



A new subfamily, *Bothriocrotoninae* n. subfam., for the genus *Bothriocroton* Keirans, King & Sharrad, 1994 status amend. (Ixodida: Ixodidae), and the synonymy of *Aponomma* Neumann, 1899 with *Amblyomma* Koch, 1844

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Abstract

Evidence suggesting polyphyly of the traditionally recognised tick genus *Aponomma* Neumann, 1899 is summarized. Continued recognition of this genus in its current concept leaves a polyphyletic genus *Aponomma* and a paraphyletic genus *Amblyomma* Koch, 1844. To improve the correlation between our understanding of phylogenetic relationships in metastriate ticks and their classification, a few changes in classification are proposed. The members of the 'indigenous Australian *Aponomma*' group (sensu Kaufman, 1972), *A. auruginans* Schulze, 1936, *A. concolor* Neumann, 1899, *A. glebopalma* Keirans, King & Sharrad, 1994, *A. hydrosauri* (Denny, 1843) and *A. undatum* (Fabricius, 1775), are transferred to *Bothriocroton* Keirans, King & Sharrad, 1994, which is raised to full generic rank. The remaining members of *Aponomma* are transferred to *Amblyomma*. Uncertainty remains on relationships of *Bothriocroton* to other metastriate lineages and on the systematic position of the two species formerly included in the 'primitive *Aponomma*' group, *A. elaphense* Price, 1959 and *A. sphenodonti* Dumbleton, 1943.

Introduction

Generic classification in the hard ticks, family Ixodidae, has been remarkably stable over the last 50 years. Although a few new genera have been proposed (*Anomalohimalaya* Hoogstraal, Kaiser & Mitchell, 1970, *Dermacentonomma* Dias 1978); only *Anomalohimalaya* is generally recognised. Apart from some discussion on the validity of *Anocentor* Schulze, 1937, as part of, or separate from, *Dermacentor* Koch, 1844 (e.g. Borges et al., 1998; Crosbie et al., 1998), ixodid classification has not really been challenged. However, a recent upsurge in interest in tick systematics, fuelled in part by the use of more rigid methodology and the addition of molecular data sets, is prompting a re-assessment of ixodid generic classification. One of the most challenging problems involves *Aponomma* Neumann, 1899. Neumann (1899) created this genus for ticks of reptiles with the following characteristics: 'Pas

d'yeux. Base du rostre ordinairement pentagonal, à bords latéraux très courts du côté dorsal. Palpes longs' (Neumann, 1899, p. 180). Of these characteristics the shape of the basis capituli and the long palps are shared with, respectively, most and all *Amblyomma*, leaving the lack of eyes as the defining character for *Aponomma*. Although some authors (Camicas & Morel, 1977; Nuttall & Warburton, 1911) suggested that its constituent species should be included in *Amblyomma* Koch, 1844, most recent studies have recognized *Aponomma* at the generic level (Dias, 1993; Filippova, 1997; Keirans, 1992; Keirans & Robbins, 1999). The main motivation for recognition of *Aponomma* as a genus separate from *Amblyomma* appears to be common usage, rather than phylogenetic relationships (Camicas & Morel, 1977). A close relationship between *Aponomma* and *Amblyomma* is acknowledged by the grouping of the two genera in the subfamily Amblyomminae (see Hoogstraal &

Aeschlimann, 1982) or subtribe Amblyommini (see Filippova, 1997).

The root cause of the systematic problems associated with *Aponomma* is the question of monophyly of the genus. Although widely recognised, the genus is still poorly defined. In the most comprehensive revision of *Aponomma*, Kaufman (1972) proposed the following definition of the genus: without eyes (1); scutum of the male usually broader than long (2), suboval or subquadrate (3), ornate or inornate (4), lateral grooves present or absent (5); scutum of the female cordiform, usually broader than long (6), with or without conspicuous indentations of posterolateral margin (7), ornate or inornate (8); trochanters with or without subterminal spurs (9); basis capituli (=gnathosomal base) pentagonal or subtriangular (10); and palps elongate, more or less subcylindrical (11). Of these characters five (4, 5, 7, 8, 9) are uninformative because they include all possible states, and two (10, 11) are plesiomorphic (=‘primitive’) for the Metastriata. What remains are scutal shape characters (2, 3, 6), all commonly occurring within *Amblyomma*, and the absence of eyes (1). In short, the genus remains defined mainly by the lack of eyes.

