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Review of the cave-dwelling species of *Pseudotyrannochthonius* Beier (Arachnida: Pseudoscorpiones: Pseudotyrannochthoniidae) from mainland Australia, with description of two troglobitic species

Danilo Harms^{1,2*} and Mark S Harvey^{1,2,3,4}

¹School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.

²Department of Terrestrial Zoology, Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia.

³Division of Invertebrate Zoology, American Museum of Natural History, 79th Street at Central Park West, New York, NY, 10024–5192, USA.

⁴Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94103–3009, USA.

Abstract

Based on morphology we review the cave-dwelling species of the pseudoscorpion genus *Pseudotyrannochthonius* (family Pseudotyrannochthoniidae) from mainland Australia and provide a brief account of their distribution and ecomorphology. *Pseudotyrannochthonius eberhardi* sp. n. is described from the Stockyard Creek karst in northern New South Wales and *P. jonesi* (Chamberlin 1962) is redescribed and illustrated from the Jenolan karst in Central New South Wales based on females. Both species show morphological features reminiscent of troglomorphism and appear to be short-range endemics that are restricted to their respective karsts. All other species previously recorded from subterranean habitats in mainland Australia are facultative cave dwellers that do not show major morphological adaptations towards life underground.

Key words

cave, Chelonethi, short-range endemism, taxonomy, troglomorphic.

INTRODUCTION

The Pseudotyrannochthoniidae is a small family of pseudoscorpions with a global distribution that includes five genera: *Allochthonius* Chamberlin, 1929 (14 species), *Afrochthonius* Beier, 1930b (7 species), *Centrochthonius* Beier, 1931 (3 species), *Pseudotyrannochthonius* Beier, 1930a (20 species) and *Selachochthonius* Chamberlin, 1929 (3 species) (Harvey 2011; Hu & Zhang 2011) (Table 1). Species belonging to Pseudotyrannochthoniidae are known from mesic forest systems in Asia, Australia, Chile, Madagascar, North America, South Africa and Sri Lanka (Harvey & Štáhlavský 2009) (Fig. 1). They are generally slender chthonioid pseudoscorpions (1–3 mm long) with prominent chelicerae (Fig. 8) and with trichobothria *ib* and *isb* situated distally near the base of the fixed finger of the pedipalpal hand so that the hand appears to be devoid of trichobothria (Fig. 5a,b,e). This arrangement is unique among extant chthonioid pseudoscorpions (Harvey 1992) but is shared exclusively with the stem-group pseudoscorpion *Dracochela deprehendor* Schawaller *et al.* 1991 from the middle Devonian some 370–380 mya (Schawaller *et al.* 1991; Shear 1991; Judson 2012), perhaps indicating an old ancestry for Pseudotyrannochthoniidae.

Although most species of Pseudotyrannochthoniidae are known from forests in temperate and subtropical biomes, some species are psychrophilic and have been collected from high-altitude regions in the Himalaya, the Japanese Alps and during winter in the cool temperate forests of western North America (Redikorzev 1918; Schuster 1966; Muchmore 1967; Benedict & Malcolm 1970; Schawaller 1991; Sakayori 1999, 2000; Harvey 2011) (Fig. 1, Table 1). The ability to withstand low temperatures and the preference for habitats with constantly high levels of humidity has resulted in diverse karst faunas in Japan, South Africa, South Korea and Tasmania (Lawrence 1935; Morikawa 1954, 1960, 1970; Chamberlin 1962; Dartnall 1970; Eberhard *et al.* 1991; Hong *et al.* 1996).

The most diverse genus in the family, *Pseudotyrannochthonius*, has a bipolar distribution with species occurring in Australia, Chile, eastern Asia and the USA (Fig. 1). In Australia, *Pseudotyrannochthonius* species have been recorded exclusively from mesic forests along the coastlines of eastern and southern Australia, and in cave systems (Beier 1966, 1968, 1969, 1971; Harvey 2011).

