

# ***Bothriocroton oudemansi* (Neumann, 1910) n. comb. (Acari: Ixodida: Ixodidae), an ectoparasite of the western long-beaked echidna in Papua New Guinea: redescription of the male and first description of the female and nymph**

Lorenza Beati · James E. Keirans · Lance A. Durden ·  
Muse D. Opiang

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**Abstract** Specimens of *Amblyomma oudemansi* (Neumann, 1910) were collected in Papua New Guinea from an endangered monotreme, *Zaglossus bruijini* (Peters & Doria), the western long-beaked echidna. These ticks were compared morphologically and molecularly with species formerly assigned to *Aponomma* Neumann, 1899 (now included in *Bothriocroton* Keirans, King, & Sharrad, 1994 or *Amblyomma* Koch, 1844), and a phylogeny was generated. Based on our results, we reassign this tick to *Bothriocroton*, as *B. oudemansi* (Neumann, 1910) n. comb. Original descriptions are provided for the female and the nymph of this species and the male is redescribed. A revised list of all *Bothriocroton* records and holdings in the US National Tick Collection is also provided.

## **Introduction**

Ticks from echidnas were first described by Lucas (1878), when he described *Ixodes acanthoglossi* (Lucas, 1878), collected from what was then called *Acanthoglossus bruijini*, the New Guinean long-beaked echidna, now *Zaglossus bruijini* (Peters & Doria). Unfortunately, his description is rather unspecific and was not accompanied by detailed diagnostic illustrations. Referring to the note published by Lucas, Oudemans (1906) included *I. acanthoglossi* in the recognised ixodid fauna of New Guinea. *I. acanthoglossi* was, however, listed as a rejected tick name by Camicas, Hervy, Adam & Morel (1998), probably because its description did not correspond to any known tick and because the Lucas types, to the best of our knowledge, were unavailable for comparison.

Neumann (1910) described and illustrated *Aponomma oudemansi* (Neumann, 1910), based on male specimens collected from the skin of a specimen of “*Zaglossus (Proechidna) bruyini nigroaculeatus*”. These ticks are deposited in the Zoological Museum of Amsterdam (ZMAM) of Amsterdam University, The Netherlands. Among other features, Neumann (1910) described the presence of spiracular plates extruding from the lateral border of the body anterior to the first festoon and a 2 ½/2 ½ hypostomal dental formula.

Schulze (1936) described female ticks deposited in the Berlin Museum, Germany, which had been

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L. Beati (✉) · J. E. Keirans  
United States National Tick Collection, Institute of  
Arthropodology and Parasitology, Georgia Southern  
University, Statesboro, GA 30460, USA  
e-mail: lorenzabeati@georgiasouthern.edu

L. A. Durden  
Department of Biology, Georgia Southern University,  
Statesboro, GA 30460, USA

M. D. Opiang  
Wildlife Conservation Society, PO Box 277,  
Goroka, EHP, Papua New Guinea

collected from *Echidna aculeata*, now *Tachyglossus aculeatus* (Shaw), from an unknown geographical region. Because his specimens had a similar hypostomal dentition ( $2 \frac{1}{2}/2 \frac{1}{2}$ ) and host preference, he deduced that these were the missing *A. oudemansi* females. He later subdivided the taxon into two subspecies, *A. o. oudemansi* (Neumann, 1910) (the nominate subspecies), for the specimens he described in 1936, and *A. oudemansi galactites* Schulze, 1941, for two female ticks collected from an unknown animal at Sydney, Australia, which were characterized by the presence of heavy white markings on the scutum (Schulze, 1941). Much later (Kaufmann, 1972), *A. oudemansi* was synonymised with *Aponomma concolor* Neumann, 1899. However, after examining a syntype male of *A. oudemansi* (Nuttall No. 2878, RML111755) in the Nuttall Collection of the Natural History Museum [then the British Museum (Natural History)] in London, Keirans (1985) noted that this tick did not have ventral lobes on palpal articles II, which are typical for *A. concolor*. Dias (1993), after examining the specimens at the ZMAM, concurred with Keirans (1985) in considering *A. oudemansi* to be a valid tick name. Later, Camicas et al. (1998) again included *A. oudemansi* in the synonymy list of *A. concolor*, but did not provide any justification for doing so.

Based on molecular data and larval morphology, the genus *Aponomma* Neumann, 1899 has now been split in two groups of taxa (Klompen, Dobson & Barker, 2002). The newly elevated genus *Bothriocroton* Keirans, King & Sharrad, 1994, originally described as a subgenus of *Aponomma* by Keirans, King & Sharrad (1994) includes the so-called “Australian endemic” former *Aponomma* species, *B. auruginans* (Schulze, 1936), *B. concolor* (Neumann, 1899), *B. hydrosauri* (Denny, 1843), *B. glebopalma* (Keirans, King & Sharrad, 1994) and *B. undatum* (Fabricius, 1775). All remaining *Aponomma* species were reassigned to *Amblyomma* Koch, 1844, partly confirming Koch’s (1844) opinion that *Aponomma* were simply eye-less *Amblyomma*. Klompen, Oliver, Keirans & Homsher (1997) and Klompen et al. (2002) also found a synapomorphic character that distinguishes members of *Bothriocroton*: all *Bothriocroton* larvae, with the exception of *B. undatum* larvae which were not available for examination, have three pairs of large wax glands (formerly known as sensilla

sagittiformia) on each side of the idiosoma near setae *s6* anterior to the first festoon. *Aponomma oudemansi* was recently transferred to *Amblyomma* and not included in *Bothriocroton* (see Horak, Camicas & Keirans, 2002; Barker & Murrell, 2004).

Eye-less ticks from long-beaked echidnas in Papua New Guinea were recently collected by one of us (MDO) as part of an ecological study of this monotreme. Herein, we describe the results obtained by comparing these ticks with former *Aponomma* species based on morphological analyses. Because we lack larval specimens of *B. oudemansi* to check for the morphology of large wax glands, we performed molecular phylogenetic analyses to establish the systematic position of this tick species.

Moreover, the name *Aponomma tachyglossi* Roberts, 1953, formerly treated as a junior synonym of *B. hydrosauri*, was recently resurrected for ticks collected from echidnas (*Tachyglossus aculeatus*) along the eastern coast of Queensland, Australia (Andrews, Beveridge, Bull, Chilton, Dixon & Petney, 2006). Therefore, in order to verify the identification of *Bothriocroton* ticks from echidnas maintained in the US National Tick Collection (USNTC), we reexamined all our *Bothriocroton* holdings and include a synoptic list.