The value of the absence or presence of eyes as an identification marker is obvious, but this character may have less significance as an indicator of phylogenetic relationships. When the character is defined more precisely, it refers to the presence or absence of lenses. The innervation for eyes appears to be present in all ixodids examined, including the eye-less *Ixodes holocyclus* Neumann, 1899, *Haemaphysalis longicornis* Neumann, 1901 and *Aponomma auruginans* Schulze, 1936 (see Binnington, 1972). Moreover, it is now clear that the lack of eyes is plesiomorphic for the Ixodida (see Klompen & Oliver, 1993; Lehtinen, 1991). Within Ixodidae, this characteristic is shared with all instars of *Haemaphysalis* Koch, 1844 and *Ixodes* Latreille, 1795, and with the postlarval instars of *Anomalohimalaya*.

A possible problem with the monophyly of *Aponomma* was anticipated in Kaufman’s (1972) revision. He proposed that *Aponomma* consisted of three well-defined groups: ‘typical’ (16 species), ‘indigenous Australian’ (4 species) and ‘primitive’ (2-3 species). He also suggested that two of these groups, the ‘indigenous Australian’ species and the ‘primitive’ species might represent new genera. Kaufman (1972) did not use modern cladistic methods, but a phylogenetic analysis of morphological and developmental features of the Metastriata (Klompen et al., 1997)

supported the idea that the ‘primitive *Aponomma*’ (represented by *A. elaphense* Price, 1959) do not group with the ‘typical *Aponomma*’ or most *Amblyomma*, but rather with an odd species of *Amblyomma*, *A. quadricavum* (Schulze, 1941). Confusion about the status of *A. quadricavum* is illustrated by the fact that this species was described as an *Aponomma*, and has only recently been transferred to *Amblyomma* based on the presence of poorly developed eyes (Keirans & Klompen, 1996). Klompen et al. (1997) failed to provide support for monophyly of the remaining groupings of *Aponomma*, the indigenous Australian and typical forms. However, the level of support for the various hypotheses of relationships for these lineages was very low.

Additional data sets, specifically DNA sequence data, have resolved relationships sufficiently to merit a further review of the systematic status of *Aponomma*. Based on the evidence summarised below, it is clear that the genus as currently defined is polyphyletic. We propose that the ‘indigenous Australian *Aponomma*’ are recognised as a distinct genus and the synonymy of the ‘typical’ and ‘primitive *Aponomma*’ with *Amblyomma*.

Evidence

Molecular evidence

The strongest evidence for polyphyly of *Aponomma* is derived from sequence data. Although none of these studies included members of the ‘primitive *Aponomma*’ group, they did consider the status of the ‘indigenous Australian’ versus the ‘typical *Aponomma*’. Dobson & Barker (1999) considered two species of ‘indigenous Australian *Aponomma*’, *A. concolor* Neumann, 1899 and *A. undatum* (Fabricius, 1775), two species of ‘typical *Aponomma*’, *A. fimbriatum* (Koch, 1844) and *A. latum* (Koch, 1844), and five species of *Amblyomma*, in an analysis of 18S nuclear rDNA sequences from 33 Ixodida. Both the genus *Aponomma* and the subfamily Amblyomminae appeared polyphyletic as the two ‘indigenous Australian *Aponomma*’ formed a monophyletic lineage (100% bootstrap support) that formed the sister-group to the remaining Metastriata. The ‘typical *Aponomma*’ spp. and *Amblyomma* spp. formed a monophyletic lineage (100% bootstrap support) that was quite distinct from a lineage including the ‘indigenous Australian *Aponomma*’. Dobson & Barker (1999) suggested that

a new genus and a new subfamily should be created for the 'indigenous Australian *Aponomma*' once the remaining three species of 'indigenous Australian *Aponomma*' had been studied.