The first species to be described was *P. solitarius* (Hoff 1951) from Victoria and placed in its own genus *Tubbichthonius* Hoff, 1951 until Beier (1966) pointed out the similarities between species of *Pseudotyrannochthonius* from Chile and *Tubbichthonius* from Australia ('It is not possible to separate the Chilean and Australian species generically') and synonymised both genera, with *Pseudotyrannochthonius* gaining

*d.harms01@googlemail.com

Table 1 List of Pseudotyranochthoniidae genera, their distributions, number of described species and references

Genus	Distribution	Number of described species and reference
<i>Allochthonius</i> Chamberlin, 1929	Asia (China, Japan, South Korea)	15 species (Ellingsen 1907; Chamberlin 1929; Morikawa 1954, 1956, 1970; Beier 1979; Lee 1982; Sato 1984; Schawaller 1995; Sakayori 1999, 2000, 2002)
<i>Afrochthonius</i> Beier, 1930b	Madagascar, Africa (Lesotho, South Africa; Swaziland), Sri Lanka	7 species (Beier 1930b, 1931, 1955, 1958, 1973; Ellingsen 1912; Heurtault 1986)
<i>Centrochthonius</i> Beier, 1931	Central Asia (China, Kyrgyzstan, Nepal)	3 species (Redikorzev 1918, 1934; Beier 1979; Schawaller 1991)
<i>Pseudotyranochthonius</i> Beier, 1930a	Australia, Asia (Japan, South Korea), North America (USA), South America (Chile)	20 species (Ellingsen 1905; Beier 1930a, 1964, 1966, 1968, 1969, 1971; Hoff 1951; Morikawa 1954, 1956, 1970; Chamberlin 1962; Schuster 1966; Muchmore 1967; Benedict and Malcom 1970; Dartnall 1970)
<i>Selachochthonius</i> Chamberlin, 1929	Africa (Lesotho, South Africa)	3 species (Ellingsen 1912; Lawrence 1935; Beier 1955)

For details of references, see Harvey (2011).

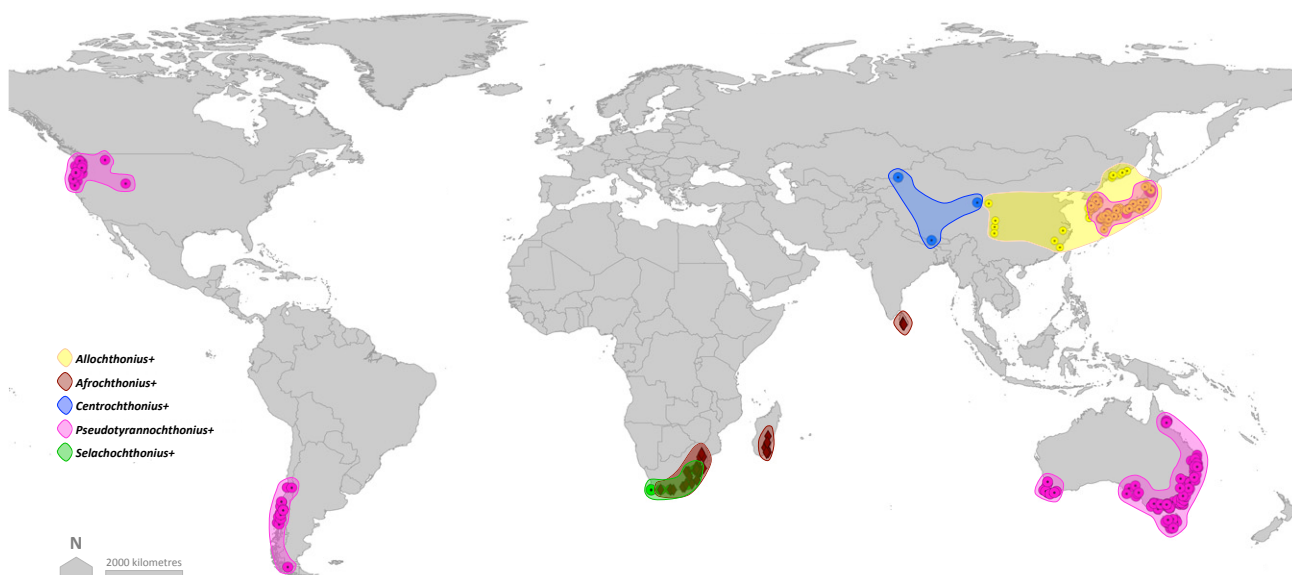


Fig. 1. World map showing current distribution of Pseudotyranochthoniidae genera compiled from the literature and museum records. The genus *Pseudotyranochthonius* currently shows a transglobal distribution with species occurring in Australia, Chile, Japan, South Korea and the United States of America.

