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The first cryptic genus of Ixodida, *Cryptocroton* n. gen. for *Amblyomma papuanum* Hirst, 1914: a tick of North Queensland, Australia, and Papua New Guinea

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Abstract

We describe a new genus *Cryptocroton* **n. gen.** for *Amblyomma papuanum* Hirst, 1914, a tick of North Queensland, Australia, and Papua New Guinea.

Key words: new genus, Ixodida, Papua New Guinea, Australia, echidna, cassowary

Introduction

The possible existence of cryptic species is often spoken about in the tick literature (e.g. Burger *et al*. 2014; Mohamed *et al*. 2022; Kelava *et al*. 2023) but so far, there is only one case of cryptic species of ticks being described: the six species of the *Amblyomma cajennense* (Fabricius, 1787) species complex (Beati *et al*. 2013; Nava *et al*. 2014). This

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is testament to the diagnostic power of the morphology of ticks: there are, however, many cases of cryptic species in other groups of animals (e.g. Fiser *et al*. 2018). The discovery of a cryptic species of ticks is remarkable: even more remarkable perhaps is the discovery of a cryptic genus of ticks. Here we describe *Cryptocroton* **n. gen.**, a genus of *Amblyomma*-like ticks with eyes, which was previously confused with ticks of the genus *Amblyomma* Koch, 1844. We discovered *Cryptocroton* **n. gen.** since it clustered with the species of *Haemaphysalis* Koch, 1844 and *Bothriocroton* Keirans, King & Sharrad, 1994 in our trees from mitochondrial (mt) genomes and nuclear rRNA.

Materials and Methods

Microscopy

Ticks were studied with a stereoscopic microscope (Olympus SZX16, Olympus Corporation, Tokyo, Japan).

Sequencing and assembly of mitochondrial genomes

Three slightly different protocols were used. First, DNA was extracted from individual specimens of *Am*. (*Cernyomma*) *nitidum* Hirst & Hirst, 1910 and *Am*. (*C*.) *postoculatum* Neumann, 1899 with the blackPREP Tick DNA/RNA kit (Analytik Jena, Germany). Then the protocol of Barker *et al*. (2022) was followed. Overlapping fragments (12–13 kb and 1.5–2.5 kb) by long-range and short-range PCR were amplified to span entire mt genomes. PrimeSTAR® GXL DNA Polymerase (Takara-Bio, Shiga, Japan) and Tks Gflex™ DNA Polymerase (Takara-Bio) were used to amplify the long-range and short-range fragments respectively. Illumina sequence libraries were constructed using the Nextera DNA Library Prep Kit (Illumina, Hayward, CA) and the Illumina MiSeq platform with the MiSeq reagent kit v3. CLC Genomics Workbench v12.0.3 (Qiagen, Hilden, Germany) was used to assemble Illumina sequence reads.

Second, individual specimens of *Am*. (*C*.) *albolimbatum* Neumann, 1907 and *C. papuanum* (Hirst, 1914) (B5524, B6707) were cut in half then digested with Proteinase K for 24 hrs. DNA was extracted with the QIAGEN DNeasy Blood and Tissue kit. Then the protocol of Kelava *et al*. (2021) was followed. Nanodrop and Qubit instruments were used to ensure the minimum threshold of 200 ng of DNA was recovered. DNA was sent to Novogene Singapore for library construction and sequencing with the Illumina Novaseq 6000 platform. Assembly of tick mt genomes from sequencing reads was with Geneious Prime build 2022–11–28 (Kearse *et al*. 2012).

Third, individual specimens of *Am*. (*C*.) cf. *calabyi* Roberts, 1963 and *C. papuanum* (Hirst, 1914) (B7103) were homogenised or bisected, respectively, and DNA extracted using the QIAGEN DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany), with an initial digestion in Proteinase K at 56°C for 16 hours. DNA concentration was assessed using the Qubit dsDNA Broad Range kit, and paired-end sequencing libraries produced from genomic DNA with the Illumina DNA Prep kit (Illumina, Hayward, CA), and sequenced with the Illumina Novaseq 6000 platform at the Genome Discovery Unit, ACRF Biomolecular Resource Facility, The John Curtin School of Medical Research, Australian National University. Paired-end reads were quality filtered and trimmed with *fastp* (Chen *et al*. 2018) and *de novo* assembled with *metaSPAdes* (Nurk *et al*. 2017). The resulting contigs were then mapped to the complete mitochondrial genomes of closely related taxa with *minimap2* (Li, 2018) using the *map-ont* present as an efficient way of extracting mitochondrial contigs from the assembly; in all cases a single complete mitochondrial genome contig was identified.

Annotation of mitochondrial genomes and alignment of mitochondrial genome sequences

We annotated mitochondrial genomes with Geneious Prime build 2022–11–28 (Kearse *et al*. 2012). First, the location of protein-coding, tRNA and rRNA genes was predicted with the MITOS Web Server (Bernt *et al*. 2013). Protein-coding genes and rRNA genes were then verified by BLAST searches of GenBank (Chen *et al*. 2015). We used tRNAscan-SE Search Server v1.21 (Lowe & Chan 2016) for a final check of the tRNAs. Entire mt genome alignments were made with the MAFFT v7.490 program using the FFT-NS-I x1000 algorithm; and trimAl v1.2; and Capella-Gutiérrez *et al*. (2009) was used to remove gaps and highly variable regions in the alignments.

Assembly and alignment of nuclear rRNA sequences

Nuclear 18S and 28S ribosomal RNA genes were assembled with Geneious Prime build 2022-11-28 (Kearse *et al*. 2012). Sequence read libraries (see "Sequencing and assembly of mitochondrial genomes" section above) were mapped to previously published tick 18S and 28S rRNA sequences with the inbuilt Geneious map-to-reference assembly program. Alignments of 18S and 28S rRNA genes were made with the MAFFT v7.490 program using the FFT-NS-I x1000 algorithm, trimAl v1.2 (Capella-Gutiérrez *et al*. 2009) was used to remove gaps and highly variable regions in the alignments.

Phylogenetic methods

Phylogenetic trees were inferred from the 11 protein-coding genes of the mitochondrial genomes of 87 species of ticks (Table 1). RAXML-HPC2 v 8.2.12 (Stamatakis 2014) was used to infer Maximum Likelihood (ML) phylogenies whereas MrBayes v3.2.6 (Ronquist *et al*. 2012) was used to infer Bayesian Inference (BI) trees. Partitionfinder v2.1.1 (Lanfear *et al*. 2016) was used to select the best substitution model for each phylogenetic run. For the ML phylogenies, ultrafast bootstrap (Hoang *et al*. 2018) of 1000 replicates was executed. For the BI phylogenies, three heated and one cold chain for 1 million generations were run with sampling every 1000 MCMC steps (first 25% discarded as burn-in). Effective sample size and run convergence were observed in Tracer v1.5 (Rambaut 2009). FigTree v1.4.4 was used to display the phylogenetic trees and their bootstrap and posterior probability support (Rambaut 2012). Species of *Ixodes* Latreille, 1795 were set as the outgroup.

TABLE 1. National Centre for Biotechnology Information (NCBI) accession numbers and details of entire mitochondrial (mt) genome, 18S rRNA and 28S rRNA sequences used to infer our phylogenetic trees. The sequences in **bold** were generated in the present study. The sequences that are **not** labelled 18S & 28S rRNA were mt genome sequences. All of the *C. papanum* material listed in Table 1 was examined.

Genus (subgenus) Species	Location	MT/18S/28S Accession/Voucher	#bp
Allocerαea colasbelcouri	China, Qujing	OM368290	14,885
Al. inermis	Romania	NC_020335, B2345	14,846
Al. inermis	Romania	OL741739	14,848
Al. kitaokai	Japan, Nara	MT371803, B5237	15,033
Al. kitaokai	China, Wenzhou	OM368280	14,936
Amblyomma (*Adenopleura*) *javanense*	China	MK229166	14,780
Am. (*Amblyomma*) *americanum*	USA, Georgia	NC_027609	14,709
Am. (*Amblyomma*) *cajennense*	Brazil, Balneário do Sol	NC_020333	14,780
Am. (*Amblyomma*) *sculptum*	Brazil	NC_032369	14,780
Am. (*Anastosiella*) *maculatum*	USA	MW719251	14,803
Am. (*Anastosiella*) *ovale*	Columbia	MT554103	14,756
Am. (*Aponomma*) *fimbriatum*	Australia, Lizard Island, Qld	NC_017759	14,705
Am. (*Aponomma*) *gervaisi*	Sir Lanka	B6928, OL741734	14,709
Am. (*Aponomma*) *latum*	Ghana	OL741735	14,658
Am*. (*Cernyomma*) *albolimbatum	**Australia, Middleback Range, SA**	**B5607, OR350524**	**15,049**
Am*. (*Cernyomma*) cf. *calabyi	**Australia, Alice Springs, NT**	**B7021.P26F, OR350525**	**14,818**
***Am*. (*Cernyomma*) cf. *calabyi* 18S & 28S rRNA**	**Australia, Alice Springs, NT**	**B7021.P26F, OR936201, OR948507**	**1815, 4045**
Am. (*Cernyomma*) *geoemydae*	Japan, Okinawa	MT371797, B5231	14,791
Am*. (*Cernyomma*) *nitidum	**Japan, Okinawa**	**B7194.AN26, OR350526**	**14,884**