Klompen et al. (2000) used a total evidence approach to infer the phylogeny of the Ixodidae from a combination of morphological, developmental, and molecular (18S and 28S nuclear, and 16S mitochondrial, rRNA nucleotide sequences) characters. In addition to the taxa considered by Dobson & Barker (1999), this study considered 18S data for two more 'indigenous Australian *Aponomma*': *A. hydrosauri* (Denny, 1843) and the recently described *A. glebopalma* Keirans, King & Sharrad, 1994. Unfortunately, coverage for the other genes was less extensive, with only one species, *A. glebopalma*, sequenced for 28S and two, *A. glebopalma* and *A. hydrosauri*, for 16S. Even so, results for these other genes were at least consistent with the 18S data, in that the representatives of 'indigenous Australian' and 'typical *Aponomma*' never clustered together. The 'indigenous Australian *Aponomma*' formed a monophyletic lineage with 100% bootstrap support in the total evidence trees (Klompen et al., 2000, Figure 4). This led these authors to conclude that their results strengthened previous conclusions about the distinctness of the indigenous Australian species of *Aponomma* (see Dobson & Barker, 1999), and the polyphyly of *Aponomma* in general (Dobson & Barker, 1999; Klompen et al., 1997). Both of these studies found the 'typical *Aponomma*' nested within *Amblyomma*, suggesting paraphyly of the genus *Amblyomma* unless the 'typical *Aponomma*' were included.

Despite these well supported results, these analyses do not resolve the phylogenetic position of all of the *Aponomma* spp. Although 18S data indicate that the 'indigenous Australian *Aponomma*' are the sister-group to the remaining Metastriata (100% bootstrap support; Dobson & Barker, 1999), this arrangement was not supported in the total-evidence analysis (Klompen et al., 2000). So we consider the relationships of the 'indigenous Australian *Aponomma*' to the other Metastriata to be unresolved. Such a conservative approach is also desirable because neither of these studies had a representative of the so-called 'primitive *Aponomma*': *A. elaphense* and *A. sphenodonti* Dumbleton, 1943. It is quite possible that inclusion of the 'primitive *Aponomma*' may have considerable influence on branching patterns among early-diverging Metastriata.

Absence of data on the fifth and last member of the 'indigenous Australian *Aponomma*', *A. auruginans* Schulze, 1936, is no longer a problem, as one of us (SJD), recently obtained 18S sequence data for that species (GenBank accession number AF479768). Analyses including this taxon confirmed the monophyly of the 'indigenous Australian *Aponomma*' and the grouping of 'typical *Aponomma*' within *Amblyomma* s.l. (Figure 1). Extraction, amplification, and sequencing protocols for *A. auruginans* followed Dobson & Barker (1999). The analyses included all ixodid species considered by either Dobson & Barker (1999) or Klompen et al. (2000), plus *A. auruginans*. Outgroups were as in Klompen et al. (2000). All analyses (gaps treated as missing or 5th state, including or excluding regions that presented minor alignment problems) generated essentially the same results, which are consistent with previous analyses. Support for monophyly of all 'indigenous Australian *Aponomma*' is always strong (100% jackknife support; Figure 1). Similarly, enforcing monophyly of all *Aponomma* included in this analysis (5 'indigenous Australian' and 2 'typical') always required numerous extra steps (e.g. 25 extra steps in the analysis shown in Figure 1). On the other hand, support for relationships within 'indigenous Australian *Aponomma*' or among major lineages of the Metastriata (Figure 1) is insufficient to allow firm conclusions. These results are also similar to those in the previous analyses (Dobson & Barker, 1999; Klompen et al., 1997).

Morphology

While the molecular evidence for separate status of the indigenous Australian taxa is strong, evidence from morphological and developmental data has been less convincing. Kaufman (1972) listed the following combination of characters to describe his 'indigenous Australian *Aponomma*' [this did not include *A. glebopalma*, which was not described until later (Keirans et al., 1994)]: basis capituli subpentagonal in shape (shared with 'typical *Aponomma*', triangular in 'primitive *Aponomma*') (1); hypostomal dentition 3/3 or 2/2 (3/3 or more in 'typical *Aponomma*', 2/2 in *A. transversale* (Lucas, 1845), 2/2 in *A. elaphense*, 3/3, but internal row almost gone in *A. sphenodonti*) (2); single subterminal spur on the trochanter (absent in all other *Aponomma* and *A. glebopalma*) (3); lateral grooves on the scutum of the male partial or complete (absent in 'typical *Aponomma*', *A. elaphense*, and *A. glebopalma*, but present in

