstraal and Kim, 1985). The structurally primitive *Haemaphysalis* (see above) include four subgenera: *Alloceraea*, *Allophysalis*, *Aboimisalis* and *Sharifiella* (Hoogstraal and Kim, 1985; Geevarghese and Mishra, 2011).

In a review of Paul Schulze's contributions to tick systematics, Guglielmone *et al.* (2017) compiled all the information about *Alloceraea*, which Schulze originally proposed as a genus for the Palearctic species *H. inermis* Birula (1895) – the type species for the subgenus *Alloceraea* – which possesses some morphological characteristics suggestive of *Aponomma*. Thereafter, *Alloceraea* was generally considered a subgenus of *Haemaphysalis*, but he later (Schulze, 1942) returned it to full genus rank and it was also treated as a valid genus by Zumpt (1951). Currently, *Alloceraea* is considered again a subgenus of *Haemaphysalis* (e.g. Camicas and Morel, 1977; Hoogstraal and Kim, 1985; Filippova, 1997; Camicas *et al.* 1998). The subgenus *Alloceraea* contains the species *H.* (*A.*) *aponommoides* from India; *H.* (*A.*) *inermis* from Europe and Asia; *H.* (*A.*) *kitaokai*, *H.* (*A.*) *verticalis* and *H.* (*A.*) *primitiva* from Asia; and *H.* (*A.*) *colasbelcouri* from the Orient (Feider, 1965; Filippova, 1997; Geevarghese and Mishra, 2011; Guglielmone *et al.* 2014). As noted above, our new fossil tick most resembles these *Alloceraea* species in being small ticks which, like our fossil, lack eyes (Nicholson *et al.* 2009).

The 11 well-defined festoons in the new amber specimen (Fig. 3B) are all more or less the same size. This is the third tick with 11 festoons found in Burmese amber; the others being *C. burmanicum* (Poinar and Buckley, 2008) and *A. birmitum* (Chitimia-Dobler *et al.* 2017). Most extant *Haemaphysalis* species also have 11 festoons (e.g. Feider, 1965; Filippova, 1997; Geevarghese and Mishra, 2011), but there are also species with nine, e.g. *Haemaphysalis* (*Herpetobia*) *sulcata* Canestrini and Fanzago (1877), *Haemaphysalis* (*Segalia*) *parva* Neumann (1897) – previously also known as *Haemaphysalis otophila* Schulze (1919) – and *Haemaphysalis* (*Ornithophysalis*) *pavlovskyi* Pospelova-Shtrom (1935) (Feider, 1965; Filippova, 1997).

In the mouthparts, the dental formula of the hypostome in the new specimen is not entirely clear, but numerous denticles can be observed (almost 8–10 in a single file) and a rosette is visible distally (Fig. 3D). The fossil larva described as *C. vetulum* has a 2/2 dental formula (Poinar and Buckley, 2008), as does *A. birmitum* (Chitimia-Dobler *et al.* 2017) which is an adult female. Structurally advanced *Haemaphysalis* species usually have a 2/2 dental formula when immature, although in some species it can be 3/3 or 4/4. As adults they usually have a 4/4 arrangement, but exceptionally they can have a 3/3 or 5/5 to 7/7 dental formulae. In this respect, our new fossil is again closest to structurally primitive *Haemaphysalis*, and in particular to nymphs which have a 2/2 dental formula with only 8–12 denticles in each file. Compared with modern *Alloceraea* species, *H. aponommoides* has a 3/3 dental formula with eight denticles in a file as a nymph, *H.* (*A.*) *kitaokai* has a 2/2 dental formula with 4–5 denticles in a file as a nymph and *H.* (*A.*) *inermis* has a 2/2 dental formula with 6–8 denticles in a file as a nymph (Feider, 1965; Hoogstraal, 1969; Geevarghese and Mishra, 2011).