......*Continued on the next page*

TABLE 1. (Continued)

Genus (subgenus) Species	Location	MT/18S/28S Accession/Voucher	#bp
Am. (Cernyomma) postoculatum	**Australia, Halls Creek, WA**	**B5475, OR350527**	**14,749**
Am. (*Cernyomma*) *triguttatum*	Australia, Queensland	NC_005963	14,740
Am. sp.	China, Jinhua	OM368313	14,760
Am. (*Xiphiastor*) *hebraeum*	South Africa, Soutpan	KY457513	14,654
Am. (*Xiphiastor*) *marmoreum*	South Africa, Grahamstown	KY457516	14,677
Am. (*Xiphiastor*) *nuttalli*	Kenya, Masai Mara	SRR12168527	14,682
Am. (*Xiphiastor*) *testudinarium*	Japan, Nara	MT371798	14,829
Am. (*Xiphiastor*) *tholloni*	South Africa: Kruger National Park	KY457521	14,642
Archaeocroton sphenodonti	New Zealand, Stephens Island	NC_017745	14,772
Bothriocroton auruginans	Australia, Benalla, Vic	B4505, OR350528	14,761
B. concolor	Australia, Kangaroo Island	NC_017756	14,809
B. concolor	**Australia, Beerwah, Qld**	**B7019.F10, OR936202, OR948508**	**1815, 3974**
18S & 28S rRNA			
B. hydrosauri	Australia, Bundey Bore, SA	B6695, OR350529	14,763
B. undatum	Australia, Frazer Island, Qld	NC_017757	14,769
B. undatum	**Australia, Blue Mt, NSW**	**B7018.F, OR387374, OR387383**	**1815, 3964**
18S & 28S rRNA			
Cryptocroton papuanum	**Australia, Julatten, Qld**	**B5524, OR350530**	**14,757**
Cr. papuanum **18S & 28S rRNA**	**Australia, Julatten, Qld**	**B5524, OR387375, OR387385**	**2386, 3065**
Cr. papuanum	**Australia, Innisfail, Qld**	**B6707, OR350531**	**14,754**
Cr. papuanum **18S & 28S rRNA**	**Australia, Innisfail, Qld**	**B6707, OR387376, OR387384**	**3381, 3666**
Cr. papuanum	**Australia, Cairns, Qld**	**B7103. 48005260.F1, OR350532**	**14,753**
Cr. papuanum **18S & 28S rRNA**	**Australia, Cairns, Qld**	**B7103. 48005260.F1, OR387377, OR387386**	**2385, 3664**
Dermacentor (*Amblyocentor*) *rhinocerinus*	South Africa, Kruger National Park	KY457526	14,708
D. (*Anocentor*) *nitens*	Brazil, Campo Grande	NC_023349	14,839
D. (*Dermacentor*) *marginatus*	China, Jinghe	OM368303	15,178
D. (*Dermacentor*) *nuttalli*	China, Jinghe	OM368307	15,086
D. (*Dermacentor*) *silvarum*	China, Yakeshi	OM368309	15,086
D. (*Indocentor*) *steini*	China, Nanchang	OM368300	14,785
D. (*Indocentor*) *taiwanensis*	Japan, Wakayama	MT371800	14,793
Haemaphysalis (*Aboimisalis*) *punctata*	China, Jinghe	OM368285	14,697
Ha. (*Aborphysalis*) *formosensis*	Japan, Nishinomiya, Hyôgo	NC_020334	14,676
Ha. (*Allophysalis*) *danieli*	China, Haidong	OM368292	14,739
Ha. (*Allophysalis*) *tibetensis*	China, Lhasa	OM368293	14,715
Ha. (*Haemaphysalis*) *campanulata*	China, Wuhan	OM368277	14,691
Ha. (*Haemaphysalis*) *concinna*	China, Heilongjiang	NC_034785, B2057	14,675
Ha. (*Haemaphysalis*) *flava*	China	MG604958	14,689
Ha. (*Haemaphysalis*) *japonica*	China	NC_037246	14,685
Ha. (*Haemaphysalis*) *megaspinosa*	Japan, Miyazaki	MT371804, B5238	14,678

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TABLE 1. (Continued)

Genus (subgenus) Species	Location	MT/18S/28S Accession/Voucher	#bp
Ha. (*Haemaphysalis*) *pentalagi*	Japan, Kagoshima	MT371805, B5239	14,703
Ha. (*Herpetobia*) *nepalensis*	China, Yunnan	NC_064124	14,720
Ha. (*Herpetobia*) *sulcata*	China, Jinghe	OM368284	14,679
Ha. (*Kaiseriana*) *bancrofti*	Australia	MH043268	14,673
Ha. (*Kaiseriana*) *cornigera*	Japan, Wakayama	MT371802, B5236	14,680
Ha. (*Kaiseriana*) *hystricis*	China	NC_039765	14,716
Ha. (*Kaiseriana*) *longicornis*	China, Qingzhou	NC_037493	14,718
Ha. (*Kaiseriana*) *mageshimaensis*	China: Haikou	OM368289	14,721
Ha. (*Kaiseriana*) *novaeguineae*	Iron Range	B5081b, OR350533	14,681
Ha. (*Kaiseriana*) *yeni*	Japan	OL741745	14,714
Ha. (*Ornithophysalis*) *doenitzi*	China, Wuhan	OM368275	14,671
Ha. (*Herpetobia*) *qinghaiensis*	China, Haidong	OM368294	14,683
Ha. (*Segalia*) *montgomeryi*	China, Yunnan	MW751681	14,681
Hyalomma (*Hyalomma*) *asiaticum*	China	MW219608	14,723
Hy. (*Hyalomma*) *impeltatum*	Palestine, Jericho	SRR7984992	14,694
Hy. (*Hyalomma*) *rufipes*	South Africa, Meyerton	KY457528	14,748
Hy. (*Hyalomma*) *truncatum*	South Africa, Vereeniging	KY457529	14,731
Ixodes (*Ixodes*) *persulcatus*	Japan, Hokkaido	NC_004370	14,539
I. (*Pomerantzevella*) *simplex*	South Africa, Bakwena Cave	KY457532	14,551
I. (*Eschatocephalus*) *vespertilionis*	China, Huangshi	OM368263	14,548
I. (*Sternalixodes*) *confusus*	Australia, Mt Molloy	OL614953, B5531A	14,939
I. (*Sternalixodes*) *holocyclus*	Australia, Sydney, NSW	NC_005293	15,007
Rhipicentor nuttalli	South Africa	MF818020	14,779
Rhipicephalus (*Boophilus*) *australis*	Australia, Bunya, Qld	NC_023348	14,891
R. (*Boophilus*) *decoloratus*	South Africa, Uitspanning	KY457525	14,782
R. (*Boophilus*) *geigyi*	Burkina Faso	NC_023350	14,948
R. (*Boophilus*) *microplus*	Brazil, Mato Grosso do Sul	KC503261	14,905
R. (*Digineus*) *evertsi*	South Africa, Uitspanning	KY457538	14,740
R. (*Rhipicephalus*) *appendiculatus*	South Africa, OVI colony	KY457536	14,733
R. (*Rhipicephalus*) *camicasi*	Saudi Arabia, Riyadh	MZ323229	14,725
R. (*Rhipicephalus*) *haemaphysaloides*	China, Ganzhou	OM368324	14,744
R. (*Rhipicephalus*) *linnaei*	Egypt, Esna City	OM994389	14,713
R. (*Rhipicephalus*) *maculatus*	South Africa, Phinda	KY457540	14,714
R. (*Rhipicephalus*) *praetextatus*	Kenya, Lakipia County	SRR14589127	14,728
R. (*Rhipicephalus*) *pravus*	Kenya, Lakipia County	SRR5184711	14,734
R. (*Rhipicephalus*) *pulchellus*	Kenya, Lakipia County	SRR14589135	14,713
R. (*Rhipicephalus*) *sanguineus*	USA, Oklahoma	NC_002074	14,710
R. (*Rhipicephalus*) *simus*	South Africa, Bathurst	KY457542	14,721
R. (*Rhipicephalus*) *turanicus*	Palestine, Tubas	SRR7985002	14,733
R. (*Rhipicephalus*) *zambeziensis*	South Africa, Marakele	KY457544	14,691
Robertsicus elaphensis	Texas, USA	NC_017758	14,627