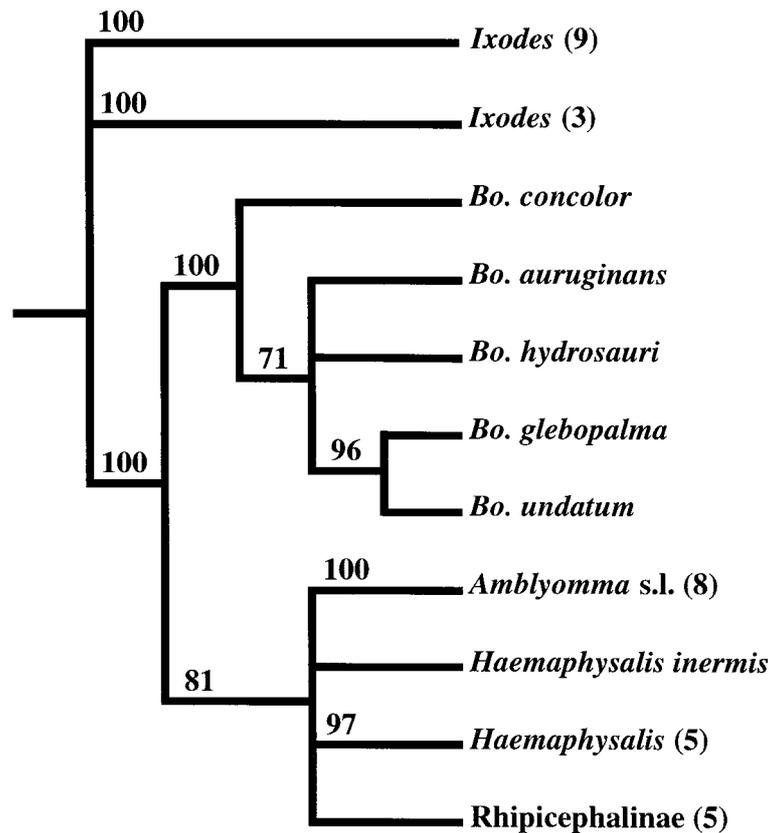


Figure 1. Strict consensus tree of relationships between *Bothriocroton* species (= 'indigenous Australian *Aponomma*') and other Ixodidae, collapsed to well supported branches. Analysis based on 18S rRNA sequence data. Results shown for an analysis including all characters and with gaps treated as missing characters (36 equally most parsimonious trees; length 1124, ri: 0.76). Numbers above the branches reflect jackknife support (100 repetitions, each with 10 random taxon additions); numbers after taxon names indicated the number of species of that lineage included in the analysis. Abbreviation: Bo, *Bothriocroton*.

A. sphenodonti) (4); iridescent scutal ornamentation absent (also absent in some 'typical *Aponomma*' and in 'primitive *Aponomma*', some white ornamentation is present in *A. glebopalma* and *A. undatum*) (5); scutum of female with conspicuous posterolateral indentations formed by confluence of larger punctations (6). None of these characters are unique apomorphies for 'indigenous Australian *Aponomma*'. The shape of the basis capituli (1) is a plesiomorphic character for early-diverging Metastriata (Klompen et al., 1997), and is thus of very little value at this level, but for setting the 'primitive *Aponomma*' apart. Characters 3 and 4 would seem to be reliable phylogenetic markers, but they are not shared by *A. glebopalma*. However, by refining the character definition, hypostomal dentition (2) may provide a derived character for 'indigenous Australian *Aponomma*'. In the adults, these taxa are characterised by the reduction in size of the teeth of the internal row of denticles, relative to the

size of the outer rows. The 3/3 then 2/2 dentition of *A. auruginans* and the 2/2 dentition of *A. glebopalma* might be the culmination of this trend, resulting in the absence of the entire inner row of denticles. This character state, reduction of the size of the teeth of the internal row of denticles on the hypostome relative to the outer rows, is also found in 'primitive *Aponomma*', especially *A. sphenodonti*.

Perhaps the most promising diagnostic character for the 'indigenous Australian *Aponomma*' is found in the larvae. Larvae of *A. glebopalma*, *A. hydrosauri*, *A. auruginans* and *A. concolor* (larvae of *A. undatum* were not available for study) have a multiplication of large wax glands (3) laterally near setae *s6* (Md3 of Clifford et al. (1961)) and anterior to the first festoons (Klompen et al., 1996). Other metastriate larvae have at most one large wax gland in that position, while the Prostriata lack large wax glands altogether. Secondly, unlike the condition in *Amblyomma*, 'typical

Aponomma' and nearly all *Haemaphysalis*, 'indigenous Australian *Aponomma*' lack large wax glands on festoons 5 (segment XIII) (Klompen et al., 1996). This condition is shared with 'primitive *Aponomma*'. It is unclear whether the absence or presence of large wax glands in that position is derived.