priority (Beier 1966). Several species from Australia were described during the following two decades (Chamberlin 1962; Beier 1966, 1968, 1969, 1971; Dartnall 1970) and 10 species are currently recognised (Harvey 2011, also Table 2). Many species have originally been described from caves, namely *P. gigas* Beier, 1969, *P. giganteus* Beier, 1971, *P. hamiltonsmithi* Beier, 1968, *P. jonesi* (Chamberlin 1962), *P. tasmanicus* Dartnall, 1970 and *P. typhlus* Dartnall, 1970 (Table 2). The epigean fauna, although potentially rich in species, remains imperfectly known, and the only described species from forest habitats in Australia are *P. australiensis* Beier, 1966, *P. bornemisszai* Beier, 1966, *P. queenslandicus* Beier, 1969 and *P. solitarius* (Hoff 1951).

The aim of this paper is twofold: First, we describe and name a troglomorphic species of *Pseudotyranochthonius* from the Stockyard Creek karst in north-eastern New South Wales (Fig. 2) and redescribe and re-illustrate *P. jonesi*

(Chamberlin 1962) from the Jenolan karst in the Blue Mountains based on morphology. Second, we review the status of species previously recorded from caves on the Australian mainland (Table 2) and provide a brief account of their distribution and ecomorphology. We have not included the karst fauna of the continental island of Tasmania because this fauna is very diverse, both in morphological and molecular terms (Harms unpubl. data 2012), and requires a more comprehensive taxonomic approach beyond the scope of this study.

MATERIALS AND METHODS

All specimens examined are lodged in the Australian Museum, Sydney (AMS) or the American Museum of Natural History, New York (AMNH). Terminology and measurements follow the standard (Chamberlin 1931), except for the nomenclature

Table 2 Described species belonging to *Pseudotyranochthonius* in Australia ordered by state and type locality

Species	State and type locality	Coordinates	Ecology
<i>P. australiensis</i> Beier, 1966	New South Wales: south-east Edith (unspecified locality)	33°49'S, 149°59'E	E
<i>P. eberhardi</i> sp. n.	New South Wales: The Castles Nature Reserve, Stockyard Creek Karst, Rolys Cave (SC-9)	30°57'S, 152°19'E	TB
<i>P. jonesi</i> (Chamberlin 1962)	New South Wales: Jenolan Karst Conservation Reserve, Jenolan Karst, Imperial Cave (J-4)	28°15'S, 150°00'E	TB
<i>P. queenslandicus</i> Beier, 1969	Queensland: Tamborine National Park	27°55'S, 153°13'E	E
<i>P. tasmanicus</i> Dartnall, 1970	Tasmania: Hastings Caves State Reserve, King George V Cave (H-214)	43°23'S, 146°51'E	TB
<i>P. typhlus</i> Dartnall, 1970	Tasmania: Mole Creek Karst, Georgies Hall Cave (MC-201)	41°36'S, 146°24'E	TB
<i>P. bornemisszai</i> Beier, 1966	Victoria: ~1.5 km south-west of Boolarra: old line homestead 'Laughing Waters'	38°24'S, 146°16'E	E
<i>P. gigas</i> Beier, 1969	Victoria: Mount Napier State Park, Byaduk Lava Caves, Harman I Cave (H-11)	37°54'S, 141°58'E	E/TP
<i>P. hamiltonsmithi</i> Beier, 1968	Victoria: Skipton, Mount Widderin Cave (H-1)	37°44'S, 143°21'E	E/TP
<i>P. solitarius</i> (Hoff 1951)	Victoria: Kinglake National Park, Mount Slide	37°33'S, 145°23'E	E
<i>P. giganteus</i> Beier, 1971	Western Australia: Cape-Leeuwin-Naturaliste National Park, Witchcliffe Karst, Calgardup Cave (WI-49)	34°03'S, 115°02'E	E/TP

Coordinates are rounded to the nearest minute.