We inferred phylogenies from the mitochondrial genomes of 87 species of Ixodidae. These 87 species were from: (i) five of the nine subgenus level taxa of *Amblyomma* listed in Camicas *et al*. (1998): *Adenopleura* Macalister, 1872; *Amblyomma* Koch, 1844; *Aponomma* Neumann, 1899; *Cernyomma* Santos Dias, 1963; *Xiphiastor* Murray, 1877 (Camicas *et al*. 1998); and (ii) species of *Archaeocroton* Barker & Burger, 2018; *Allocerаea* Schulze, 1918; *Bothriocroton* Keirans, King & Sharrad, 1994; *Cryptocroton* **n. gen.**; *Dermacentor* Koch, 1844; *Haemaphysalis* Koch, 1844; *Hyalomma* Koch, 1844; *Rhipicentor* Nuttall & Warburton, 1908; *Rhipicephalus* Koch, 1844; *Robertsicus* Barker & Burger, 2018; and *Ixodes* Latreille, 1795 (Table 1). Three of the nine subgenera of *Amblyomma* were not represented in our trees: *Anastosiella* Santos Dias, 1963; *Dermiomma* Rondelli, 1939; and *Walkeriana* Santos Dias, 1963.

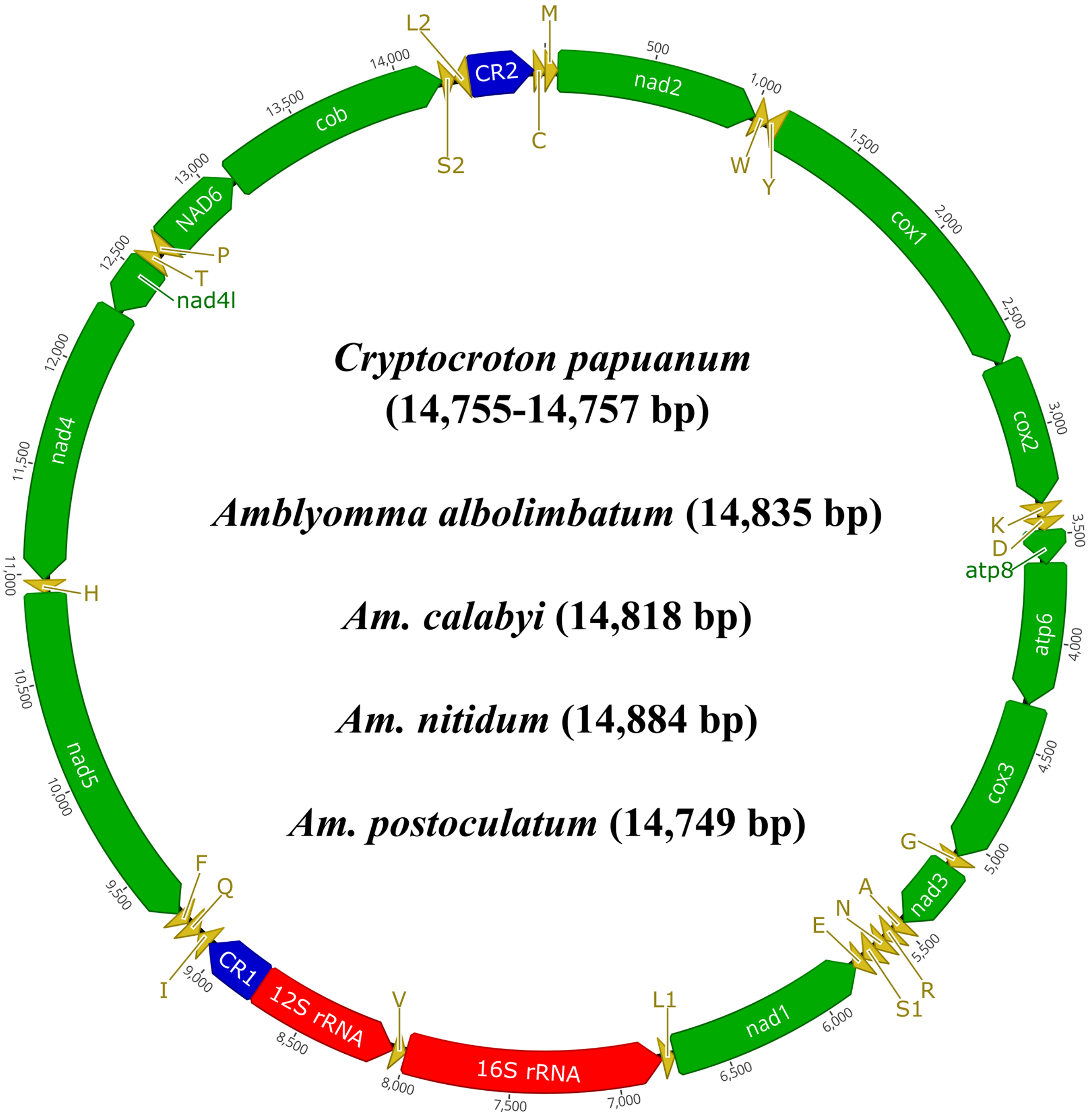

FIGURE 1. The mitochondrial genomes of *Cryptocroton papuanum*, *Amblyomma* (*Cernyomma*) *albolimbatum*, *Am*. (*C*.) cf. *calabyi*, *Am*. (*C*.) *nitidum* and *Am*. (*C*.) *postoculatum*. Protein-coding genes are in green, tRNAs are in yellow, rRNAs are in red, and the two control regions are in blue. Protein-coding genes are labelled by their four-character abbreviations, tRNAs are labelled by their one-letter amino-acid abbreviations, control regions are labelled as CR1 and CR2. The sizes of the mt genomes are indicated in brackets.

Results

Mitochondrial genomes and nuclear rRNA

Seven mitochondrial genomes from four species are presented for the first time (Fig. 1, Table 1): (i) *C. papuanum* (Hirst, 1914)—ticks from Cairns, Innisfail and Julatten, Queensland (Qld), Australia; (ii) *Am.* (*Cernyomma*) *albolimbatum*; (iii) *Am.* (*C.*) cf. *calabyi*; (iv) *A.* (*C.*) *nitidum*; and (v) *Am.* (*C.*) *postoculatum*. These seven mitochondrial genomes had the typical gene-content and gene-arrangement of the mitochondrial genomes of metastriate Ixodidae: 13 protein-coding genes, two ribosomal RNAs, 22 tRNAs and two control regions (Fig. 1) (Campbell & Barker 1998; Shao & Barker 2007). We also present for the first time the entire 18S and 28S rRNA of: (i) *C. papuanum* (Hirst, 1914) (Cairns, Innisfail and Julatten); (ii) *Am.* (*C.*) cf. *calabyi* Roberts, 1963; (iii) *Bothriocroton undatum* (Fabricius, 1775); and (iv) *B. concolor* (Neumann, 1899) (Table 1, Fig. 2).