Structurally primitive *Haemaphysalis* show some distinctive morphological characters: each developmental stage – or only the larvae and nymphs – presents a lateral convexity of the basis capituli or a projection from each side of the basis capituli; the palps are elongate and compact, but not basolaterally salient, and capitular and leg-spur development is (with a few notable exceptions) exceedingly slight (Hoogstraal and Kim, 1985; Geevarghese and Mishra, 2011). Structurally primitive *Haemaphysalis*, and the other non-rhipicephaline ixodids, differ distinctly from other haemaphysaline species in other subgenera. For example, life stages from the subgenus *Alloceraea* have a laterally convex or otherwise laterally projecting basis capituli, lacking cornua, and elongate (clavate) pedipalpi lacking a ventral spur

(Geevarghese and Mishra, 2011). Our new fossil has some of these *Alloceraea* characteristics, such as elongate pedipalpi, absence of a ventral spur on the pedipalps and lacking cornua, but can be differentiated from the living species in that it does not show the convex or laterally projecting basis capituli (Fig. 3C and D). The new fossil is perhaps morphologically closest to *H.* (*A.*) *inermis*, which also lacks a lateral projection (Feider, 1965) and both this species and the fossil present six setae on the palps; the setae being longer in our fossil. The various spur or spur-like angles of the body appendages are obsolete or only very slightly developed in each *Alloceraea* stage. Extant *Alloceraea* species uniquely have a leathery cuticle, which is probably adapted for water conservation (Geevarghese and Mishra, 2011). The identification of species within the subgenus *Alloceraea* is rather difficult. Different authors sometimes consider conspecific ticks collected in the same region as different species. Therefore, the data on the precise distribution of *H.* (*A.*) *aponommoides*, *H.* (*A.*) *inermis*, *H.* (*A.*) *kitaokai* and *H.* (*A.*) *colasbelcouri* in the territory of China is rather inconsistent (Kolonin, 2009).

In conclusion, we concede that our new fossil is not a typical *Haemaphysalis*, but we propose that it most closely resembles members of the extant *Haemaphysalis* subgenus *Alloceraea*; albeit differing from living taxa in some features. The basis capitulum of our fossil is dorsally 2.6 times as broad as long (length from palpal insertion to posterior margin of basis 83.7 μM, width 239.6 μM) (Fig. 3C). It is four times as broad as long in *H.* (*A.*) *aponommoides*, 2.9 times as broad as long in *H.* (*A.*) *kitaokai*, five times as broad as long in *H.* (*A.*) *garhwalensis* and broader than long in *H.* (*A.*) *inermis* (Feider, 1965; Hoogstraal, 1969; Geevarghese and Mishra, 2011). The scutum of our new fossil is 1.2 times as broad as long (Fig. 3A), but with margins broadly rounded, no evidence of punctuations, the scapulae are acute-angled and resemble elongate sharp prongs; the cervical grooves are deep and linear anteriorly (Fig. 2A) and diverge posteriorly where they can be traced along the whole length of the scutum. In *H.* (*A.*) *aponommoides*, the scutum is approximately 1.4 times as broad as long, few punctuations are seen and the cervical grooves form deep arcs. In *H.* (*A.*) *kitaokai*, the scutum is 1.25 times as broad as long, cordiform, punctations are few, shallow, small and of moderate size; cervical grooves are slightly converging anteriorly, slightly diverging posteriorly and extend to the posterior margin of scutum. In *H.* (*A.*) *garhwalensis*, few punctuations are present, numbering eight to ten and the cervical grooves are linear, extending to almost to the posterior margin of the scutum (Hoogstraal, 1969; Geevarghese and Mishra, 2011). The scutum of *H.* (*A.*) *inermis* is 1.4 times as broad as long, cordiform with the posterior part converging, deep and uniform spread punctuations are seen, and the cervical grooves are deep, almost reaching the margin of the scutum (Feider, 1965). These morphological differences justify treating the Cretaceous fossil tick is an extinct *Haemaphysalis* species.

Haemaphysalis *host taxa*

Haemaphysalis ticks typically parasitize mammals, and to a lesser extent birds, in most regions of the world (Nicholson *et al.* 2009). Frogs, etc. (Anura), and crocodiles have not been recorded as hosts for any life stage of *Haemaphsysalis* species, while lizards and snakes (Squamata) and tortoises (Testudines) make only a relatively minor contribution (Guglielmone *et al.* 2014). Of the closest living matches for our fossil, adult *H.* (*A.*) *inermis* ticks feed on a variety of mammals, while the immature stages feed on small mammals and reptiles (Feider, 1965; Manilla, 1998; Perez-Eid, 2007). *Haemaphysalis* (*A.*) *aponommoides* adults feed on domestic and wild mammals (including the flying squirrel), while the immature stages feed on lizards, shrews, rodents and birds (Geevarghese and Mishra, 2011). *Haemaphysalis* (*A.*) *kitaokai* adults have been collected from cattle, horse, Japanese serow and sika deer in the Honshu and Kyushu islands (Hoogstraal, 1969). *Haemaphysalis* (*A.*) *colasbelcouri* adults have been collected from cattle and deer, for *H.* (*A.*) *verticalis* two females were collected from the domestic dog in Shansi, but mostly occur on ground squirrels and sometimes from another rodent, the long-clawed jird (Emel'yanova and Hoogstral, 1973). The normal hosts are squirrels (Sciuridae) for all life stages, and exceptionally birds (Guglielmone *et al.* 2014).