E, epigean species; TB, troglobite; TP, troglophile.

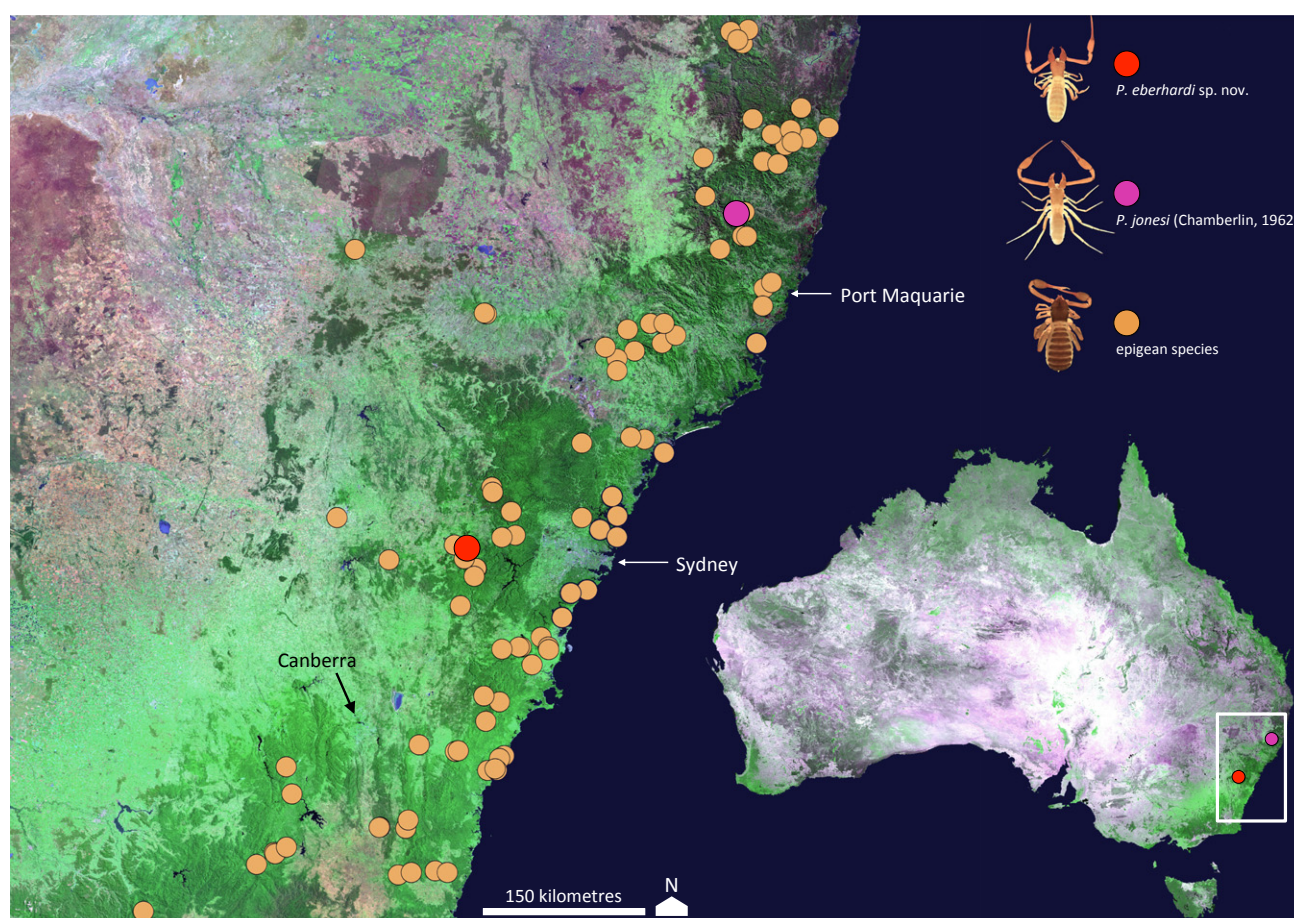


Fig. 2. Map showing type localities of *Pseudotyranochthonius eberhardi* sp. n. (pink circle) and *P. jonesi* (Chamberlin 1962) (red circle) plus epigean records of species occurring in New South Wales, Australia. The epigean records are based on a complete investigation of specimens lodged with Australian museums.