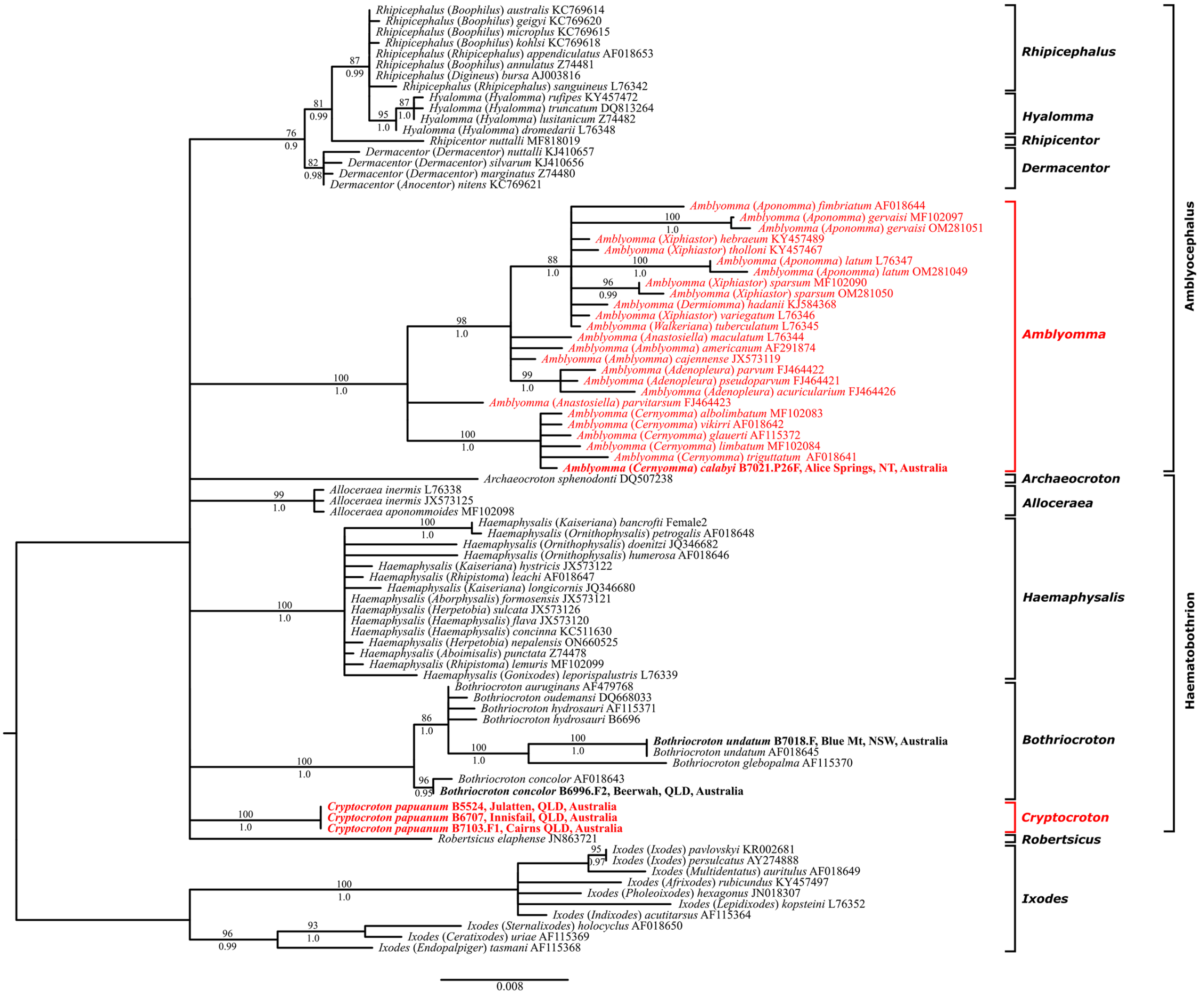

FIGURE 2. Phylogenies inferred from the nucleotide sequences from entire 18S rRNA (1,708 bp alignment). Maximum Likelihood (ML) bootstrap support are shown above branches and Bayesian Inference (BI) posterior probabilities are shown below branches. Branches that had less than 70% ML and less than 0.8 BI were collapsed. The *Cryptocroton* and *Amblyomma* species are in red.

Phylogenetic trees and pairwise (%) genetic differences among the mitochondrial genomes of 32 species (34 individuals) of ticks

Our phylogenies from the 11 protein-coding genes of mitochondrial genome sequences (ca. 15,000 bps) were well resolved. Indeed, many branches had bootstrap support of 100% and posterior probabilities of 1 out of 1 (Fig. 3). Our phylogenies from entire 18S rRNA (ca. 1,700 bps) also had many well resolved branches (Fig. 2) but the phylogeny from part of the 28S rRNA (ca. 670 bps) was far less resolved (Fig. 4).

The mean pairwise genetic difference among the six genera we studied was 26.1 % (Table 3). *Cryptocroton* was 25.0–28.8 % different to the five other genera we studied (*Alloceraea*, *Amblyomma*, *Archaeocroton*, *Bothriocroton* and *Haemaphysalis*; Table 3).

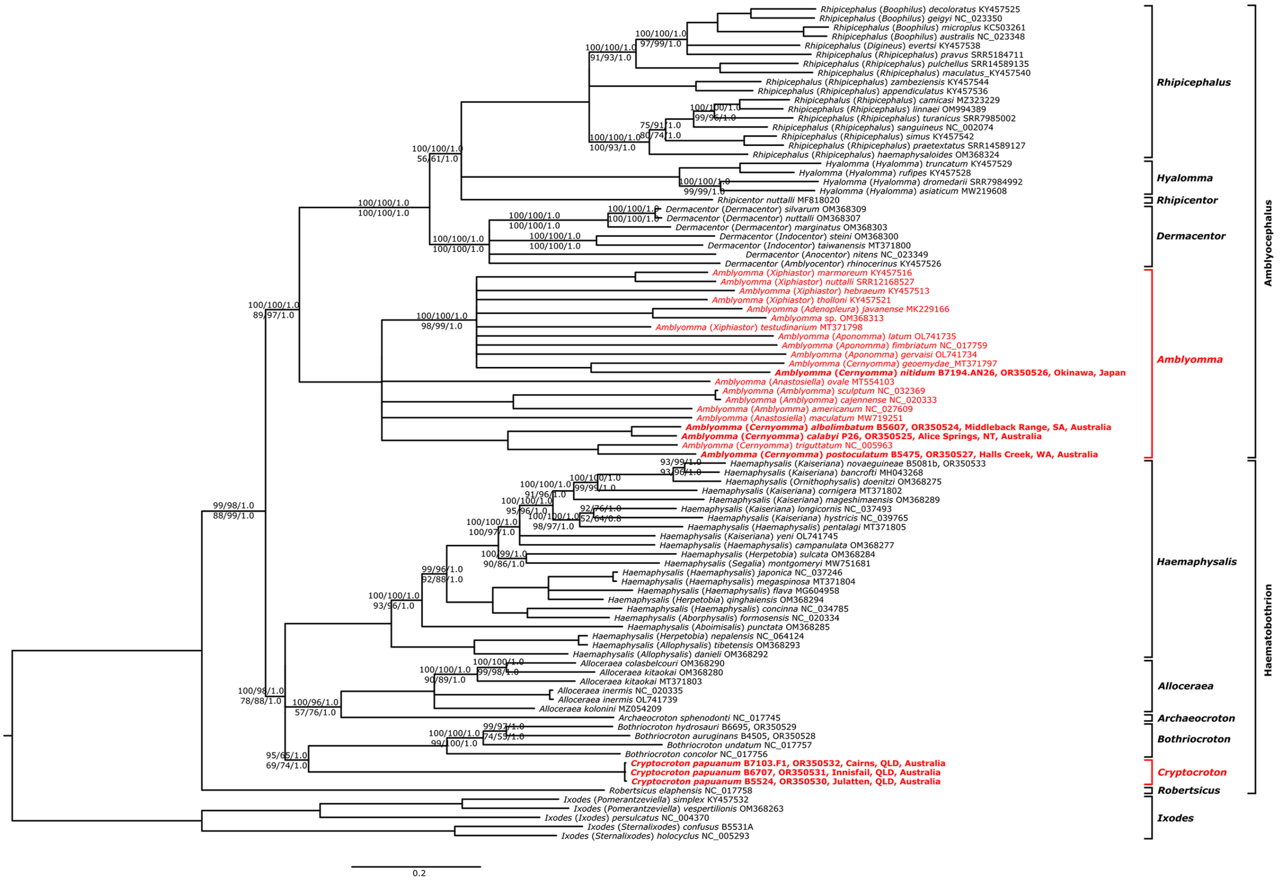

FIGURE 3. Phylogenies inferred from the 11 protein-coding genes of mitochondrial genomes (10,398 bp, 2,855 aa alignments) with bootstrap values and posterior probabilities from six sets of trees. Branch support for nucleotide trees is shown above branches, support for the amino acid trees is below branches. Branch support above branches is shown in the order (left to right) (i) RAxML Maximum likelihood (ML) bootstrap support; (ii) IQtree Maximum likelihood (ML) bootstrap support; (iii) MrBayes Bayesian Inference. Branch support below branches is (left to right) (i) RAxML Maximum likelihood (ML) bootstrap support; (ii) IQtree (ML) bootstrap support; (iii) MrBayes (BI) posterior probability. Branches that had less than 70% and less than 0.7 posterior probability in three or more of the six sets of trees were collapsed. Branches without values had 100% bootstrap support and 1.0 posterior probability for all six sets of trees. The 21 *Amblyomma* spp. and *Cryptocroton papuanum* are in red.

TABLE 2. A. Matrix of genetic-differences (%) of pairs of entire mitochondrial genomes of 17 species of *Amblyomma*, *Cryptocroton papuanum*, four species of *Bothriocroton*, *Archaeocroton sphenodonti*, seven species of *Haemaphysalis* and two species of *Alloceraea*.