Our new fossil is a nymph, and so could potentially have used lizards, birds, (small) dinosaurs or mammals as hosts. However, we might predict that the adult of *H.* (*A.*) *cretacea* sp. nov. was primarily a parasite of Cretaceous mammals; similar to the modern members of this subgenus. This makes it potentially one of the oldest pieces of evidence for an arthropod parasitizing a mammal. We should add that other data suggest that parasitic insect groups such as lice (Smith *et al.* 2011) and fleas (Huang *et al.* 2012) may have been present on Late Cretaceous mammals too.

Structurally primitive *Haemaphysalis* species represent approximately 10% of the total number of known species in the genus. Ecologically and geographically, all except one species of this group are confined to temperate zones of North America – *H.* (*Aboimisalis*) *chordeilis* Packard (1869) – and Eurasia. *Haemaphysalis* (*Sharifiella*) *theilerae* Hoogstraal (1953) is the only exception, being present in the tropical climate of Madagascar. Low temperatures and slow reproductive rates appear to be partially responsible for the preservation of the primitive morphotype and perhaps also for the survival of certain species that have changed little, if at all, since the genus first originated; see Hoogstraal and Wilson (1966) for further discussion. In terms of biogeography, the species in the *Alloceraea* subgenus have different distributions. *Haemaphysalis* (*A.*) *aponommoides* is closer to Myanmar, having been partially found in Southeast Asia: namely Iran, India, Nepal, Taiwan and Japan (Geevarghese and Mishra, 2011). *Haemaphysalis* (*A.*) *inermis* has been recorded from the former Soviet Union, Turkey, Iran, Romania, Albania, Greece, Bulgaria, Czech Republic, Germany and France (Feider, 1965; Manilla, 1998). *Haemaphysalis* (*A.*) *colasbelcouri* (*vietnamensis*) has been recorded only in the Vietnam highlands (Hoogstraal and Wilson, 1966). *Haemaphysalis* (*A.*) *kitaokai* has been reported from Japan and Taiwan (Hoogstraal, 1969). *Haemaphysalis* (*A.*) *verticalis* has been recorded from China (Emel'yanova and Hoogstral, 1973).

The fossil record of ticks compared to their hosts

The Mesozoic is popularly referred to as the 'Age of Reptiles'. This is somewhat misleading, as there were also increasing numbers of both birds and mammals from the Jurassic onwards (see below) but, as noted above, living species of *Amblyomma*, the extant tick genus found previously in Burmese amber (Grimaldi *et al.* 2002; Chitimia-Dobler *et al.* 2017), do largely use reptiles as their hosts today. By contrast, *H.* (*A.*) *cretacea* sp. nov. appears to be closest to ticks, which in modern ecosystems feed on (placental) mammals as adults, and mammals, lizards and birds when immature. Hoogstraal (1965) postulated that *Haemaphysalis* ticks arose alongside reptiles in the Late Paleozoic or Early Mesozoic in warm, humid forests of tropical Southeast Asia. In this hypothesis, severe competition from numerous more advanced forms led to most structurally primitive haemaphysalids becoming extinct. This scenario touches on the wider question of to what extent there has been coevolution between these parasites and their hosts. A caveat here is that lineages may have originated on groups that are now extinct or they may have changed hosts over deep geological time. Thus, Klompen *et al.* (1996) cautioned against the assumption that host phylogeny should determine tick phylogeny. Bearing this in mind, it may still be instructive to compare the fossil record of ticks with records of their vertebrate hosts, as well as molecular clock estimates for when the parasite and/or host lineages may have originated.