Cytogenetics and host-associations

The 'indigenous Australian *Aponomma*' differ from the 'typical *Aponomma*' in a number of other characteristics. While sharing the XX XO sex determination system of most of the Metastrata, *A. concolor*, *A. hydrosauri* and *A. undatum* have unusually low chromosome numbers, relative to most Metastrata. Most male Metastrata, including a representative of the 'typical *Aponomma*', *A. fimbriatum* and most *Amblyomma*, have a diploid number of 21, but *A. hydrosauri* males have $2N=17$, while male *A. concolor*, *A. undatum*, the Australian endemic *Amblyomma triguttatum* Koch, 1844, and a primitive *Haemaphysalis*, *H. (Alloceraea) kitaokai* Hoogstraal, 1969, share $2N=19$ (Oliver, 1977). Data for *A. auruginans* and *A. glebopalma* are currently unavailable.

Ecologically there may also be some distinctions. 'Typical *Aponomma*' are invariably associated with varanid lizards and snakes, but the 'indigenous Australian *Aponomma*' show a much wider host range. While *A. glebopalma* and *A. undatum* are most commonly associated with varanids [there is one report of infestation by *A. undatum* of an echidna (Roberts, 1970)], *A. auruginans* is an associate of wombats (Marsupialia), *A. concolor* is associated with echidnas (Monotremata) and *A. hydrosauri* can be associated with either echidnas (North East Australia) or lizards (Southern Australia) (Roberts, 1970).

Conclusion

There is considerable evidence suggesting that *Aponomma* in its traditional concept is polyphyletic. While the 'typical *Aponomma*' generally cluster with or within *Amblyomma*, the 'indigenous Australian *Aponomma*' form a very distinct lineage. This distinct status is not based on sequence data only, but is backed up by morphological characters, ecology and, possibly, cytogenetic data. In order to improve the match between our understanding of systematic relationships and classification we propose to reclassify the 'typical *Aponomma*' as *Amblyomma* and to recognise the 'indigenous Australian *Aponomma*' as a distinct genus which is described below.

Monophyly of the new genus, *Amblyomma* (*sensu lato*) (that is including 'typical *Aponomma*'), *Haemaphysalis* and the Rhipicephalinae [including the Hyalomminae, as suggested by Klompen et al. (1997) and Murrell et al. (2001)] is well supported (although for *Amblyomma* this is based on sequence data only), but any hypothesis of relationships among these four is not. In order to minimise the number of changes to the classification, we therefore propose to place the new genus in its own subfamily, while retaining the Haemaphysalinae, Amblyomminae (without the 'indigenous Australian *Aponomma*') and Rhipicephalinae.

The status of the 'primitive *Aponomma*' remains unclear. *A. sphenodonti* shares several characters with the 'indigenous Australian *Aponomma*' (e.g. the reduction of the internal row of hypostomal denticles and the presence of lateral grooves on the scutum of the male), but is set apart from that lineage by the triangular shape of the basis capituli (Dumbleton, 1943; Kaufman, 1972). A re-examination of the larvae of *A. sphenodonti* might be instructive in this context, focusing on their currently undocumented distribution pattern of large wax glands. Both this species and *A. elaphense* are tentatively placed with the 'typical *Aponomma*' in *Amblyomma*, until further evidence relating them to other ixodid lineages is generated.

Taxonomy

Bothriocrotoninae n. subfam.

Diagnosis. With characteristics of its sole constituent genus, *Bothriocroton* Keirans, King & Sharrad, 1994.

***Bothriocroton* Keirans, King & Sharrad, 1994 status amend.**

Syn. *Aponomma* (*Bothriocroton*) Keirans, King & Sharrad, 1994

Diagnosis

Hypostomal dentition in the adults 2/2 or 3/3 with internal row much smaller than other rows; larvae with three large wax glands lateral near setae *s6*.

Other stages:

Postlarval instars. Scutum broader than long. In female and nymphs with conspicuous posterolateral indentations formed by confluence of larger punctations. Scutum of the males with partial or complete lateral grooves, formed by a confluence of larger punctations

(absent in *B. glebopalma*). Iridescent ornamentation on the scutum absent, but *B. glebopalma* and *B. undatum* have white ornamentation. Eyes absent. Basis capituli subpentagonal in shape. Palps elongate. Coxae with two spurs in all instars. Trochanters with a single subterminal ventral spur (absent in *B. glebopalma*).