		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	*Amblyomma* (*Adenopleura*) *javanense* MK229166	-	23.1	23.5	25	25.9	25.8	25.4	24.4	23	23.5	24.4	24.4	24.1	25.2	25.3	26.7	25.7
2	*Amblyomma* (*Aponomma*) *latum* OL741735	23.1	-	22.9	24.3	25.1	25	25.2	23.6	22.6	23	24	24.2	23.7	24.4	24.5	25.5	24.9
3	*Amblyomma* (*Aponomma*) *gervaisi* OL741734	23.5	22.9	-	24.7	25.9	25.8	25.3	24	23.1	23.9	24.3	24.7	24.2	25.3	25.3	26.1	25.4
4	*Amblyomma* (*Amblyomma*) *americanum* NC_027609	25	24.3	24.7	-	21.2	21.1	24.4	25.1	23.7	24	25.2	25.3	25	24.7	24.8	25	24.6
5	*Amblyomma* (*Amblyomma*) *cajennense* NC_020333	25.9	25.1	25.9	21.2	-	0.8	25.4	25.9	24.2	24.8	25.7	25.8	25.5	24.9	24.8	25.8	24.7
6	*Amblyomma* (*Amblyomma*) *sculptum* NC_032369	25.8	25	25.8	21.1	0.8	-	25.3	25.8	24.1	24.7	25.5	25.7	25.5	24.8	24.6	25.7	24.6
7	*Amblyomma* (*Anastosiella*) *ovale* MT554103	25.4	25.2	25.3	24.4	25.4	25.3	-	25.8	23.9	24.3	25.2	25.5	25.4	25.3	25	25.5	25
8	*Amblyomma* (*Aponomma*) *fimbriatum* NC_017759	24.4	23.6	24	25.1	25.9	25.8	25.8	-	23.4	24.3	22.9	24.6	24.8	25.6	25.8	26.5	25.8
9	*Amblyomma* (*Xiphiastor*) *hebraeum* KY457513	23	22.6	23.1	23.7	24.2	24.1	23.9	23.4	-	17.3	21.3	23.3	22.7	24.6	24.2	24.8	24.3
10	*Amblyomma* (*Xiphiastor*) *marmoreum* KY457516	23.5	23	23.9	24	24.8	24.7	24.3	24.3	17.3	-	22	23.6	23.3	25.1	24.7	25.5	25.1
11	*Amblyomma* (*Xiphiastor*) *tholloni* KY457521	24.4	24	24.3	25.2	25.7	25.5	25.2	22.9	21.3	22	-	25	24.2	26.3	25.9	26.9	26.3
12	*Amblyomma* (*Cernyomma*) *geoemydae* MT371797	24.4	24.2	24.7	25.3	25.8	25.7	25.5	24.6	23.3	23.6	25	-	20.2	26	26	26.6	25.8
13	***Amblyomma* (*Cernyomma*) *nitidum* AN26, OR350526**	24.1	23.7	24.2	25	25.5	25.5	25.4	24.8	22.7	23.3	24.2	20.2	-	25.6	26	26.3	25.7
14	***Amblyomma* (*Cernyomma*) *albolimbatum* B5607, OR350524**	25.2	24.4	25.3	24.7	24.9	24.8	25.3	25.6	24.6	25.1	26.3	26	25.6	-	8.8	19.8	18.8
15	***Amblyomma* (*Cernyomma*) cf. *calabyi*_P26, OR350525**	25.3	24.5	25.3	24.8	24.8	24.6	25	25.8	24.2	24.7	25.9	26	26	8.8	-	19.4	18.8
16	***Amblyomma* (*Cernyomma*) *postoculatum*_B5475, OR350527**	26.7	25.5	26.1	25	25.8	25.7	25.5	26.5	24.8	25.5	26.9	26.6	26.3	19.8	19.4	-	13.1
17	*Amblyomma* (*Cernyomma*) *triguttatum* NC_005963	25.7	24.9	25.4	24.6	24.7	24.6	25	25.8	24.3	25.1	26.3	25.8	25.7	18.8	18.8	13.1	-
18	***Cryptocroton papuanum* B5524, OR350530**	29.2	28.3	28.5	28.5	28.5	28.4	29.3	29.4	28	29	29.8	29.3	29.1	28.5	28.6	29.2	28.4
19	***Cryptocroton papuanum* B6707, OR350531**	29.2	28.4	28.5	28.5	28.5	28.4	29.3	29.3	28	29	29.8	29.3	29	28.5	28.6	29.2	28.4
20	***Cryptocroton papuanum* B7103.F1, OR350532**	29.2	28.4	28.5	28.5	28.5	28.4	29.3	29.3	28.1	29	29.8	29.3	29	28.5	28.6	29.2	28.4
21	*Bothriocroton auruginans*_B4505, OR350528	28.7	28.5	28.5	28	28.3	28.2	28.5	29.7	27.9	28.7	29.1	29.3	28.7	28.2	27.9	28.6	27.8
22	*Bothriocroton hydrosauri* B6695, OR350529	28.5	28	28.1	27.5	28	27.9	28.7	29.4	27.7	28.1	29.2	28.7	28.8	27.8	27.6	28.5	27.4
23	*Bothriocroton undatum* NC_017757	29.6	28.7	28.6	28.4	28.5	28.4	29	29.7	28.4	28.9	30	29.3	29.1	28.3	28.2	28.9	28

......*Continued on the next page*

TABLE 2. (Continued)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
24	*Bothriocroton concolor* NC_017756	30.2	29.3	29.7	28.7	29	29	29.3	30.2	29	29.2	30.3	29.9	29.5	29	28.9	29.2	28.9
25	*Haemaphysalis* (*Aboimisalis*) *punctata* OM368285	27.4	27	27.6	27	28.3	28.2	28	28.2	26.9	27.7	28.2	28.2	28.3	27.5	27.4	27.8	26.9
26	*Haemaphysalis* (*Aborphysalis*) *formosensis* NC_020334	27.3	27.3	27.7	27.2	27.9	27.8	27.9	28.5	26.6	27.4	28.8	28.2	27.9	27.4	27.2	27.9	27
27	*Haemaphysalis* (*Haemaphysalis*) *megaspinosa* MT371804	27.8	27.3	27.7	27	28.2	28.1	28.2	28.4	27.2	27.8	28.5	28.7	28.1	27.4	27.2	28.4	27.6
28	*Haemaphysalis* (*Kaiseriana*) *longicornis* NC_037493	28.1	27.4	28.2	28	28.9	28.8	28.5	29	27.7	28.3	28.9	28.8	28.8	27.9	27.8	28.8	27.8
29	*Haemaphysalis* (*Ornithophysalis*) *doenitzi* OM368275	28.1	27.5	28.6	27.8	28.6	28.5	28.6	29.3	27.7	28.4	29	28.7	28.5	27.8	27.6	28.9	28.2
30	*Haemaphysalis* (*Allophysalis*) *tibetensis* OM368293	28.3	27.5	28.1	27.7	28.5	28.4	28.3	28.6	27.6	28	28.5	28.6	28.5	27.6	27.2	28.4	27.5
31	*Haemaphysalis* (*Herpetobia*) *nepalensis* NC_064124	28.5	27.7	28.3	27.9	28.7	28.5	28.4	28.8	27.7	28.3	28.8	28.7	28.7	27.7	27.4	28.6	27.7
32	*Alloceraea inermis* OL741739	27.3	26.6	26.8	26.5	26.7	26.6	27.1	27.6	26.2	26.9	27.9	27.6	27.4	26.7	26.6	27.1	26.5
33	*Alloceraea kitaokai* MT371803	27	26.5	26.9	26.6	26.9	26.8	27.2	28.1	26.1	26.9	28.1	27.3	27	26.7	26.6	27.5	26.8
34	*Archaeocroton sphenodonti* NC_017745	28.8	27.3	27.8	27.6	28.5	28.5	28.5	29	27.9	28.3	29.1	28.9	29	27.6	27.2	28.1	27.5

TABLE 2. (Continued)