Tick origins

For a recent review of tick origins, and their probable relationships to other mites, see Mans *et al.* (2016). Modern ticks are ectoparasites on terrestrial and semi-aquatic vertebrates (Guglielmone *et al.* 2014), thus an obvious question is who their initial hosts were? Dobson and Barker (1999), Barker and Murrell (2002) and Barker *et al.* (2014) argued for Devonian labyrinthodont amphibians (i.e. tetrapods), specifically those living in Australia, as the original host species. The lungfish–tetrapod split has been estimated to the Early Devonian (408–419 Ma, Müller and Reisz, 2005), although both groups were presumably still (primarily) aquatic at this time. Although not Australian, fossils such as *Tiktalik* from the Late Devonian (ca. 375 Ma) of Canada (Daeschler *et al.* 2006) are essentially fish with several transitional characters towards the tetrapod condition. Slightly younger fossils from the Late Devonian (ca. 365 Ma) of Greenland, such as *Acanthostega* or *Ichthyostega*, can be considered true tetrapods and may offer an upper constraint on the appearance of potential hosts for ancestral ticks (Table 1). However, these early tetrapods are also thought to have been essentially aquatic (reviewed by Clack, 2012), and are sometimes referred to as ‘fish with legs’. In other words, could a Devonian tick have lived on a primarily aquatic host? Some modern ticks have been documented surviving for weeks or even months underwater (e.g. Smith, 1973), thus the labyrinthodont hypothesis should not be dismissed out of hand. Nevertheless, tetrapods may have only been habitually terrestrial from the Early Carboniferous (330–345 Ma, Smithson *et al.* 2012) onwards. This partly overlaps with Mans *et al.*’s (2012) molecular estimate of 350 ± 23 Ma for when the ticks diverged from mesostigmatid mites (Table 1); although it should be noted that these authors regarded Holothyrida – for which molecular data were not available – as the sister group of Ixodida. Mans *et al.* (2016) also favoured tick origins in the Carboniferous or Permian as opposed to an older Devonian date.

An alternative scenario would constrain ticks to hosts within the Amniota, i.e. vertebrates who did not need to return to water to breed, and presumably spent most (if not all) of their time on land. Some authors have indeed suggested the initial tick hosts were Palaeozoic reptiles (e.g. Hoogstraal and Aeschlimann, 1982). The oldest unequivocal amniote fossils – which also provide a maximum age for reptiles in general – date to the Late Carboniferous (ca. 311 Ma, e.g. Modesto *et al.* 2015). Amniota is thought to have diverged a little earlier (e.g. Reisz and Fröbisch, 2014) to form two main lineages, both of which regularly host ticks today. Of these, Sauropsida (which includes all modern reptiles) would also later lead to birds, while Synapsida would eventually produce the mammals. However, molecular estimates for what is essentially the bird–mammal split are not well constrained (see comments in Müller and Reisz, 2005), partly because the Late Carboniferous amniote fossil record is too sparse to bracket this divergence with any confidence. Published estimates include, e.g. 323–326 Ma for the diapsid–synapsid split (Pereira and Baker, 2006) and younger dates of ca. 285 Ma (Hugall *et al.* 2007) for the bird–lizard split, reflecting the origins of crown-group reptiles. In summary, amniotes probably evolved and diversified at some point in the Late Carboniferous (298–323 Ma), and this approximate date is consistent with Mans *et al.*’s (2012) 319 ± 25 Ma molecular estimate for when the ticks began to diverge from one another.

Nuttalliellidae

Nuttalliella namaqua Bedford (1931) is the only representative of the remarkable family Nuttalliellidae and shares several characteristics with both hard ticks (Ixodidae) and soft ticks (Argasidae). It has thus been envisaged as a ‘missing link’ between the other two tick families (e.g. Bedford, 1931; El Shoura, 1990; Latif *et al.* 2012; Mans *et al.* 2016). Recent studies have recovered *N. namaqua* as the sister group of all other ticks (Mans *et al.* 2012), or sister group to Ixodidae only (Burger *et al.* 2014) to the exclusion of the soft ticks. Early studies suggested that the preferred hosts of *N. namaqua* could be rock hyraxes (*Procavia capensis*), swallows, rodents and meerkats (Bedford, 1931; Keirans *et al.* 1976), while *Agama* or other lizards were also considered (Hoogstraal, 1985). Efforts to feed females and nymphs on chickens, pigeons, rabbits, rats or mice were unsuccessful (Hoogstraal, 1985). Later, Mans *et al.* (2011) and Horak *et al.* (2012) collected *N. namaqua* larvae from different murid rodent species; while a gut meal analysis from field-collected female ticks showed that it had fed on lizards. In conclusion, it seems likely that *N. namaqua* is a multi-host tick.