of the segments of the pedipalps and legs (Harvey 1992), the replacement of the term flagellum with 'rallum' for the chelicer blades (Judson 2007), the nomenclature of the trichobothria (Edward & Harvey 2008; Harvey 1992) and alterations to the terminology of the chelal teeth (Harvey 2009). The term 'coxal blades' is used instead of the widely used 'coxal spines' to account for the shape of the respective structures on the first coxae.

Specimens used for morphological examination were preserved in 70–75% ethanol. General morphological examinations were carried out using a Leica MZ16A stereomicroscope. Digital images were taken using a Leica DFC 500 digital camera attached to a Leica MZ16A stereomicroscope, using the Leica Application Suite Version 2.5ORI software. This program allows the alignment of images taken at different focal planes (c. 20–100 images, depending on size of the imaged structure) and combines them into a single image. For investigation of fine structures and imaging of the coxae and coxal blades, specimens were immersed in 100% glycerol and temporarily mounted on microscope glass slides with 12-mm coverslips supported by microneedles (diameter according to size of specimen). An Olympus BH-2 compound microscope was used to study structures under high magnification. Line drawings were made on tracing paper using printed automontage images as a template. To assure accuracy, all drawings were rechecked against the respective original structures.

Measurements are expressed in millimetres and were taken with an ocular graticule at the highest possible magnification. All measurements were taken in dorsal view, except those of coxae and manducatory process, which were taken in ventral view. Total length measurements exclude the chelicerae.

Images were edited and formatted in Adobe Photoshop, Version CS5. Distribution maps were produced using ESRI ArcGIS 9.3.1 software and edited using Adobe Photoshop, Version CS5. The GPS coordinates for the caves have been rounded to the minute to protect the caves. Caves numbers follow the system established by Matthews (1985).

SYSTEMATICS

Family Pseudotyranochthoniidae Beier, 1932

Pseudotyranochthoniini Beier, 1932: 69; Roewer, 1937: 240; Hoff, 1951: 9.

Pseudotyranochthoniinae Beier: Harvey, 1992: 1399; Harvey, 1996: 256.

Pseudotyranochthoniidae Beier: Judson, 1993: 697.

Diagnosis. Species of Pseudotyranochthoniidae differ from other members of the superfamily Chthonioidea by the following combination of characters: trichobothria *ib* and *isb* in subdistal position on the chelal hand near trichobothria *esb* and *ist*; trichobothria *sb* on movable chelal finger in subdistal position, and near trichobothria *b* and *t* (Figs 5a,b,e); coxal blades present on coxa I only (Figs 3d, 6d); apical process of coxa I

broadly rounded and not elongate (Figs 4g, 7g); subapical seta of manducatory process reduced and ~1/3 length of apical seta.

Remarks. Pseudotyranochthoniidae currently comprises 47 described species in five genera (Harvey 2011; Hu & Zhang 2011). The number of recognised species is, however, a gross underestimation of the actual alpha diversity, and our investigations suggest that there are several dozen putative epigean species awaiting formal scientific description in Australia alone (Harms unpubl. data 2012). Most species were described in the early to mid-20th century (1910–1970, Table 1), and only a few species have been added since from eastern Asia (Lee 1982; Sato 1984; Schawaller 1995; Sakayori 1999, 2000, 2002; Hu & Zhang 2011).

Pseudotyranochthonius Beier, 1930a

Pseudotyranochthonius Beier, 1930a: 207–208.

Tubbichthonius Hoff, 1951: 10–11 (synonymised by Beier 1966, p. 285).