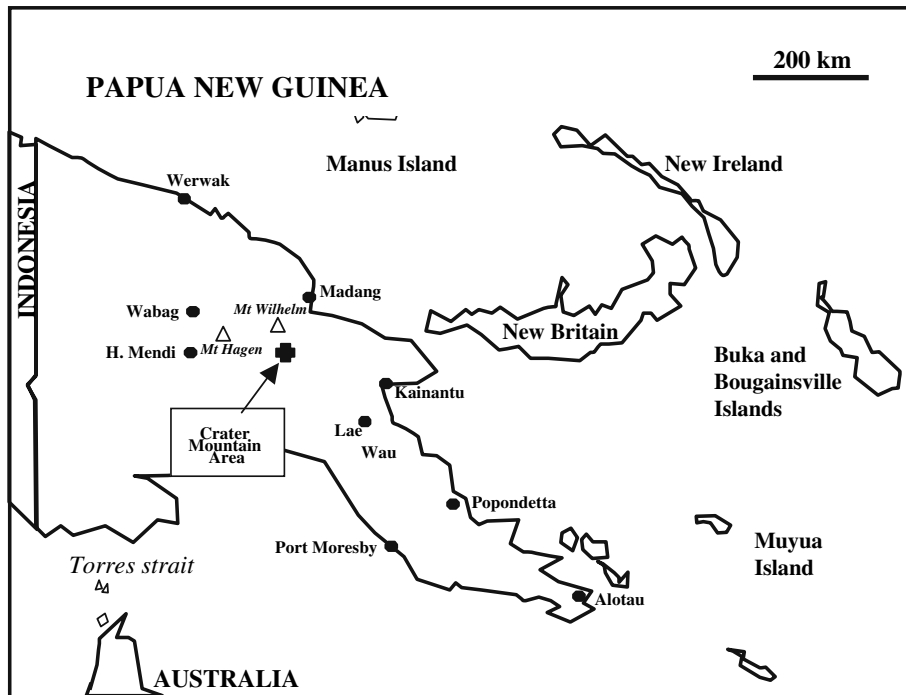
## Materials and methods

### *Preparation of specimens for morphological examinations*

All measurements (8 males, 5 females and 2 nymphs) in the following descriptions are in micrometres and given as the range is followed by the mean in parentheses. Specimens were prepared for scanning electron microscopy using the method of Corwin, Clifford & Keirans (1979).

### *Material studied*

RML numbers refer to USNTC accession numbers. All fresh samples were collected from *Zaglossus bruijni* in Papua New Guinea (Fig. 1). Eight males and 1 nymph (RML123103) were collected in Chimbu Province, north of Haia. Additional specimens, all collected in the Crater Mountain Wildlife Management Area in Eastern Highlands Province, included: 1 female (RML123610); 2 males, 7 females and 1 nymph (RML123611); 2 females (RML123612); 2 females



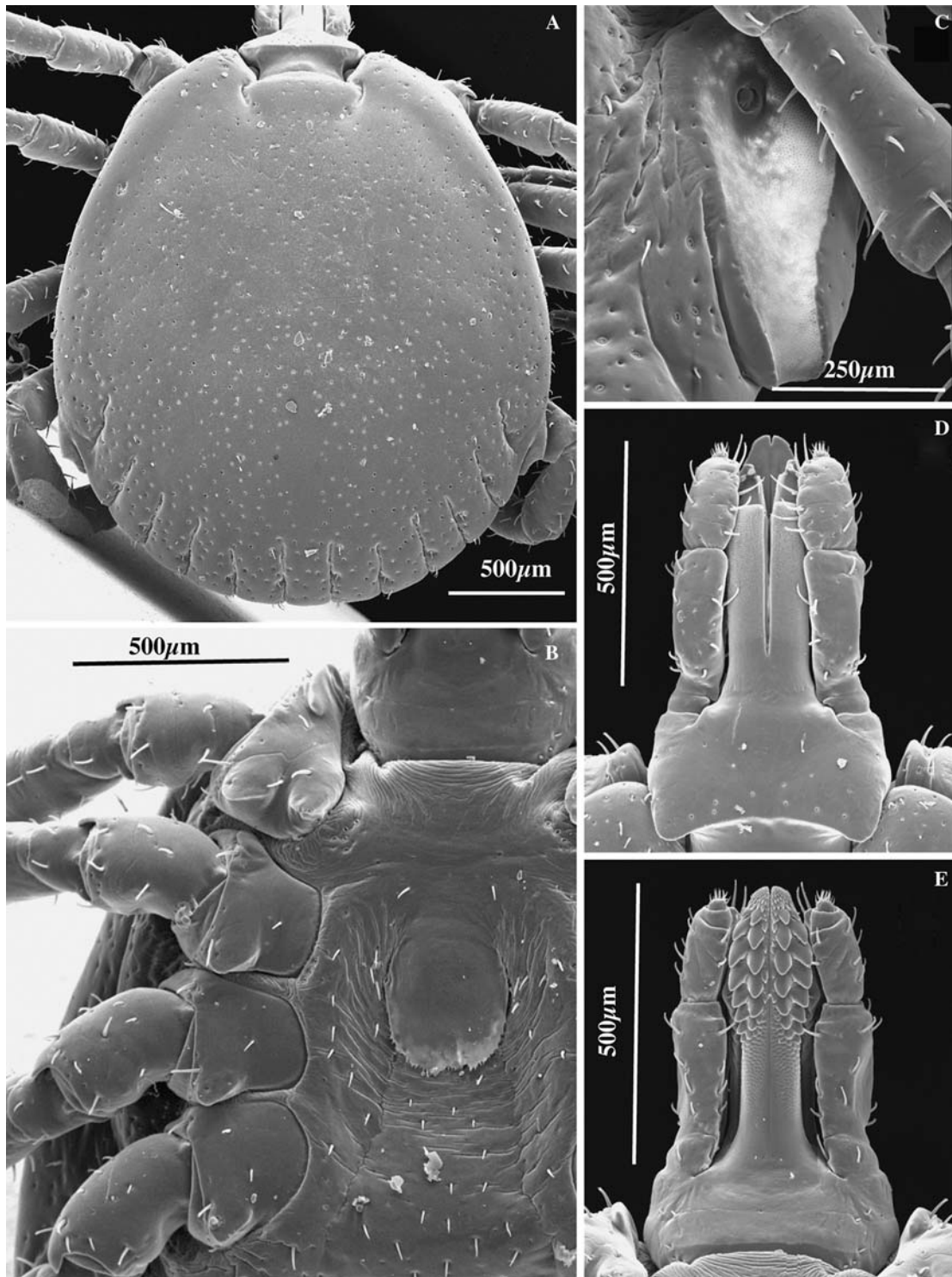
**Fig. 1** Geographical map of Papua New Guinea showing the Crater Mountain Area (cross) where the *Bothriocroton oudemansi* specimens were collected. Black circles correspond to locality and white triangles to mountains

(RML123613); and 2 males and 7 females (RML123614). The male lectotype and 13 male paralectotypes, designated in 1982 by Dias (1993), of Neumann's *Aponomma oudemansi*, were borrowed from the ZMAM for comparison with our specimens. The females described by Schulze in 1936 are deposited in the USNTC (RML49311). These and all other USNTC collections re-examined in this study and their associated collection data are listed in Table 1.

#### Molecular analysis

DNA was extracted using DNAeasy tissue kits (Qiagen, Valencia, CA) and a previously described modified protocol, which is particularly effective when working with alcohol-preserved, blood-fed arthropods (Beati & Keirans, 2001; Beati, Cáceres, Galati, Lee & Munstermann, 2004). A portion of the 18S rDNA gene was amplified and sequenced from a nymph (RML123611) in order to establish whether this tick is a *Bothriocroton* or an *Amblyomma*. The 18SrRNA gene fragment was amplified using the primer pair NS1 and NS8, and sequenced with primers NS1, NS8, NS4 and NS 58.1 (Black,

Klompen & Keirans, 1997). The 18S rDNA gene sequence was manually aligned with homologous sequences from Genbank by using McClade4 (v. 4.07) (Maddison & Maddison, 2000). Phylogenetic reconstructions were inferred by using PAUP (v. 4.0b10) with Maximum Parsimony (MP) and maximum likelihood (ML) (Swofford, 2000). Sequence divergence values were calculated based on the model evaluated by maximum likelihood. Node support was assessed by bootstrap analysis (MP with 1,000 replicates). The Genbank accession numbers of all 18S rDNA sequences included in the analysis are listed in Fig. 5 with the tick names. Fragments of the 12S rDNA and of the 28S rDNA genes of one male (RML123614), one female (RML123612) and one nymph (RML123611) of the New Guinea ticks, one *B. glebopalma* (RML121855), one *B. undatum* (RML83244) and one *B. concolor* (RML100403) were amplified and sequenced by using primers TIB and T2A (Beati & Keirans, 2001) and 28SV and 28SX, respectively (Hillis & Dixon, 1991). Other sequences used for comparisons are 12S rDNA fragments of *B. hydrosauri* (U95860) and *B. glebopalma* (U95858) from Genbank.