Nuttalliella namaqua has been called a ‘living fossil’ (Mans *et al.* 2012), although it lacks a fossil record itself. Several authors consider the nuttalliellid lineage to have split off first from the argasid/ixodid ticks, and as noted above, Mans *et al.* (2012) dated this to the Late Carboniferous (319 ± 25 Ma). The alternative (*Nuttalliella* + *Ixodidae*) hypothesis is not yet associated with a date estimate. Of the known nuttalliellid hosts, lizards are the oldest potential group. The origins of Lepidosauria (i.e. lizards, snakes and the tuatara) are probably to be found in the Triassic. The oldest unequivocal lizards come from the mid-Jurassic (e.g. Evans, 1998). Lepidosaur origins were reviewed in some detail by Jones *et al.* (2013) who noted that published molecular estimates ranged from the Early Jurassic (ca. 179 Ma) to the Early Permian (ca. 294 Ma). They themselves favoured a mid-Triassic estimate of about 238–250 Ma. In this scenario, there is a discrepancy of some 80 million years between the time when the lineage, which includes *N. namaqua*, may have originated and the expected appearance of at least some of the hosts they are known to use today. The implication is that nuttalliellids initially had to use other (extinct) reptile groups – perhaps for tens of millions of years – before adopting at least some of the hosts they use today.

Deinocrotonidae

Although nuttalliellids lack a fossil record, a recent and remarkable discovery (Peñalver *et al.* 2017) was the extinct family Deinocrotonidae described from Burmese amber with a single species *D. draculi*. The authors documented several characteristic features of deinocrotonids – including the structure of the integument, the palp, the shape of the preanal groove and a uniquely discontinuous genital groove – but suggested that Deinocrotonidae and Nuttalliellidae may be sister taxa, sharing synapomorphes such as a subterminal hypostome and the presence of a pseudoscutum. If this hypothesis is correct, the (Deinocrotonidae + Nuttalliellidae) clade must be at least 99 million years old, although a possible deinocrotonid was mentioned by Peñalver *et al.* (2017) from the slightly older (ca. 105 Ma) Spanish amber, which awaits formal description. As noted above, molecular data suggest a much older (Carboniferous) date for when nuttalliellids split from the clade encompassing both the hard and soft ticks.

With respect to their ecology, the *Deinocroton* fossils were found associated with specialized hairs (hastisetae) typical for larvae of the beetle family Dermestidae, which today are often found in bird nests. This discovery led Peñalver *et al.* (2017) to infer that

Deinocroton may also have been also associated with nest ecosystems and may thus have parasitized feathered dinosaurs. The age of the oldest feathered dinosaur is not so easy to resolve as there was almost certainly a gradation from downy filaments though to the fully developed flight feathers of birds (cf. Prum, 1999); see also discussion of the oldest birds below. Several Jurassic fossils show evidence of feather-like structures and a similar date, approaching 200 Ma, was adopted by Peñalver *et al.* (2017: Fig. 10).

Argasidae

Argasids are sometimes referred to as 'bird ticks', but this is misleading because, as a group, they are multi-host parasites with several genera utilizing mammals. Five argasid genera are currently recognized traditionally divided into the subfamilies Argasinae and Ornithodorinae. The argasines are restricted to the genus *Argas*, which includes parasites of both birds and bats (Nicholson *et al.* 2009). Of the four ornithodorine genera, *Ornithodoros* feeds on a range of both marsupial and placental mammals, and occasionally on birds and reptiles, *Otobius* has two species which feed, respectively, on rabbits and several domestic animals, while *Antricola* and *Nothoaspis* specifically parasitize bats. Note that most of the *Carios* species (currently an invalid genus) are now considered to belong to *Ornithodoros* or *Argas* (11 species) or to *Antricola* and *Nothoaspis* (see Estrada-Peña *et al.* 2010; Guglielmone *et al.* 2010).