Larvae. Idiosomal setation pattern generally as in other *Metastrata*. Setae *Zv4* and *Sv1* absent in, respectively, *B. glebopalma* + *B. hydrosauri* and *B. glebopalma*. Large wax glands on festoons 5 (segment XIII) absent (present in *Amblyomma*, ‘typical *Aponomma*’, and nearly all *Haemaphysalis* (Klompen et al., 1996)). Leg and palpal chaetotaxy as in *Amblyomma* s.l.

Type-species: *Bothriocroton glebopalma* Keirans, King & Sharrad, 1994 (by original designation).

Other included species:

B. auruginans (Schulze, 1936) n. comb (from *Aponomma*)

B. concolor (Neumann, 1899) n. comb.(from *Aponomma*)

B. hydrosauri (Denny, 1843) n. comb. (syn. *Aponomma trachysauri* Neumann, 1899)

B. undatum (Fabricius, 1775) n. comb. (syn. *Aponomma decorosum* (Koch, 1867))

Remarks

Keirans, King & Sharrad (1994) erected the subgenus *Bothriocroton* for the species *Aponomma (Bothriocroton) glebopalma* Keirans, King & Sharrad, 1994. As the oldest (and only) available genus group name, including any of the ‘indigenous Australian *Aponomma*’ the name *Bothriocroton* therefore has priority (ICZN, 1999). However, the diagnosis of the genus has had to be expanded (see above) to include all ‘indigenous Australian *Aponomma*’. The name *Bothriocroton* is derived from the Greek words for pitted (bothrio) and tick (croton) (Keirans et al., 1994).

Amblyomma Koch, 1844

Syn. *Aponomma* Neumann, 1899, new synonymy

Remarks

Two of the three groups of Kaufman (1972), ‘typical’ and ‘primitive *Aponomma*’, are included in *Amblyomma*. While support for the inclusion of ‘typical *Aponomma*’ in *Amblyomma* is strong, there is less support for including the ‘primitive *Aponomma*’, so the addition of the ‘primitive *Aponomma*’ to *Amblyomma* is provisional, pending further investigation.

Discussion

The proposed changes in classification of the members of the former genus *Aponomma* raise some very significant classification problems. The main problem in this context is the status of *Amblyomma* s.l. (*sensu lato*), that is *Amblyomma* s.s. (*sensu stricto*; the traditional genus) plus the ‘typical’ and ‘primitive’ groups of *Aponomma* as defined by Kaufman (1972). There are no obvious derived morphological characters for *Amblyomma* s.l. The presence of a marginal groove in the male might be a derived character state, but is shared with some members of *Bothriocroton*. We acknowledge this problem, but point out that there are no derived morphological characters for *Amblyomma* s.s. Commonly listed characters are: (1) presence of eyes, (2) elongated palps, and (3) presence of ornamentation. Characters (1) and (3) are derived at the level of *Amblyomminae* + *Rhipicephalinae*, and (2) is plesiomorphic for the *Metastrata*. Moreover, (3) is variable within *Amblyomma* s.s. Thus neither character is diagnostic for *Amblyomma*. It is clear that focused studies on the status of, and relationships within, *Amblyomma* s.l. are needed. One question that needs particular attention is the status of the ‘primitive *Aponomma*’. Morphological data (Klompen et al., 1997) hint at a phylogenetic position separate from *Amblyomma* s.l. and *Bothriocroton*, but support for this idea is relatively weak. Resolution of this problem may have repercussions far beyond the classification of *Amblyomma*. Confirmation of the morphology-based hypothesis that ‘primitive *Aponomma*’ is the sister-group to the *Rhipicephalinae* (see Klompen et al., 1997) would have considerable implications for our understanding of the evolution of that major lineage of ticks.

The recognition of *Bothriocroton* at full generic level is the first step towards resolving the considerable systematic problems surrounding the *amblyommine* lineage. While acknowledging the problems associated with changes of classification, we believe that a better match between phylogenetic position and classification advances overall understanding of a taxon. In this particular case, the recognition of *Bothriocroton* resolves a number of unexplained observations on biogeography, host-associations and cytogenetics of the former *Aponomma*.

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