**Fig. 2** *Bothriocroton oudemansi* (male, RML123103): A. Scutum; B. Coxae I-IV, ventral view; C. Spiracular plate; D. Capitulum, dorsal view; E. Capitulum, ventral view. Scale-bars: A,B,D,E, 500 μm; C, 250 μm

**Table 1** Taxonomic status and collection data for *Bothriocroton* spp. examined during this study

RMLNo.	Location	Species	Host family	Host genus	Origin	Latitude	Longitude
39530	USNTC	<i>B. auruginans</i>	Vombatidae	<i>Vombatus hirsutus</i>	AUS, NSW	34°32'49"S	150°22'20"E
112187	BMNH	<i>B. auruginans</i>	Vombatidae	<i>V. ursinus</i> or <i>Lasirhinus</i> sp.	AUS, ?	n/a	n/a
112561	BMNH	<i>B. auruginans</i>	Vombatidae	<i>Vombatus ursinus</i>	AUS, NSW	n/a	n/a
121302	USNTC	<i>B. auruginans</i>	Vombatidae	<i>Vombatus ursinus</i>	AUS, TAS	41°16'31"S	144°44'27"E
31463	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	USA, imported	n/a	n/a
33564	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, VIC	38°23'30"S	143°02'31"E
37715	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, NSW	33°29'44"S	151°19'27"E
37721	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, ?	n/a	n/a
37723	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, ?	n/a	n/a
37727	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, NSW	33°25'30"S	151°20'38"E
49311	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	Unknown	n/a	n/a
83241	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus</i>	AUS, NSW	32°01'13"S	146°20'10"E
83242	USNTC	<i>B. concolor</i>	Unknown	Unknown	AUS, NSW	32°01'13"S	146°20'10"E
100402	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, NSW	34°45'19"S	149°43'06"E
100403	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, QLD	28°11'50"S	151°55'49"E
112558	BMNH	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, ?	n/a	n/a
121300	USNTC	<i>B. concolor</i>	Peramelidae	<i>Perameles gunnii</i>	AUS, TAS	41°13'57"S	146°52'37"E
21541	MISSING	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus</i> sp.	AUS, VIC	38°19'55"S	145°00'35"E
37716	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, NSW	33°25'30"S	151°20'38"E
37720	USNTC	<i>B. concolor</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	AUS, NSW	33°25'30"S	151°20'38"E
46021	BMNH	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	17°54'00"S	137°53'00"E
46022	NTM	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	15°51'00"S	129°03'00"E
46023	NTM, USNTC	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	13°29'00"S	132°54'00"E
46024	NTM, USNTC	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	16°05'00"S	135°22'00"E
46025	NTM	<i>B. glebopalma</i> (paratypes)	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	15°45'00"S	129°05'00"E
46028	NTM	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	17°56'00"S	137°01'00"E
118531	USNTC	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	15°23'00"S	124°21'00"E
120440	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	n/a	n/a
120443	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	15°23'00"S	125°19'00"E
120447	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	n/a	n/a
120448	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	15°19'00"S	125°35'00"E
120452	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	14°18'00"S	126°38'00"E
120453	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	12°19'00"S	133°03'00"E
120454	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	15°32'00"S	125°14'00"E
120456	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	16°11'00"S	123°37'00"E
120457	BMNH	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, WA	16°15'00"S	123°31'00"E
120482	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glauerti</i>	AUS, WA	14°15'00"S	126°40'00"E
120484	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glauerti</i>	AUS, WA	15°07'00"S	125°33'00"E
120485	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glauerti</i>	AUS, WA	14°35'00"S	125°45'00"E
120486	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glauerti</i>	AUS, WA	14°44'00"S	126°56'00"E
120487	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glauerti</i>	AUS, WA	15°20'00"S	124°56'00"E
120488	WAMU	<i>B. glebopalma</i>	Varanidae	<i>Varanus glauerti</i>	AUS, WA	15°22'00"S	124°21'00"E

**Table 1** continued

RMLNo.	Location	Species	Host family	Host genus	Origin	Latitude	Longitude
121855	USNTC	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	12°51'00"S	132°52'00"E
121856	USNTC	<i>B. glebopalma</i>	Varanidae	<i>Varanus glebopalma</i>	AUS, NT	12°51'00"S	132°52'00"E
20946	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Trachydosaurus</i> sp.	AUS, SA	36°51'51"S	139°50'02"E
21534	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Trachydosaurus rugosus</i>	AUS, VIC	35°05'57"S	142°02'45"E
21540	MISSING	<i>B. hydrosauri</i>	Unknown	Unknown	AUS, VIC	n/a	n/a
25549	USNTC	<i>B. hydrosauri</i>	Agamidae	<i>Physignathus leseuerii</i>	AUS, NSW	33°52'06"S	151°12'31"E
37730	USNTC	<i>B. hydrosauri</i>	Elapidae	<i>Notechis scutatus</i>	AUS, TAS	40°18'00"S	147°52'00"E
37735	USNTC	<i>B. hydrosauri</i>	Elapidae	<i>Notechis scutatus</i>	AUS, TAS	40°18'00"S	147°52'00"E
83236	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua rugosa</i>	AUS, NSW	n/a	n/a
83237	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Trachydosaurus</i>	AUS, SA	34°55'36"S	138°35'57"E
83238	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Trachydosaurus rugosus</i> or <i>Tiliqua nigrolutea</i>	AUS, NSW	n/a	n/a
83239	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua rugosa</i>	AUS, NSW	n/a	n/a
83240	Missing	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua rugosa</i>	AUS, NSW	34°27'30"S	149°29'02"E
102035	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Trachydosaurus rugosus</i>	AUS, SA	36°07'34"S	139°38'51"E
104763	BMNH	<i>B. hydrosauri</i>	Scincidae	<i>Trachydosaurus rugosus</i>	AUS, SA	34°55'36"S	138°35'57"E
105901	BMNH	<i>B. hydrosauri</i>	Varanidae	<i>Varanus gouldi</i>	AUS, ?	n/a	n/a
109256	BMNH	<i>B. hydrosauri</i>	Unknown	Unknown	AUS, SA	n/a	n/a
110681	BMNH	<i>B. hydrosauri</i>	Elapidae	<i>Notechis scutatus</i>	AUS, TAS	n/a	n/a
110686	BMNH	<i>B. hydrosauri</i>	Elapidae	<i>Denisonia superba</i>	AUS, TAS	n/a	n/a
112557	BMNH	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua scincoides</i>	AUS, VIC	38°06'17"S	145°08'19"E
112565	BMNH	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua scincoides</i>	AUS, VIC	38°06'17"S	145°08'19"E
121295	USNTC	<i>B. hydrosauri</i>	Elapidae	<i>Austrelaps superba</i>	AUS, TAS	41°26'00"S	147°08'39"E
121347	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua nigrolutea</i>	AUS, TAS	n/a	n/a
121348	USNTC	<i>B. hydrosauri</i>	Elapidae	<i>Notechis ater</i>	AUS, TAS	41°48'21"S	147°22'51"E
121349	USNTC	<i>B. hydrosauri</i>	Muridae	<i>Mus musculus</i>	AUS, TAS	41°04'21"S	145°56'48"E
121591	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua rugosa</i>	AUS, SA	37°21'23"S	140°42'21"E
123724	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua nigrolutea</i>	AUS, ?	n/a	n/a
123726	USNTC	<i>B. hydrosauri</i>	Scincidae	<i>Tiliqua nigrolutea</i>	AUS, ?	n/a	n/a
88313	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bartoni</i>	PNG, SHP	6°19'52"S	144°08'49"E
111755	USNTC, BMNH	<i>B. oudemansi</i>	Tachyglossidae	<i>Tachyglossus aculeatus</i>	INDN, PP	2°56'24"S	132°17'53"E
123103	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bruijini</i>	PNG, CP	6°42'00"S	145°06'00"E
123610	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bruijini</i>	PNG, EHP	6°50'00"S	145°00'00"E
123611	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bruijini</i>	PNG, EHP	6°50'00"S	145°00'00"E
123612	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bruijini</i>	PNG, EHP	6°50'00"S	145°00'00"E
123613	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bruijini</i>	PNG, EHP	6°50'00"S	145°00'00"E
123614	USNTC	<i>B. oudemansi</i>	Tachyglossidae	<i>Zaglossus bruijini</i>	PNG, EHP	6°50'00"S	145°00'00"E
31923	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus salvator</i>	AUS, QLD	n/a	n/a
37718	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, NSW	33°32'43"S	151°18'25"E
83243	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus</i> sp.	AUS, QLD	20°28'05"S	148°28'09"E
83244	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus</i> sp.	AUS, QLD	n/a	n/a
105849	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus gouldi</i>	AUS, ?	n/a	n/a
109251	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus</i> sp.	Unknown	n/a	n/a