Mans *et al.* (2012) estimated an Early Permian (290 ± 23 Ma) split between Argasidae and Ixodidae, and a Late Triassic (234 ± 25 Ma) split between Argasinae and Ornithodorinae. *Argas* currently lacks a fossil record (Table 1). Of the groups it parasitizes today (birds and bats), the oldest fossil traditionally recognized as a bird is still *Archaeopteryx* from the Late Jurassic (ca. 150 Ma) of Germany, although there is debate in the literature about precisely where to draw the line between birds and the non-avian (feathered) dinosaurs from which they evolved. A corollary of this is that argasids may have been hosted previously by other groups (e.g. dinosaurs), which would be consistent with Mans *et al.*'s Triassic origination date. At some stage, *Argas* shifted to bird hosts, and while several Jurassic fossils are evidently close to bird origins, the fragility of bird skeletons means that their subsequent Cretaceous record is poor (Brocklehurst *et al.* 2012). This ambiguity in the fossil record makes it hard to calibrate molecular estimates for when birds first appeared. For example, Pereira and Baker (2006) could only confidently bracket the split at the base of the archosaurs (i.e. crocodiles, dinosaurs and birds) to ca. 258 Ma and the split between the palaeognath and neognath bird lineages (both crown-group clades with living species) to at least 139 Ma; which is obviously younger than the current fossil record for the Aves total group. A similar point about the lack of robust calibrations for bird origins was made by Prum *et al.* (2015) who also stressed that, on their data, most modern birds radiated after the end Cretaceous mass extinction. For bats, the oldest unequivocal fossils are Eocene in age (ca. 52 Ma); see, e.g. Simmons *et al.* (2008). Molecular data (Teeling *et al.* 2005) support the hypothesis that bats originated shortly after the K–T extinction event (ca. 64 Ma).

Among the ornithodorines, *Ornithodoros* (as *Carios*) is known from Late Cretaceous (ca. 94 Ma) New Jersey amber (Klompen and Grimaldi, 2001) and the ca. 16 Ma Miocene Dominican Republic amber (Poinar, 1995). *Otobius*, *Antricola* and *Nothoaspis* lack a fossil record. As noted above, ornithodorine ticks usually parasitize mammals. Identifying the oldest unequivocal fossil mammal is also difficult, as there is an obvious gradation from synapsid reptiles through to modern mammal groups. Mammals evolved from a broader group, usually referred to as the Mammaliaformes, whose origins are to be found in the mid- to Late Triassic. Thus depending on the author, and the definition of Mammalia they use, the oldest mammals may be cited at Triassic or Jurassic in age; see Williamson *et al.* (2014) for a review. An estimate of ca. 160–208 Ma would encompass the oldest putative mammal fossils through to the oldest unequivocal members of the group (e.g. Luo *et al.* 2011). As with birds, debate about the exact position of certain fossils hinders effective calibration of molecular trees, but Phillips *et al.* (2009), e.g. estimated the split between monotremes and all other mammals to 161–217 Ma; with a caveat that other dates can be found in the literature. *Otobius* is only found on placental mammals. The origins of crown placental mammals is also controversial (e.g. dos Reis *et al.* 2014 and references therein), with dates both before and after the K–T extinction being proposed. The oldest unequivocal placental fossil dates to the Paleogene (ca. 65 Ma), while dos Reis *et al.* (2014) proposed Cretaceous origins for placental mammals based on the molecular data between 72 and 108 Ma; depending on the calibration method used.

Translating this into an evolutionary scenario for Argasidae, early members of this family could have been hosted by one of several groups of Late Palaeozoic or Early Mesozoic reptiles, and there is a gap of at least 50 million years between the inferred origins of argasids and the appearance of at least extinct relatives of their modern host groups. The inferred Late Triassic split into the subfamilies Argasinae (with bird/bat hosts) and Ornithodorine (mostly with mammal hosts) is particularly interesting. It corresponds well with the time at which dinosaurs, which eventually gave rise to birds, were thought to have been evolving from the other archosaurs, and is also the time when the mammaliaform/mammal lineage emerged from the synapsids. A deep (Triassic) split in host preferences between the argasid subfamilies is thus plausible; see also comments in Mans *et al.* (2012). Bats are geologically much younger (Paleogene/Eocene) and the shift to bat hosts by members of both the argasines and the ornithodorines must have occurred more than once. In general, we should not forget that hosts almost certainly changed over time and that modern associations of a given tick species with particular living bird or (placental) mammal group must also be geologically quite young. Both the fossil record and molecular data strongly imply that modern mammal and bird lineages radiated after the Cretaceous (dos Reis *et al.* 2014; Prum *et al.* 2015).