Spelaeochthonius Morikawa, 1954: 83–84 (synonymised by Muchmore 1967, p. 134).

Type species

Chthonius (*Chthonius*) *silvestrii* Ellingsen, 1905, by original designation.

Diagnosis. This genus currently includes 20 species from four continents (Harvey 2011; Hu & Zhang 2011), but it is difficult to diagnose in the absence of a global generic revision of the family. The two species treated later are, however, very similar in overall morphology to other described species of *Pseudotyranochthonius* from the eastern Australian mainland and share a unique arrangement of the coxal blades (Figs 4g, 7g,h): (1) blades arranged in a diagonal row and consisting of four to six distinct, spaced groups; (2) blades of the distal group(s) basally fused and, on common, spatulate elevations; (3) most distal elevation hand-shaped and with three to six basally fused blades; and (4) individual blades terminally trifurcate, hence their assignment to *Pseudotyranochthonius*.

Distribution. Species belonging to this genus have been described from four continents in both the Northern and Southern hemisphere (Fig. 1): Australia (10 species), eastern Asia (Japan and South Korea – 4 species), North America (USA – 3 species) and South America (Chile – 3 species).

P. eberhardi sp. n.

Figures 2–4, 5d, e, 8a–c.

Type. *Australia: New South Wales:* Holotype ♀, Rolys Cave (SC–9), Stockyard Creek karst, The Castles Nature Reserve (30.57°S, 152.19°E), 5.v.1995, deep zone of cave, coll. S.M. Eberhard (AM KS.118361).

Diagnosis. Adults of *P. eberhardi* differ from all epigean species by their troglomorphic features: total lack of eyes (Figs 3a,b, 4a,d), reduction of body pigment (Figs 8a–c), elongate body appendages and high number of chelal teeth (30 on