**Table 1** continued

RMLNo.	Location	Species	Host family	Host genus	Origin	Latitude	Longitude
110779	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus</i> sp.	AUS, NSW	31°29'31"S	145°51'09"E
110780	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, NSW	32°14'49"S	148°36'07"E
110781	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, NSW	32°14'49"S	148°36'07"E
110782	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, NSW	32°14'49"S	148°36'07"E
111051	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, QLD	n/a	n/a
111450	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, QLD	25°22'02"S	151°07'33"E
111880	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus</i> sp.	AUS, VIC	n/a	n/a
111881	BMNH	<i>B. undatum</i>	Varanidae	<i>Varanus</i> sp.	AUS, NSW	30°59'28"S	150°15'48"E
123722	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, NSW	32°01'15"S	151°58'01"E
123723	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, NSW	32°01'15"S	151°58'01"E
123725	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, ?	n/a	n/a
123727	USNTC	<i>B. undatum</i>	Varanidae	<i>Varanus varius</i>	AUS, ?	n/a	n/a

Origin: AUS, Australia; INDN, Indonesia; PNG, Papua New Guinea; USA, United States of America; NSW, New South Wales; QLD, Queensland; TAS, Tasmania; VIC, Victoria; NT, Northern Territory; WA, Western Australia; SA, South Australia; SHP, Southern Highlands Province; EHP, Eastern Highlands Province; CP, Chimbu Province; PP, Papua Province

Museums: Natural History Museum (London, UK), BMNH; Northern Territory Museum (Darwin, Australia), NTM; WAMU, Western Australian Museum (Perth, Australia); USNTC, US National Tick Collection (Statesboro, USA)

### ***Bothriocroton oudemansi* (Neumann, 1910)**

#### **n. comb.**

Syns *Aponomma oudemansi* Neumann, 1910; *Amblyomma oudemansi* (Neumann, 1910) Horak, Camicas & Keirans, 2002

#### Comments on synonymy

For lack of conclusive proof that *Ixodes acanthoglossi* (Lucas, 1878) is the same tick species, and in agreement with Camicas et al. (1998), we will not include this name in this synonymy and consider it a *nomen dubium*. *Aponomma concolor* was not included in the synonymy list because Kaufmann (1972) synonymised *A. oudemansi* and *A. concolor* while looking at what Schulze thought were female *A. oudemansi* (1936), but were in fact female *B. concolor*. Morphological comparisons of our tick specimens with the lecto- and paralectotypes from the ZMAM confirm that our male ticks are identical to Neumann's (1910) *A. oudemansi* (Fig. 2A-E). Schulze's (1936) *A. oudemansi* females (RML49311) were all characterised by having ventral finger-like processes on palpal articles II, round and deep porose areas located close to the posterior margin of the basis capituli, and alloscutal punctation typical of

*B. concolor* (see Roberts, 1970; Kaufmann, 1972).

These features were not found in our females (Fig. 3A-F), which also differed from all known former Australasian *Aponomma*. While re-examining all *Bothriocroton* holding of the USNTC, we discovered an additional collection (RML88313) of ticks (males and nymphs) from the eastern long-beaked echidna *Zaglossus bartoni* (Thomas), collected in the Indonesian Province of Papua, which were identical to our samples from Papua New Guinea (Table 1).

#### Descriptions of the female and the nymph and redescription of the male (Figs. 2–4)

##### *Male* (Fig. 2A-E)

[Measurements made from 8 males.] *Body*. Small, pale yellow, subcircular, slightly longer than wide. Length from scapular apices to posterior body margin 2,342–2,718 (2,513), breadth 2,153–2,370 (2,243). *Capitulum* (Fig. 2C, E). Basis capituli 236–330 (280) long, 523–604 (568) broad, with rounded lateral margins; cornua present, 42–66 (53) long. Palps elongate, 595–772 (679) long, 177–230 (209) broad; average length of palpal article I 89, II 337 and III 259. Length of the spatulate hypostome 507 with 2 ½ : 2 ½ dentition; length of toothed portion 244–338

(294); apex of hypostome slightly narrower with numerous fine denticles. *Conscutum* (Fig. 2A). Inornate, with mid-gut typically visible through cuticle in fed specimens (Neumann, 1910); eyes absent. Regularly distributed small punctations, slightly deeper along margins and on festoons, giving scutum smooth overall appearance. Cervical grooves absent; marginal grooves barely distinguishable as shallow depressions. Venter with uniformly distributed punctations each with a fine seta; genital opening at level of coxae II and III (Fig. 2B); anal groove present, posterior to anus, broadly U-shaped. Large spiracular plates (Fig. 2C) anterior to first festoon, extruding from lateral body margin, 532–655 (591) long, 232–401 (319) broad. *Legs*. Coxa I (Fig. 2B) with 2 equally short rounded spurs; all other coxae with single stout, rounded external spur. Tarsus I (not shown) gradually tapered distally, 477–571 (51) long, 175–217 (194) broad; tarsus IV (not shown) with subapical hump, 469–590 (527) long, 140–173 (159) broad.