Ixodidae: Prostriata

Hard ticks (Ixodidae) can be divided into two main lineages: Prostriata restricted to *Ixodes*, and Metastriata containing the remaining genera. There seems to be a consensus that *Ixodes* can be divided into an Australian and a non-Australian lineage, and some authors (Klompen *et al.* 2000) have even questioned whether the genus is monophyletic. Hosts for Australian *Ixodes* species were reviewed by Barker *et al.* (2014) and include monotreme, marsupial and placental mammals, as well as sea birds. A similar pattern is seen in the remaining *Ixodes* ticks, which are usually found on mammals, but also includes species which parasitize birds and occasionally reptiles (Hoogstraal and Aeschlimann, 1982).

The oldest fossil *Ixodes* is *I.* (*Partipalpiger*) *succineus* from Eocene (ca. 44–49 Ma) Baltic amber (Weidner, 1964; Dunlop *et al.* 2016), plus a subfossil record from an owl pellet. As noted above, the Ixodidae–Argasidae split has been estimated to the Early Permian (290 ± 23 Ma). Within ixodids, Mans *et al.* (2012) placed the Prostriata–Metastriata split in the earliest part of the Triassic (249 ± 23 Ma) and the split into Australian and non-Australian *Ixodes* lineages in the Late Triassic (217 ±

24 Ma) (Table 1). The amber fossil is thus much too young to offer any insights into the origins of the genus, but the preference for mammalian hosts among several living *Ixodes* species could imply a long association, potentially beginning with the mammal-like reptiles, which belong to the broader synapsid clade. To reiterate (see above), Synapsida originated in the Late Carboniferous (Reisz and Fröbisch, 2014) when they split off from the Sauropsida, which includes extinct groups (e.g. Parareptilia) as well as the ancestors of modern reptiles and birds. The Late Carboniferous is also the time when argasids are estimated to have split from ixodids. During the Permian early members of both tick families would have had mammal-like synapsid reptiles and sauropsids as potentially available hosts, although any host preferences at this stage remain speculation.

What could be significant is the estimated split of Ixodidae into Prostriata and Metastriata at about the time of the End-Permian mass extinction. This major event fundamentally changed the tetrapod landscape. Within Synapsida, groups such as the, probably paraphyletic, pelycosaurs were replaced by the more mammal-like cynodonts; see, e.g. Rubidge and Sidor (2001) or Abadala and Ribeiro (2010) for reviews. One hypothesis would be that prostriate ticks adopted cynodonts as hosts during the Triassic, and essentially remained with them through their subsequent development into mammals in the Late Triassic or Early Jurassic. However, we should note that in several studies (e.g. Dobson and Barker, 1999; Fukunaga *et al.* 2000) species such as the Australian paralysis tick *Ixodes holocyclus* Neumann 1899 resolved in a basal position within *Ixodes*. This is a multi-host parasite found both on mammals and birds, and it is unclear to what extent this reflects the original host preferences, or a general adaptability in host choice within the genus. For example, other *Ixodes* ticks use birds when immature and switch to mammals as adults (Barker *et al.* 2014) and several *Ixodes* ticks prefer birds in general.

Ixodidae: Metastriata

Metastriata includes 11 extant and two extinct genera. Following authors such as Hoogstraal and Aeschlimann (1982) and Barker and Murrell (2002, 2004), the sequence of genera, from basal to derived, is probably along the lines of: *Bothriocroton* (the subfamily Bothriocrotoninae), *Amblyomma* (Amblyomminae), *Haemaphysalis* (Haemaphysalinae), followed by *Cosmiomma* Schulze (1919); *Dermacentor* CL Koch (1844); *Rhipicentor* Nuttall and Warburton (1908); *Nosomma* Schulze (1919); *Hyalomma* CL Koch (1844); *Anomalohimalaya*, *Rhipicephalus* and *Margaropus* Karsch (1879) (all Rhipicephalinae). For an alternative phylogeny, see Burger *et al.* (2013) who recognized two major metastriate lineages: (1) *Amblyomma* s.s. + rhipicephalines and (2) *Haemaphysalis* + *Bothriocroton* + *A. sphenodonti*. Host preferences for individual genera are given in Table 1. The important message here is that *Bothriocroton* and *Amblyomma* – representing the more basal subfamilies *sensu* Barker and Murrell (2002) – use a mixture of reptilian and mammalian hosts. For example, species previously assigned to the genus *Aponomma* invariably parasitize reptiles, but following the revision of Klompen *et al.* (2002), they were transferred to *Bothriocroton* and *Amblyomma*, respectively. As noted above, *Haemaphysalis* is usually found on mammals, but also sometimes on birds. The rhipicephalines are strongly, or exclusively (*Cosmiomma*, *Dermacentor*, *Rhipicentor*, *Nosomma* and *Anomalohimalaya*), associated with mammals throughout their life cycle.