		18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1	*Amblyomma* (*Adenopleura*) *javanense* MK229166	29.2	29.2	29.2	28.7	28.5	29.6	30.2	27.4	27.3	27.8	28.1	28.1	28.3	28.5	27.3	27	28.8
2	*Amblyomma* (*Aponomma*) *latum* OL741735	28.3	28.4	28.4	28.5	28	28.7	29.3	27	27.3	27.3	27.4	27.5	27.5	27.7	26.6	26.5	27.3
3	*Amblyomma* (*Aponomma*) *gervaisi* OL741734	28.5	28.5	28.5	28.5	28.1	28.6	29.7	27.6	27.7	27.7	28.2	28.6	28.1	28.3	26.8	26.9	27.8
4	*Amblyomma* (*Amblyomma*) *americanum* NC_027609	28.5	28.5	28.5	28	27.5	28.4	28.7	27	27.2	27	28	27.8	27.7	27.9	26.5	26.6	27.6
5	*Amblyomma* (*Amblyomma*) *cajennense* NC_020333	28.5	28.5	28.5	28.3	28	28.5	29	28.3	27.9	28.2	28.9	28.6	28.5	28.7	26.7	26.9	28.5
6	*Amblyomma* (*Amblyomma*) *sculptum* NC_032369	28.4	28.4	28.4	28.2	27.9	28.4	29	28.2	27.8	28.1	28.8	28.5	28.4	28.5	26.6	26.8	28.5
7	*Amblyomma* (*Anastosiella*) *ovale* MT554103	29.3	29.3	29.3	28.5	28.7	29	29.3	28	27.9	28.2	28.5	28.6	28.3	28.4	27.1	27.2	28.5
8	*Amblyomma* (*Aponomma*) *fimbriatum* NC_017759	29.4	29.3	29.3	29.7	29.4	29.7	30.2	28.2	28.5	28.4	29	29.3	28.6	28.8	27.6	28.1	29
9	*Amblyomma* (*Xiphiastor*) *hebraeum* KY457513	28	28	28.1	27.9	27.7	28.4	29	26.9	26.6	27.2	27.7	27.7	27.6	27.7	26.2	26.1	27.9
10	*Amblyomma* (*Xiphiastor*) *marmoreum* KY457516	29	29	29	28.7	28.1	28.9	29.2	27.7	27.4	27.8	28.3	28.4	28	28.3	26.9	26.9	28.3
11	*Amblyomma* (*Xiphiastor*) *tholloni* KY457521	29.8	29.8	29.8	29.1	29.2	30	30.3	28.2	28.8	28.5	28.9	29	28.5	28.8	27.9	28.1	29.1

......*Continued on the next page*

TABLE 2. (Continued)

		18	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
12	*Amblyomma* (*Cernyomma*) *geoemydae* MT371797	29.3	29.3	29.3	29.3	28.7	29.3	29.9	28.2	28.2	28.7	28.8	28.7	28.6	28.7	27.6	27.3	28.9
13	***Amblyomma* (*Cernyomma*) *nitidum* AN26, OR350526**	29.1	29	29	28.7	28.8	29.1	29.5	28.3	27.9	28.1	28.8	28.5	28.5	28.7	27.4	27	29
14	***Amblyomma* (*Cernyomma*) *albolimbatum* B5607, OR350524**	28.5	28.5	28.5	28.2	27.8	28.3	29	27.5	27.4	27.4	27.9	27.8	27.6	27.7	26.7	26.7	27.6
15	***Amblyomma* (*Cernyomma*) cf. *calabyi*_P26, OR350525**	28.6	28.6	28.6	27.9	27.6	28.2	28.9	27.4	27.2	27.2	27.8	27.6	27.2	27.4	26.6	26.6	27.2
16	***Amblyomma* (*Cernyomma*) *postoculatum*_B5475, OR350527**	29.2	29.2	29.2	28.6	28.5	28.9	29.2	27.8	27.9	28.4	28.8	28.9	28.4	28.6	27.1	27.5	28.1
17	*Amblyomma* (*Cernyomma*) *triguttatum* NC_005963	28.4	28.4	28.4	27.8	27.4	28	28.9	26.9	27	27.6	27.8	28.2	27.5	27.7	26.5	26.8	27.5
18	***Cryptocroton papuanum* B5524, OR350530**	-	0.3	0.3	26.3	26.1	26.7	26.8	25.9	26.3	26.1	26.8	26.7	26.4	26.6	24.9	25.1	25.8
19	***Cryptocroton papuanum* B6707, OR350531**	0.3	-	0.1	26.3	26.1	26.7	26.8	25.9	26.3	26.2	26.8	26.8	26.4	26.5	24.9	25.2	25.9
20	***Cryptocroton papuanum* B7103.F1, OR350532**	0.3	0.1	-	26.3	26.1	26.7	26.7	26	26.3	26.2	26.8	26.7	26.3	26.5	24.9	25.1	25.9
21	*Bothriocroton auruginans*_B4505, OR350528	26.3	26.3	26.3	-	16	18.6	19.8	26	25.7	26	26.4	26.3	25.7	25.8	24	23.9	25.6
22	*Bothriocroton hydrosauri* B6695, OR350529	26.1	26.1	26.1	16	-	18.3	19.5	25.5	25.1	25.3	26	25.7	25.5	25.7	23.8	23.7	24.9
23	*Bothriocroton undatum* NC_017757	26.7	26.7	26.7	18.6	18.3	-	21.3	26.2	26.8	26.5	27.2	26.9	26.7	27	24.6	24.7	25.9
24	*Bothriocroton concolor* NC_017756	26.8	26.8	26.7	19.8	19.5	21.3	-	26.6	26.4	26.2	26.8	27	26.5	26.7	24.9	24.7	25.4
25	*Haemaphysalis* (*Aboimisalis*) *punctata* OM368285	25.9	25.9	26	26	25.5	26.2	26.6	-	19.3	19.4	20.4	20.5	20.6	20.8	23.3	23.4	25.3
26	*Haemaphysalis* (*Aborphysalis*) *formosensis* NC_ 020334	26.3	26.3	26.3	25.7	25.1	26.8	26.4	19.3	-	14.7	18.6	18.9	20	20.1	22.6	23	25.3
27	*Haemaphysalis* (*Haemaphysalis*) *megaspinosa* MT371804	26.1	26.2	26.2	26	25.3	26.5	26.2	19.4	14.7	-	18.8	19.3	20	20.2	22.7	23	25.1
28	*Haemaphysalis* (*Kaiseriana*) *longicornis* NC_037493	26.8	26.8	26.8	26.4	26	27.2	26.8	20.4	18.6	18.8	-	16.1	21.1	21.3	23.5	23.7	25.1
29	*Haemaphysalis* (*Ornithophysalis*) *doenitzi* OM368275	26.7	26.8	26.7	26.3	25.7	26.9	27	20.5	18.9	19.3	16.1	-	21.6	21.9	23.5	23.8	25.6
30	*Haemaphysalis* (*Allophysalis*) *tibetensis* OM368293	26.4	26.4	26.3	25.7	25.5	26.7	26.5	20.6	20	20	21.1	21.6	-	2.2	22.9	23.3	24.8
31	*Haemaphysalis* (*Herpetobia*) *nepalensis* NC_064124	26.6	26.5	26.5	25.8	25.7	27	26.7	20.8	20.1	20.2	21.3	21.9	2.2	-	23	23.3	24.9
32	*Alloceraea inermis* OL741739	24.9	24.9	24.9	24	23.8	24.6	24.9	23.3	22.6	22.7	23.5	23.5	22.9	23	-	14.5	22.8
33	*Alloceraea kitaokai* MT371803	25.1	25.2	25.1	23.9	23.7	24.7	24.7	23.4	23	23	23.7	23.8	23.3	23.3	14.5	-	23.1
34	*Archaeocroton sphenodonti* NC_017745	25.8	25.9	25.9	25.6	24.9	25.9	25.4	25.3	25.3	25.1	25.1	25.6	24.8	24.9	22.8	23.1	-