#### Female (Fig. 3A–F)

[Measurement from 5 partly engorged specimens.] *Body*. Length from apices of scapulae to posterior body margin 2,818–3,512 (3,097), breadth 2,473–3,076 (2,718), small, pale yellow, subcircular; gut visible through cuticle in fed specimens. Large spiracular plates (Fig. 3D) extruding from body external margins, 544–612 (571) long, 403–607 (531) broad. Genital aperture U-shaped at level of coxae II and III; anal groove present, posterior to anus and broadly U-shaped. Deep alloscutal punctations homogeneously distributed dorsally and ventrally. *Scutum* (Fig. 3A,C). Length 1,417–1,530 (1,435), breadth 1,659–1,737 (1,697). Subtriangular, inornate, covered with fine punctations, slightly coarser along margins and in lateral fields; eyes absent. Cervical grooves very shallow if present at all. *Capitulum* (Fig. 3E,F). Basis capituli 265–501 (399) long, 707–756 (744) broad, trapezoid, with rounded lateral margins; cornua absent. Porose areas well delimited, depressed, pyriform, slightly divergent anteriorly, 93–143 (114) in diameter; interporose distance 52–110 (93). Palps elongate, 910–959 (933) long, 190–264 (226) broad; length of palpal segment I 117–138 (128), II 448–585 (503), and III 258–287 (270). Hypostomal dentition as in males, but hypostome anteriorly more rounded, with fine apical

denticles. Hypostome 655–721 (693) long, length of toothed portion 360–421 (386). *Legs*. Coxa I (Fig. 3B) with 2 short, rounded spurs; all other coxae with single external rounded protuberance. Tarsi I (not shown) 741–892 (824) long, 194–230 (217) broad; Tarsi IV (not shown) 690–872 (790) long, 163–204 (188) broad.

#### Nymph (Fig. 4A–E)

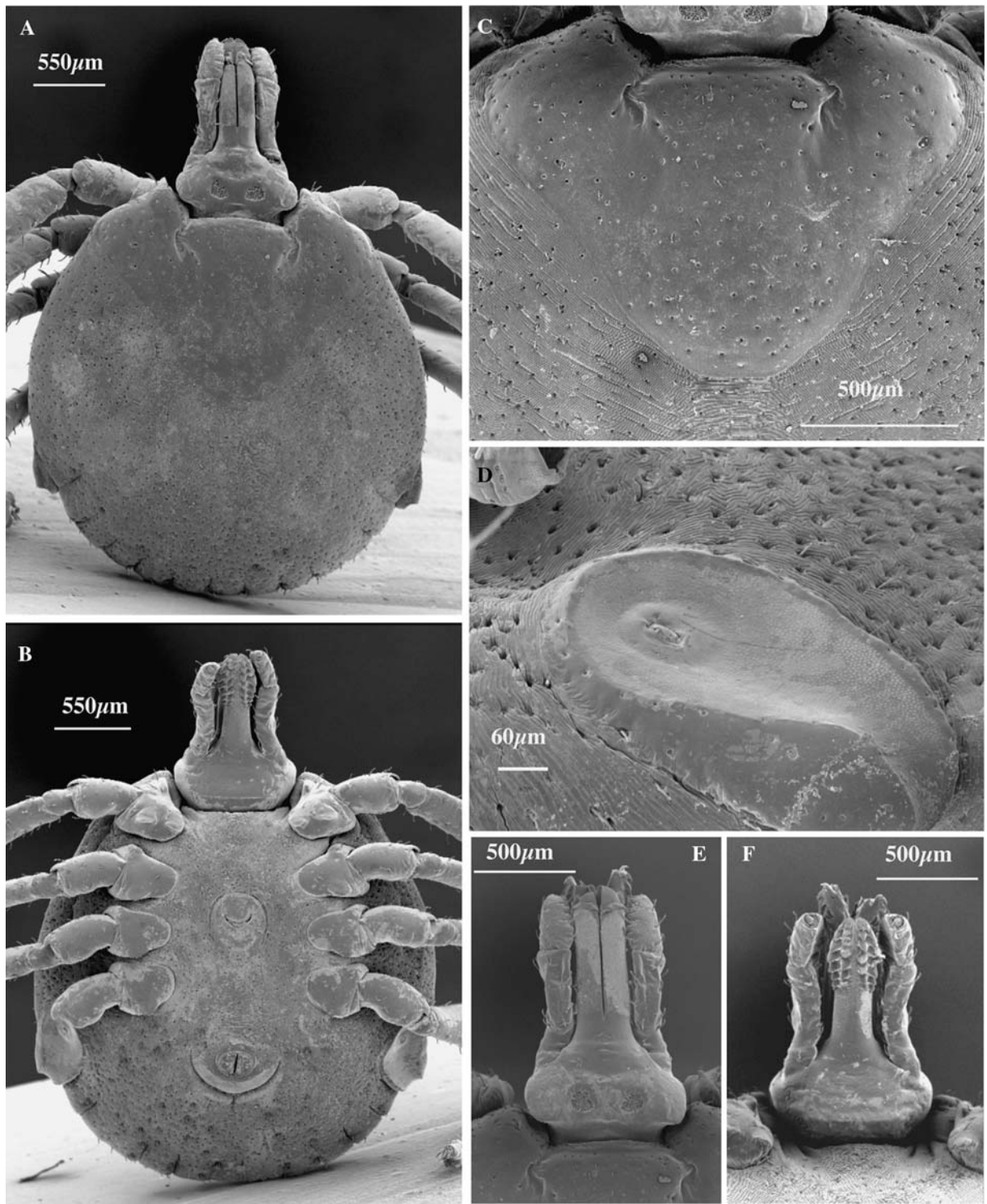
[Measurement made from 2 partly engorged specimens.] *Body*. Length from apices of scapulae to posterior body margin 1,616–2,403 (2,010), breadth 1,390–1,781 (1,586), pale yellow, subcircular, with uniform punctations; gut visible through cuticle in fed specimens. Spiracular plates extruding from lateral body margins, 274 long, 181–208 (195) broad (Fig. 4C). *Scutum* (Fig. 4E) broader – 785–915 (850) than long – 598–661 (630), subtriangular, with few scattered punctations. Cervical grooves short, shallow, slightly chagrined; eyes absent. *Capitulum* (Fig. 4A,B). Basis capituli subtriangular, laterally rounded, length 126–128 (127), breadth 332–360 (346); cornua absent. Palps 357–379 (368) long, 97–111 (104) broad; length of article I 37–45 (41), II 123–185 (154) and III 120–123 (122). Hypostome 315–326 (321) long; length of toothed portion 164–175 (170); hypostomal dentition 2/2. *Legs*. Coxa I (Fig. 4D) with 2 short rounded spurs; coxae II–IV with single short rounded external spurs. Tarsi I (not shown) 307–375 (341) long, 117–130 (124) broad; tarsi IV (not shown) 261–375 (318) long, 83–97 (90) broad.