The oldest fossil metastriate ticks include the two (99 Ma) Burmese amber records of *Amblyomma* (Chitimia-Dobler *et al.* 2017) and *Haemaphysalis* (this study). The extinct genera *Cornupalpatum* and *Compluriscutula* from Burmese amber are probably metastriates too and close to *Amblyomma*. There is evidence that *Cornupalpatum* may have fed on feathered dinosaurs and/or birds, with Peñalver *et al.* (2017) figuring a tick belonging to this extinct genus entangled in a pennaceous feather. In detail, the feather was considered as belonging to stage V of Prum's (1999) model of feather evolution and implies a host belonging to the Pennaraptora *sensu* Foth *et al.* (2014); a clade encompassing several derived genera of feathered dinosaurs as well as crown-group birds. The only other metastriate fossils are *Amblyomma* records from Miocene (ca. 16 Ma) Dominican Republic amber and a subfossil record of *Dermacentor*. As noted by Chitimia-Dobler *et al.* (2017), a published record of *Hyalomma* in Eocene Baltic amber (de la Fuente, 2003) is a misidentification. Metastriata is estimated to have split off from Prostriata in the Early Triassic (ca. 249 ± 23 Ma) with a further putative divergence (Mans *et al.* 2012) into the modern genera in the Early Cretaceous at ca. 124 ± 17 Ma. In other words, the Burmese amber fossils come from a time not long after the suggested radiation into living genera. The fossils also now encompass two of the four subfamily groups recognized by Barker and Murrell (2002, 2004): namely Amblyomminae and Haemaphysalinae.

In the Mans *et al.* (2012) scenario, there is a ca. 125 Ma hiatus from the Triassic through to the Early Cretaceous during which metastriate ticks should have been present, but had not yet diversified into their modern genera. Several reptilian and mammal-like reptile groups, as well as eventually mammals and birds, would have been available as potential hosts during this time. What may be significant is that the basal metastriate ticks (*Bothriocroton* and *Amblyomma*) retain a stronger association to reptiles. While prostriates (i.e. *Ixodes*) may have adopted mammal-like reptiles as hosts back in the Triassic (see above), the first members of the metastriate lineage may have taken up other reptiles such as squamates or archosaurs as their original hosts instead.

A subsequent shift in host preferences may have taken place in the more derived haemaphysaline and rhipicephaline metastriate genera, for which *H.* (*A.*) *cretacea* sp. nov. is the oldest known putative example. In the two most derived tick subfamilies, mammals appear to play a more significant role. Unfortunately, most of the rhipicephaline genera lack a fossil record (Table 1). Molecular data from Sands *et al.* (2017) suggested that the modern *Hyalomma* species diverged towards the end of the Eocene at around 34.8–39.8 Ma – although we should caution that they were still using the erroneous Baltic amber record of this genus for calibration – with Fig. 2 of the same paper suggesting a Palaeocene *Nosomma*/*Hyalomma* split at ca. 60 ± 17 Ma and a deeper (Cretaceous) split from *Amblyomma* at 78 ± 20 Ma. We might predict that rhipicephaline evolution in general is linked to the Late Cretaceous origins of modern mammal lineages (e.g. dos Reis *et al.* 2014) and their subsequent diversification after the K–T extinction event.

Indeed some (monotypic) genera here have quite specific host preferences: *Cosmiomma* is found as adults on hippos and rhinos (Aspanaskevich *et al.* 2013) and *Nosomma* occurs on buffalo as adults and rodents when immature (Kahn *et al.* 1982). These taxa may be constrained by the appearance of their hosts. Fossil rhinos are known since the Eocene (38–42 Ma) (Cerdeño, 1998), while hippos and bovids are known from the Miocene (16 and 18 Ma, respectively), but are predicted to have originated earlier depending on their sister group (Theodor, 2004). For example, molecular origination dates of ca. 50 Ma for perissodactyls (including rhinos) and 23 Ma for bovids have been proposed (Norman and Ashley, 2000; Matthee and Davis, 2001). A final thought is that Burmese, and other Cretaceous, amber deposits may yield further ticks belonging to other (rhipicephaline?) genera, which may help to confirm and refine the hypotheses presented above.

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