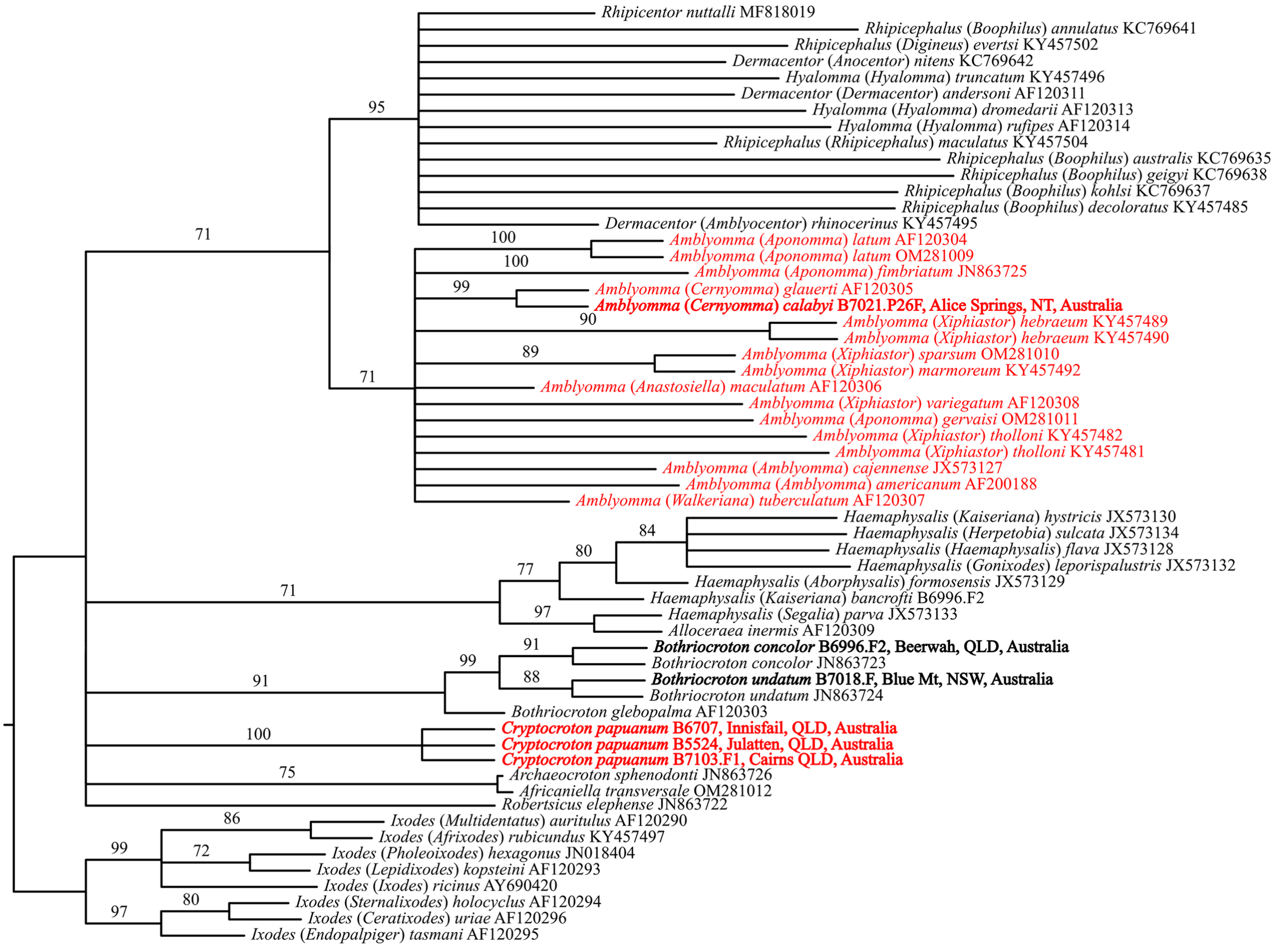

FIGURE 4. Phylogeny inferred from partial nucleotide sequences of 28S rRNA (673 bp alignment). Maximum Likelihood (ML) bootstrap support is shown above branches. Branches that had less than 70% ML were collapsed. The *Cryptocroton* and *Amblyomma* species are in red; *Ixodes* spp. were set as the outgroup. Sequences presented for the first time in this paper are in bold font.

TABLE 3. Matrix of genetic-differences (mean %, range) among genera.

	Amblyomma	***Cryptocroton***	***Bothriocroton***	***Haemaphysalis***	***Alloceraea***	***Archaeocroton***
Amblyomma	**24.1** (0.8–26.9)					
Cryptocroton	**28.8** (28–29.8)	-				
Bothriocroton	**28.7** (27.4–30.4)	**26.5** (26.1–26.8)	**18.9** (16–21.3)			
Haemaphysalis	**28** (26.6–29.3)	**26.4** (25.9–26.8)	**26.2** (25.1–27.2)	**18.8** (2.2–21.9)		
Alloceraea	**27** (26.1–28.1)	**25** (24.9–25.2)	**24.3** (23.7–24.9)	**23.2** (22.6–23.8)	-	
Archaeocroton	**28.2** (27.2–29.1)	**25.9** (25.8–25.9)	**25.5** (24.9–25.9)	**25.2** (24.8–25.6)	**23** (22.8–23.1)	-

Systematics

Family Ixodidae Murray, 1877

Genus *Cryptocroton* n. gen. Barker, S.C. & Barker, D.

http://zoobank.org/urn:lsid:zoobank.org:act:F801837F-6F60-4ACB-8E1B-9AEF390774D7

Type species: *Amblyomma papuana* Hirst, 1914, here designated.

Type depository: British Museum (Natural History) London, according to Robinson (1926).

Species included: Monotypic, *Cryptocroton papuanum* (Hirst, 1914). Guglielmone *et al*. (2020) has a list of the descriptions and redescriptions of this species.

Material examined: Table 1.

Diagnosis: With characteristics of its sole constituent species *Cryptocroton papuanum* (Hirst, 1914). Coxa II–IV of the female and male with with two widely separated spurs, and with spurs half way along trochanters II–IV (Figs 5–6; see also Roberts 1970 Fig. 61c for a drawing of the coxa and trochanters of the female).

Etymology: From the Greek: *crypto*, concealed and *croton*, tick (neuter gender).

Distribution: Australia and Papua New Guinea.

Remarks. Hirst (1914) and Roberts (1953) noted that the male of *Amblyomma papuana* is small and subcircular, similar to *Aponomma*. This was an apt description; indeed a prophetic description given that affinities of *C. papuanum* (Hirst, 1914) lie with the *Aponomma*-like ticks of the genus *Bothriocroton* not *Amblyomma* (Fig. 3). *Bothriocroton* was formerly in the genus *Aponomma*, a genus that once held all of the eyeless ticks of reptiles.

Roberts (1953) observed that the only species of Australian *Amblyomma* in which the female has two spurs on coxae II–IV is *C. papuanum* (Hirst, 1914); in the other species there is only one spur on each of these coxae (Roberts 1970; Barker & Barker 2023). However this is not a morphological synapomorphy for *Cryptocroton* since some species of *Amblyomma* from other parts of the world have two spurs on coxae II–IV. We note that morphological synapomorphies have been identified so far for only a few genera of ticks; for example, the three pairs of large wax glands on segment VIII in larvae that is a synapomorphy for the genus *Bothriocroton* (Klompen *et al*. 2002; Burger *et al*. 2012; Barker & Burger 2018).

Discussion

Cryptic genera are rare but have been discovered by molecular phylogenetics in other organisms e.g. in plants (Gagnon *et al*. 2015). Phylogenies from mitochondrial genomes and from nuclear rRNA have nourished systematic studies of the genera of soft ticks to an extraordinary extent (Mans *et al*. 2019). Yet, truly cryptic species of ticks may be rare: "cryptic" in this context refers to species with no apparent distinguishing morphological features and/or species that have morphological features that led them to be placed in the wrong genus. *Cryptocroton papuanum* is a case of tick that has morphological features (eyes, Fig. 7.) that led it to be placed in the wrong genus: *Amblyomma*. Roberts (1953) noted in passing that *C. papuanum* was an "*Aponomma*-like tick", but did not question its placement in *Amblyomma*; and indeed, did not even mention in his final taxonomic work (Roberts 1970) that *C. papuanum* was an unusual species of *Amblyomma*. The small size and poorly developed festoons of *C. papuanum* might, however, have drawn attention to its anomalous systematic position. Regardless, *C. papuanum* was considered to be a species of *Amblyomma* by all of the tick-taxonomists who crossed its path: so *Cryptocroton* was indeed hidden for well over 100 years (since 1914 when *Amblyomma papuanum* Hirst, 1914 was described).

In the Argasidae, the remarkable morphological similarity of the nymphs and adults, and even the adult males and adult females, of many species, together with the difficulty of collecting larvae, since the larvae may moult to nymphs soon after hatching (without a blood-meal), for example in *Ornithodoros* Koch, 1844 *sensu strictu*, explains why *Ornithodoros moubata* (Murray, 1877) and *Ornithodoros savignyi* (Audouin, 1827) were not recognised as complexes of cryptic species (Bakkes *et al*. 2018). The same is true for other genera of Argasidae in which cryptic species have been identified by molecular phylogenetics (Mans *et al*. 2019): for example the cryptic species in *Alectorobius capensis* (Neumann, 1901), *Carios vespertilionis* Latreille, 1796, *Chiropterargas boueti* (Roubaud & Colas-Belcour, 1933), *Ogadenus brumpti* (Neumann, 1907), and *Secretargas transgariepinus* (White, 1846) (Mans *et al*. 2019).