#### Species relationships

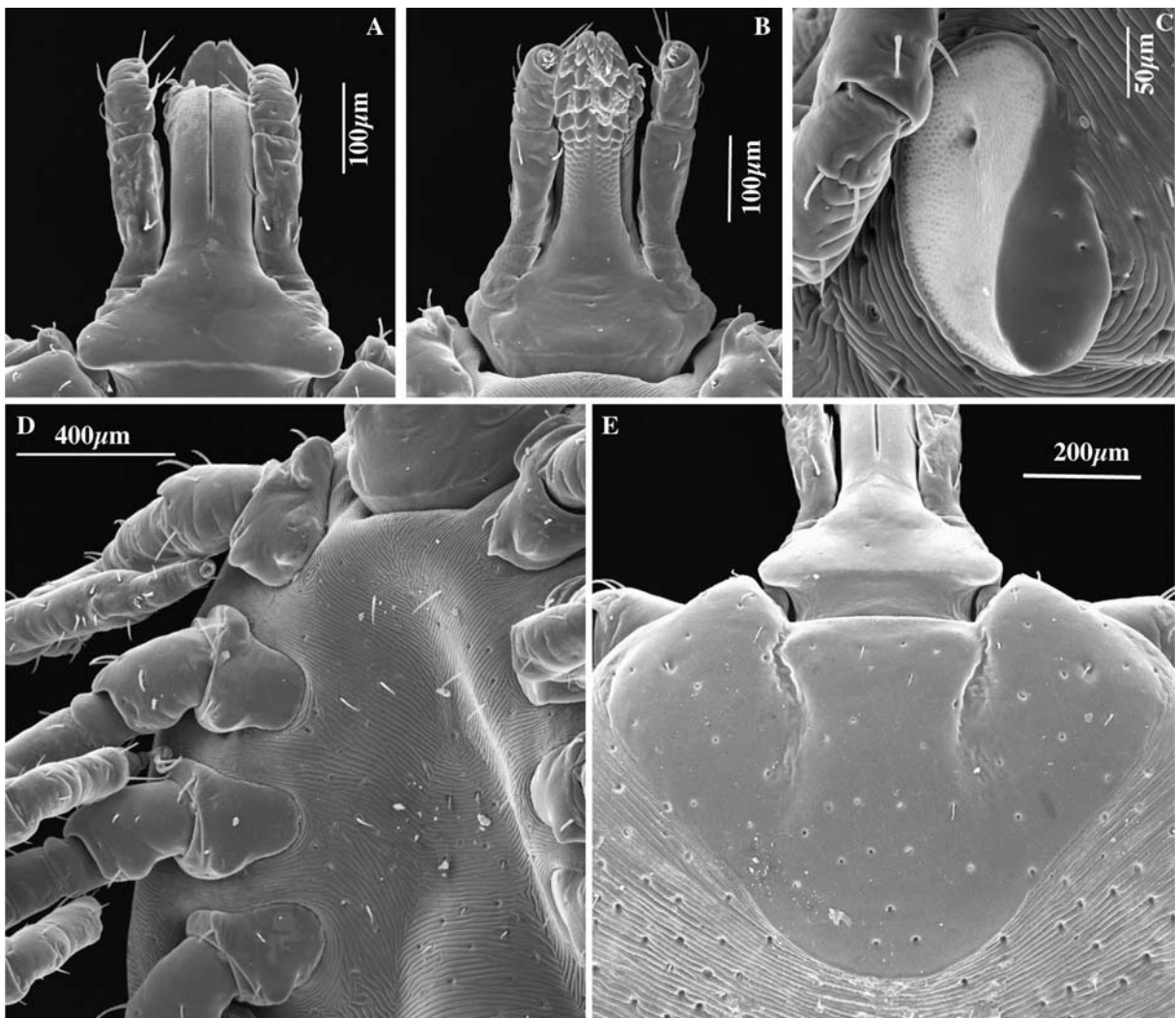
##### Molecular analyses

The 18S rDNA sequence alignment of the 29 selected taxa included 1,719 characters, 142 of which were parsimony informative. The MP heuristic search found 80 trees with identical length (342 steps). The topology of their strict consensus tree and the ML trees were totally congruent with each other and, therefore, only the MP reconstruction is shown in Fig. 5. The inferred tree shows that the New Guinea echidna tick belongs to *Bothriocroton*. Among *Bothriocroton* species, *B. concolor* constitutes the basal lineage and *B. oudemansi* clusters with *B. hydrosauri*, *B. undatum* and *B. glebopalma*. For comparison, 18S





**Fig. 3** *Bothriocroton oudemansi* (female, RML123614; two specimens): A. Scutum; B. Coxae I-IV, ventral view; C. Scutum; D. Spiracular plate; E. Capitulum, dorsal view; F. Capitulum. Scale-bars: A,B, 550  $\mu\text{m}$ ; C,E,F, 500  $\mu\text{m}$ ; D, 60  $\mu\text{m}$

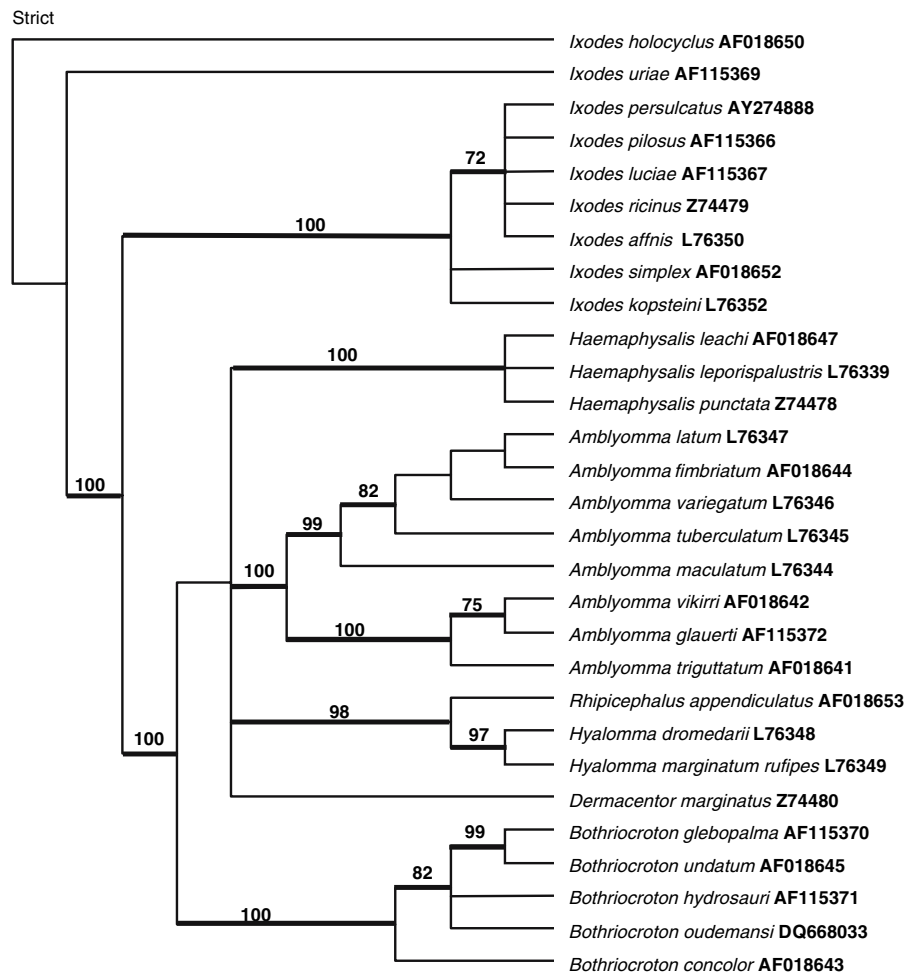


**Fig. 4** *Bothriocroton oudemansi* (nymph, RML123103). A. Capitulum, dorsal view; B. Capitulum, ventral view; C. Spiracular plate; D. Coxae I-IV, ventral view; E. Scutum. Scale-bars: A,B, 100 µm; C, 50 µm; D, 400 µm; E, 200 µm

rDNA sequence divergence between *Bothriocroton* species varied from 0.3 to 1.9%, whereas divergence of *Bothriocroton* taxa from the other considered genera varies from 5.7 to 8.7% (*Ixodes*), 2.5 to 4.4% (*Haemaphysalis*) and 3.6 to 6.0% (*Amblyomma*) (Table 2).

The 349 bp fragment of the small-subunit ribosomal mitochondrial gene sequences of the female – RML123612 (GenBank accession number: DQ668031) and the nymph – RML123611 (DQ668030) were identical and differed from the male – RML123614 sequence (DQ668032) by only 2 bp (0.3% sequence divergence). The *B. oudemansi*

sequences differed from homologous sequences of *B. hydrosauri* (U95860), *B. glebopalma* (U95858 and EF173724), *B. undatum* (EF173726) and *B. concolor* (EF173725) by 11.9–16.9%. The 12S rDNA sequence of *B. glebopalma* (RML121855; EF173724) differed from the Genbank sequence (U95858) by 0.3%. The 28S rDNA sequences (EF064255, EF064256, and EF064257) of the female, male and nymph *B. oudemansi* were identical and differed from the homologous fragment of *B. concolor* (EF173727) by 0.7%, of *B. undatum* (EF173729) by 0.7% and of *B. glebopalma* (EF173728) by 1.44%. Comparing the 12S and 28S rDNA sequences of the specimens from



**Fig. 5** Strict consensus maximum parsimony tree based on the alignment of 18S rDNA partial sequences of 29 tick species. The heuristic search found 80 best trees: length = 342; CI = 0.708; RI = 0.883; RC = 0.625 and HI = 0.292. Bootstrap values are based on 1,000 replica and are only shown above supported branches (>78%)

New Guinea with the available homologous *Bothriocroton* sequences confirms that the New Guinea male, female and nymph all belong to a single species. *Bothriocroton* currently contains five species (Roberts, 1953, 1964, 1970; Keirans et al., 1994; Klompen et al., 2002). Our molecular results show that *Amblyomma oudemansi* is definitively not an *Amblyomma* and should be assigned to *Bothriocroton* with all the endemic Australian former *Aponomma* species.

#### Morphological comparisons

*B. oudemansi* can be distinguished from other *Bothriocroton* species by the presence of its unusually extruding and large spiracular plates and by its

geographical distribution. *B. oudemansi* is not an ornamented tick and can, therefore, be readily differentiated from both *B. undatum* and *B. glebopalma* (see Neumann, 1899; Roberts, 1970; Keirans et al., 1994). Both sexes of *B. glebopalma* are much smaller than *B. oudemansi* and are covered with deep punctations, each with stout short setae, which give them an unmistakable appearance. Their hypostomal dentition is 2/2 and all coxae bear a single spur. Furthermore, *B. glebopalma* is associated with varanid lizards in northwestern Australia and not with echidnas. *B. undatum* is a reddish-brown tick, which is also found exclusively on reptiles. In both sexes, this tick is characterised by homogeneously distributed coarse punctations, which contrast with the smooth overall

**Table 2** Pairwise distances (%) between the 18S rDNA sequences included in our phylogenetic analysis. The ML pairwise distances were calculated based on the substitution model estimated from the MP tree with the best ML score by PAUP

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28								
1 <i>B. glebopalma</i>																																				
2 <i>B. hydrosauri</i>	1.5																																			
3 <i>B. oudemansi</i>	1.6	0.3																																		
4 <i>B. concolor</i>	1.9	0.6	0.6																																	
5 <i>B. undatum</i>	1.7	1.4	1.5	1.8																																
6 <i>I. holocycclus</i> Neumann, 1899	7.1	6.2	6.0	6.1	7.3																															
7 <i>I. uriae</i> White, 1852	6.8	5.8	5.7	5.7	7.0	0.9																														
8 <i>I. persulcatus</i> Schulze, 1930	7.0	6.1	6.2	6.0	7.2	4.4	3.9																													
9 <i>I. pilosus</i> Koch, 1844	7.3	6.2	6.3	6.1	7.4	4.7	3.9	0.6																												
10 <i>I. luciae</i> Sénevet, 1940	6.9	6.1	6.2	6.0	7.0	4.5	3.9	0.5	0.8																											
11 <i>I. rictinus</i> (Linnaeus, 1758)	6.9	6.1	6.2	6.0	7.0	4.4	3.7	0.2	0.5	0.4																										
12 <i>I. affinis</i> Neumann, 1899	7.0	6.0	6.1	5.9	7.1	4.5	3.8	0.1	0.5	0.5	0.1																									
13 <i>I. simplex</i> Neumann, 1906	8.1	7.1	7.2	6.8	7.7	5.5	4.7	1.6	1.5	1.4	1.5																									
14 <i>I. kopsteini</i> Oudemans, 1926	8.7	7.3	7.4	7.1	8.3	6.5	5.5	2.7	2.9	2.6	2.8	2.7	3.0																							
15 <i>Ha. leachi</i> (Audouin, 1826)	4.1	2.8	2.7	2.5	3.8	5.4	4.7	6.4	6.4	6.4	6.3	6.9	7.3																							
16 <i>Ha. leporispalustris</i> (Packard, 1869)	4.3	2.8	2.7	2.6	4.0	5.7	4.9	6.8	6.7	6.9	6.8	7.4	7.7	0.4																						
17 <i>Ha. punctata</i> Canestrini & Fanzago, 1878	4.4	2.9	2.8	2.6	4.1	5.8	5.0	6.8	6.7	6.8	6.8	6.7	7.3	7.6	0.2	0.3																				
18 <i>A. latum</i> Koch, 1844	5.7	4.3	4.2	4.1	5.3	7.4	6.9	7.8	7.6	8.0	7.9	7.8	8.4	9.0	3.5	3.6	3.6																			
19 <i>A. fimbriatum</i> Koch, 1844	6.0	4.6	4.4	4.4	5.5	7.5	6.7	8.4	8.2	8.5	8.4	8.2	8.7	9.1	3.3	3.6	3.5	1.4																		
20 <i>A. variegatum</i> (Fabricius, 1794)	5.6	4.0	3.9	3.8	4.9	7.3	6.5	7.5	7.3	7.6	7.5	7.4	7.9	8.2	2.5	2.8	2.7	1.0	0.6																	
21 <i>A. tuberculatum</i> Marx, 1894	5.7	4.1	4.0	3.9	5.0	7.1	6.4	7.3	7.1	7.4	7.3	7.2	7.8	8.0	2.6	2.9	2.8	0.9	0.7	0.2																
22 <i>A. maculatum</i> Koch, 1844	5.3	3.8	3.7	3.6	4.7	7.2	6.4	7.1	6.9	7.2	7.1	7.0	7.5	7.8	2.5	2.8	2.7	1.3	1.0	0.5	0.4															
23 <i>A. vikirri</i> Keirans, Bull, & Duffield, 1996	5.5	4.0	3.9	3.9	4.8	6.6	6.1	7.8	7.7	7.9	7.8	7.7	8.0	8.7	2.4	2.7	2.6	2.5	2.0	1.5	1.5	1.7														
24 <i>A. glauerti</i> Keirans, King, & Sharrad, 1994	5.6	4.1	3.9	3.9	4.8	6.7	6.2	7.9	7.8	8.0	7.9	7.7	8.1	8.7	2.5	2.7	2.7	2.5	1.9	1.5	1.5	1.7	0.1													
25 <i>A. t. triguttatum</i> Koch, 1844	5.5	4.0	3.8	3.9	4.8	6.9	6.4	7.9	7.7	7.8	7.9	7.7	8.3	8.6	2.8	3.0	3.0	2.5	2.1	1.5	1.5	1.7	0.3	0.4												
26 <i>R. appendiculatus</i> Neumann, 1901	4.2	2.7	2.6	2.5	3.6	5.4	4.6	6.3	6.5	6.6	6.3	6.2	7.0	6.8	1.1	1.3	1.1	3.2	2.9	2.2	2.2	2.0	2.1	2.2	2.5											