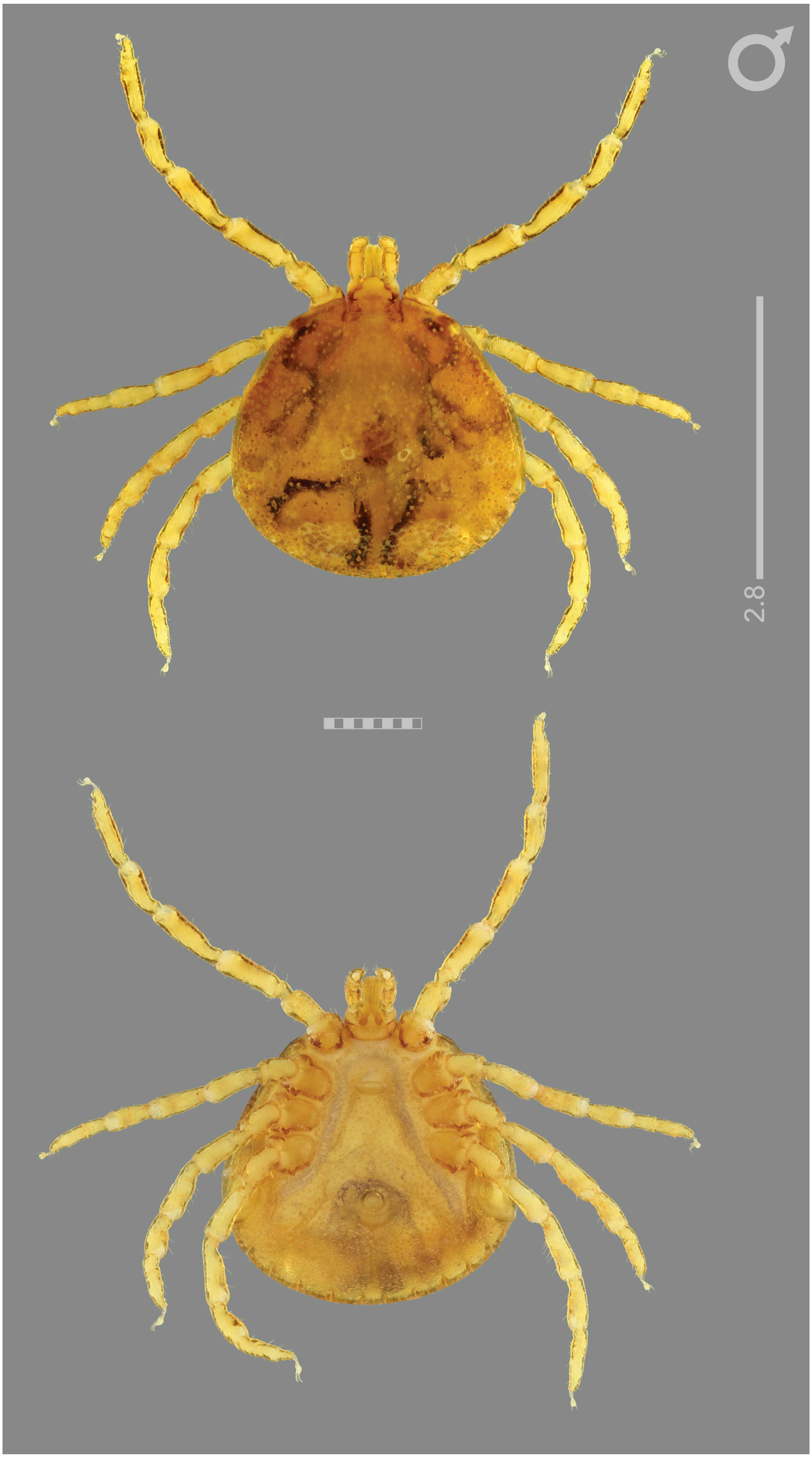

FIGURE 5. Male *Cryptocroton papuanum* B7102 (ANIC 48 000 592). Horizontal scale bar: 1 mm. Vertical scale bar indicates overall length (mm).

FIGURE 6. Female *Cryptocroton papuanum* B7102 (ANIC 48 000 592). Horizontal scale bar: 1 mm. Vertical scale bar indicates overall length (mm).

FIGURE 7. Eyes of female *Cryptocroton papuanum* B7102 (ANIC 48 000 592).

TABLE 4. Records of *Cryptocroton papuanum* (Hirst, 1914). ANIC, Australian National Insect Collection; B&B, Barker & Barker Collection, University of Queensland; and QM, Queensland Museum. PNG, Papua New Guinea; Qld, Queensland (Australia); AMNH, American Museum of Natural History. We examined the following specimens: B7102, B7103, B6707, B6640, B6639 and B5524.

Host: genus species (if known)	F	M	N	L	Place name, state	Date collected	Latitude, Longitude	Collection #	Collection/ Reference	Collector	GenBank Accession #s: mt genome/ 18S rRNA/ 28S rRNA
Tachyglossus aculeatus	1				Cairns, Qld	15 May 2013	-17.35, 145.60	B7103, 48 005 260: 40R	ANIC	I. Beveridge	OR350532, OR387377, OR387386
Tachyglossus aculeatus	1	3			Cairns, Qld	9 Oct 1901	-16.92, 145.77	B7102 48 000 592	ANIC	?	
Tachyglossus aculeatus	1				Innisfail, Qld	22 June 2021	-17.528943, 146.033121	B6707	B&B	Z. Squarei	OR350531, OR387376, OR387384
pitfall trap in eucalypt forest	1				Gordon's Mine Area, Iron Range, Cape York, Qld	12-18 Feb 1976	-12.692154, 143.334215	B6640	QM	G.B. Monteith	
pet-possibly a dog (“on collar”)		1			Iron Range National Park, Cape York, Qld	16 Dec 1942	-12.6866473, 143.3342296	B6639	QM	J.L. Wassell	
vegetation	1				Julatten, Atherton Tablelands, Qld	22 Jan 2021	-16.626787, 145.320618	B5524	B&B	S.C. Barker	OR350530, OR387375, OR387385
unknown	7	4			Iron Range, Qld	June 1948		RML45578	Robbins & Bush (2006)	Archbold Expedition (AMNH)	
Casuarius casuarius	5				Western Province, Oriomo, PNG	Oct 1958		RML99421	Robbins & Bush (2006)	F. Klekham	
Casuarius casuarius	4	2			Western Province, Fly River, Lake Daviumbu, PNG	31 Aug 1936		RML18476	Robbins & Bush (2006)	Archbold Expedition (AMNH)	
Casuarius bennetti	2			21	Norther Province, Mount Suckling (Owen Stanley Range), PNG	15 Oct 2002	- 9.32.50, 149.04.14	RML123680	Robbins & Bush (2006)	S.E. Bush	
Casuarius casuarius	?	?	?	?	PNG				Hoogstraal (1982), Wilson (1972a,b)	?	

In the Ixodidae, putative cryptic species have been identified in *Rhipicephalus* (*Boophilus*) *microplus* (Canestrini, 1888), *Amblyomma marmoreum* Koch, 1844 and *Rhipicephalus turanicus* Pomerantzev, 1940 (Burger *et al*. 2014; Mans *et al*. 2019; Bakkes *et al*. 2020 respectively). It is of course possible, perhaps even likely, that these "cryptic" species will be morphologically distinguishable after more detailed morphological and/or morphometric study of all the life stages, especially the larvae and nymphs. A species may be cryptic at the adult life-stage whereas the larvae and/or nymphs may be distinguishable or *vice versa*. Thus, molecular phylogenetics might reveal relationships that had previously been overlooked. More often than not, the species was assigned to a species-name on the basis of morphological features, and thus is indeed cryptic, until morphological differences that had either been ignored or considered part of a species continuum are brought to light by molecular phylogenetics. In this regard, a number of new species have been described recently from species complexes, since stable morphological characters have finally been found (Bakkes *et al*. 2018, 2020). Furthermore, phylogenies from mitochondrial genomes and from nuclear rRNA have revealed other cryptic higher taxa. For example, the extraordinary discovery that *Otobius lagophilus* Cooley & Kohls, 1940 belongs in the Argasinae whereas *Otobius megnini* (Dugès, 1883) belongs in the Ornithodorinae (Knuebehl *et al*. 2022): *Otobius lagophilus* had been unambiguously placed in the genus *Otobius* Banks, 1912 on account of the panduriform body-margin, spinose integument of the nymphs, the presence of well-developed denticles rather than vestigial denticles on the hypostome of the adults and nymphs, and the fact that adults do not feed (Cooley & Kohls 1940; Clifford *et al*. 1964). A new genus in the subfamily Argasinae will probably be needed for *O. lagophilus*: that genus would certainly seem to qualify as another cryptic genus. In a similar way, the recently erected and/or resurrected genera *Archaecroton*, *Robertsicus* and *Africaniella* were once cryptic genera (Barker & Burger 2018; Hornok *et al*. 2020; Kelava *et al*. 2023). New genera like these were cryptic until they were brought to the light by molecular phylogenetics and subsequent detailed morphological study.

Barker *et al*. (2021) proposed that the part of the mini-super continent Australis that became Australia was one of the theatres of evolution of the ticks. The discovery of *Cryptocroton*, which is known only from Australia and Papua New Guinea, reinforces this point of view. Finally, we note with interest that *Cryptocroton papuanum* has not been recorded from a cassowary in Australia; only from cassowaries in Papua New Guinea (Table 4). It seems, however, that few cassowaries have been examined for ticks in Australia.

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