Table 2 continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
27 <i>D. marginatus</i> (Sulzer, 1776)	4.0	2.5	2.4	2.3	3.4	5.4	4.7	6.1	6.0	6.1	6.1	6.0	6.8	6.8	1.1	1.3	1.1	2.8	2.7	2.0	2.1	1.8	2.1	2.2	2.3	0.5				
28 <i>Hy. dromedary</i> Koch, 1844	4.5	3.0	2.9	2.6	3.9	5.7	4.9	6.6	6.8	6.9	6.6	6.5	7.2	7.2	1.3	1.6	1.4	3.1	2.9	2.1	2.2	2.0	2.3	2.4	2.6	0.2	0.7			
29 <i>Hy. marginatum rufipes</i> Koch, 1844	4.3	2.8	2.7	2.5	3.7	5.7	4.9	6.6	6.8	6.9	6.6	6.5	7.2	7.3	1.3	1.6	1.4	3.3	3.0	2.3	2.4	2.1	2.5	2.6	2.8	0.4	0.8	0.1		

A, *Amblyomma*; B, *Bothriocroton*; Ha, *Haemaphysalis*; Hy, *Hyalomma*; I, *Ixodes*; R, *Rhipicephalus*; D, *Dermacentor*

appearance of *B. oudemansi*. Male *B. undatum* also present distinct non-continuous lateral grooves marked by confluent deep punctations (Neumann, 1899; Roberts, 1970). Among the echidna-associated *Bothriocroton* ticks, *B. oudemansi* can easily be differentiated from *B. concolor* and *B. hydrosauri* [or *Aponomma tachyglossi*, according to Andrews et al. (2006)]. *B. hydrosauri* is a dark brown tick, the males of which are larger than *B. oudemansi* and are characterised by a heavily punctated conscutum with continuous lateral grooves. The scutum of the female *B. hydrosauri* is dark brown, with a clearer median area, sometimes with a pale spot in the posterior angle, and with numerous punctations which are coarser laterally; the alloscutum is covered with deep punctations each with stout whitish setae. Porose areas are large and oval, almost contiguous with the posterior margin of the basis capituli (Roberts, 1970). *A. tachyglossi* is distinguished from *B. hydrosauri* only by the presence of larger punctated areas contiguous to the lateral grooves in males and by smaller porose areas in females (Andrews et al., 2006). None of these characters should constitute a problem when identifying *B. oudemansi*. Both sexes of *B. concolor* have prominent ventral finger-like processes on palpal article II, and females have small round and deep-set porose areas located close to the posterior margin of the basis capituli. The female scutum is punctate and has deep cervical grooves. Males are characterised by having a continuous lateral groove on a heavily punctate scutum (Schulze, 1936, 1941; Roberts, 1970). *B. auruginans* is generally larger than *B. oudemansi* and is a tick strictly associated with wombats. Males are oval in shape and narrower anteriorly, with a hypostomal dentition of 2/2, stout palps with palpal article II one third as wide as long and about twice as long as article III, and lateral grooves ending at the anterior margin of the external festoon. The female scutum is almost rugose, and the porose areas are very large and encroach on the posterior margin of the basis capituli (Schulze, 1936; Roberts, 1970).

#### Host, distribution and ecology

*B. oudemansi* has been collected from two of the long-beaked echidna species known to occur in New Guinea, *Zaglossus bruijnii* and *Z. bartoni* (some

consider *Z. bartoni* to be a synonym of *Z. bruijini*), but Groves (2005) treated these taxa as distinct species. These monotremes are largely insectivorous and, unlike their close relative *T. aculeatus*, which mainly feeds on termites and ants, they prefer to eat insect larvae and earthworms. *Z. bruijini* is usually found in the highland forests of New Guinea from 1,300–4,000 m, whereas *Z. bartoni* is known to occur along the central cordillera of New Guinea from its Indonesian region to the Huon Peninsula in Papua New Guinea (Flannery & Groves, 1998; Musser, 2003). Because long-beaked echidnas are endangered species, *B. oudemansi* should, therefore, also be included in endangered tick species lists (see Durden & Keirans, 1996).

## Discussion

Morphological characters typical, if not unique, for *Bothriocroton* had been listed by Kaufmann (1972), who stated: “conceivably, the indigenous Australian species and the ‘primitive’ species may represent new genera”. None of these morphological features clustering endemic Australian taxa together are, however, synapomorphic for Australian taxa and can also be found in some species of *Amblyomma*. As larval specimens of *B. oudemansi* were not available, a molecular phylogenetic analysis of its relationships with other former *Aponomma* species appeared to be the easiest way of establishing its taxonomic status. All molecular data confirm that this tick is in fact a *Bothriocroton* and allow us to determine with confidence that adult and nymphal stages in our recent collection all belong to the same species. The female specimens were, however, morphologically very different from Schulze’s (1936) description of ‘*A. oudemansi*’. Our direct examination of Schulze’s specimens confirms that they are all *B. concolor*. Schulze did not have access to female *B. concolor*, which was not fully recognised and described until much later (Roberts, 1964, 1970). Nevertheless, his misidentification is certainly at the heart of most of the taxonomic contradictions found in the literature. Kaufmann (1972) did not have access to the types, and probably based his conclusions only on the examination of Schulze’s illustrations of the females, but stated that *Aponomma oudemansi* was a synonym of *A. concolor*. He neglected to compare males of

*B. concolor* to Neumann’s illustrations (1910) and was, therefore, unable to realise how different these two species in fact are. Because both Keirans (1985) and Dias (1993) had access to Neumann’s types (all males), they did not agree with Kaufmann (1972) and considered *A. oudemansi* to be a valid tick species.

In recently published lists of valid tick names (Horak et al., 2002; Barker & Murrell, 2004), this tick was included in *Amblyomma*. The decision of reassigning this tick to *Amblyomma* can be explained by the fact that all ‘non-endemic Australian’ *Aponomma* species had then been transferred to *Amblyomma* (see Klompen et al., 2002). The use of the term ‘non-endemic Australian’ species proved to be an unfortunate choice, because the Australasian ecozone, delimited from the Indomalayan ecozone by Wallace’s line, extends well beyond Australia (Brown & Lomolino, 1998). It also includes the island of New Guinea, the eastern part of the Indonesian archipelago and several additional Pacific Islands and archipelagos. Australia and New Guinea were contiguous from about 5 million to 8,000 years ago (Pliocene to Pleistocene) across the shallow Sahul continental shelf (now occupied by the Torres Strait) when eustatic sea levels were c.30–200 m lower than at present (Parsons, 1998). Monotremes are endemic species of the Australasian ecozone and occur (as different species) as part of the native fauna in both Australia and New Guinea.

In conclusion, based on our molecular results, *Bothriocroton* now includes six recognised species: *B. auruginans*, *B. concolor*, *B. glebopalma*, *B. hydrosauri*, *B. oudemansi* n. comb. and *B. undatum*. The taxonomic status of *Amblyomma tachyglossi* (see Andrews et al., 2006) as a distinct species from *B. hydrosauri* is not totally convincing, particularly because there does not seem to be any morphological difference between immature stages of the two species. However, if this hypothesis is confirmed in future by molecular data, *A. tachyglossi* will certainly be added to the list of *Bothriocroton* species. This genus is now known to occur in the Australasian ecological zone and is not limited to the Australian continent.

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