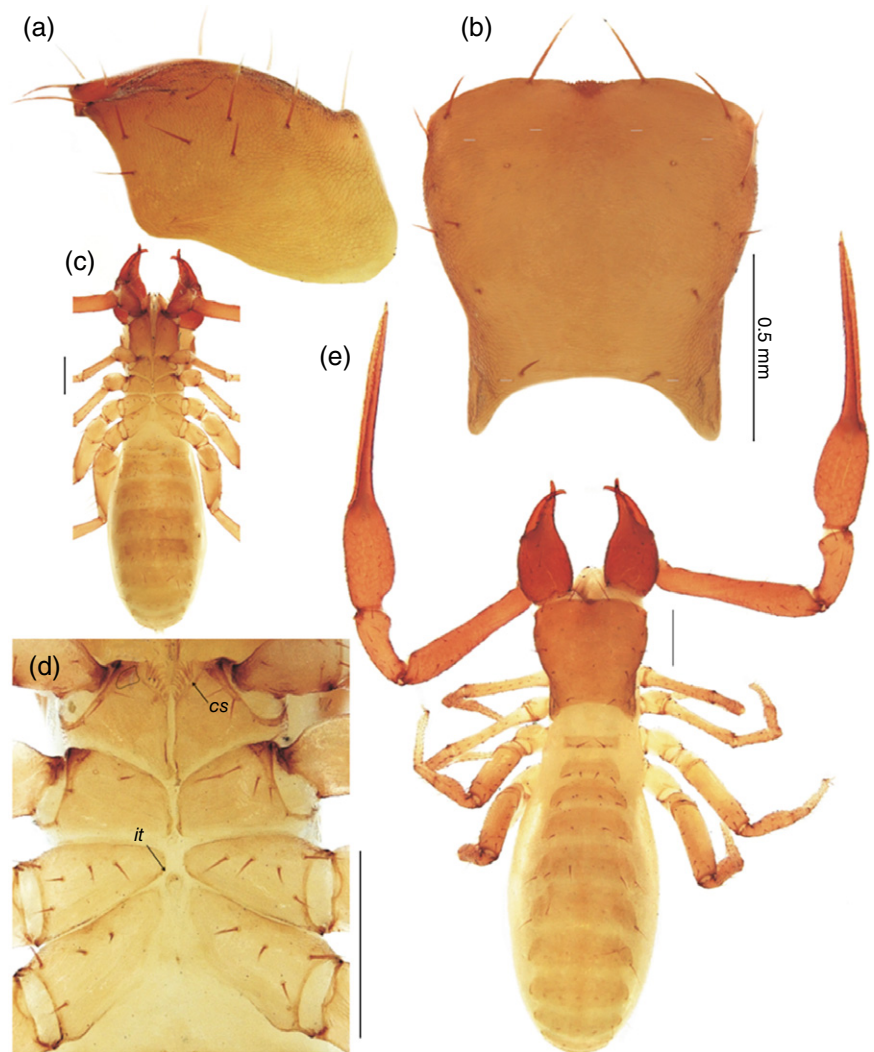


Fig. 3. *Pseudotyrannochthonius eberhardi* sp. n., holotype female (AM KS. 118361): (a) cephalothorax, lateral; (b) same, dorsal, position of lyrifissures indicated by white horizontal bars; (c) habitus, ventral; (d) coxae, ventral; (e) habitus, dorsal. cs, coxal blades; it, interoxal tubercle. Pointed line, position of dwarfed setae near apical process on coxa I.

fixed and 21 on movable finger). They differ from *P. jonesi*, the only other troglomorphic species from mainland Australia, in larger body size (3.58 mm in *P. eberhardi*, 2.98 mm in *P. jonesi*), higher number of cheliceral setae (11 in *P. eberhardi*, 9 in *P. jonesi*, Fig. 5e), distal tooth on fixed cheliceral finger smaller than in *P. jonesi*, (Fig. 4f), cephalothorax almost as broad as long (significantly longer than broad in *P. jonesi*, Fig. 3b), posterior lyrifissures on cephalothorax shifted laterally (directly behind posterior setae in *P. jonesi*, Fig. 3b), setae of cephalothorax short (Fig. 3b), eye region convex in dorsal view (rather straight or only slightly convex in *P. jonesi*, Fig. 3b), higher number of coxal blades (12–14 in *P. eberhardi*, 9–11 in *P. jonesi*, Fig. 4g), higher number of genital setae (10 in *P. eberhardi*, 6–8 in *P. jonesi*, Fig. 5d), higher number of setae on coxa II (5 in *P. eberhardi*, 4 in *P. jonesi*, Fig. 3d) and the arrangement of trichobothria on the movable chelal finger (sb/b distance 3.5 times distance b/t; less in *P. jonesi*, Fig. 5e). Males of *P. eberhardi* are unknown.

Description. Adult female (AM KS.118361).

Colour (in ethanol): Cephalothorax, pedipalps and legs orange-brown, chelicerae darker, soft body parts pale yellow (Figs 3e, 4d).

Chelicerae (Figs 4a,e,f): Relatively broad. Cuticle of hand gently granulate to squamate. Hand with 10 setae, all setae acuminate, movable finger with one seta in medial position (Fig. 4f), with three small lyrifissures in most dorsal row of setae on hand. Fixed finger with one medium-sized distal tooth and eight progressively smaller proximal teeth (Fig. 4f), with one sub-basal lyrifissure; movable finger with c. 14 continuous serrations. Galea absent; rallum with 12 blades arising from a slit-shaped depression and distally increasing in size; proximal and distal blades not paired, other blades arranged in pairs, all blades unilaterally pinnate except anterior blade that is slightly serrate; serrula exterior with 26–28 blades, serrula interior present but basal parts hidden.

Pedipalp (Figs 3e, 4d, 5d): All setae acuminate. Femur 6.15, patella 2.48, chela 6.4, hand $2.1 \times$ longer than broad; movable finger $2.1 \times$ longer than hand; without large basal apodeme. Femur without tactile setae. Palm retrolaterally with c. 15 setae in three loose rows (Fig. 5d); trichobothria *ib* and *isb* distally on dorsum of palm, fixed finger with eight trichobothria, *esb*, *ist* and *eb* forming an oblique row sublaterally to dorsally at base of fixed chelal finger, *it* and *est* distomedial and forming a pair, *it* slightly more distal than

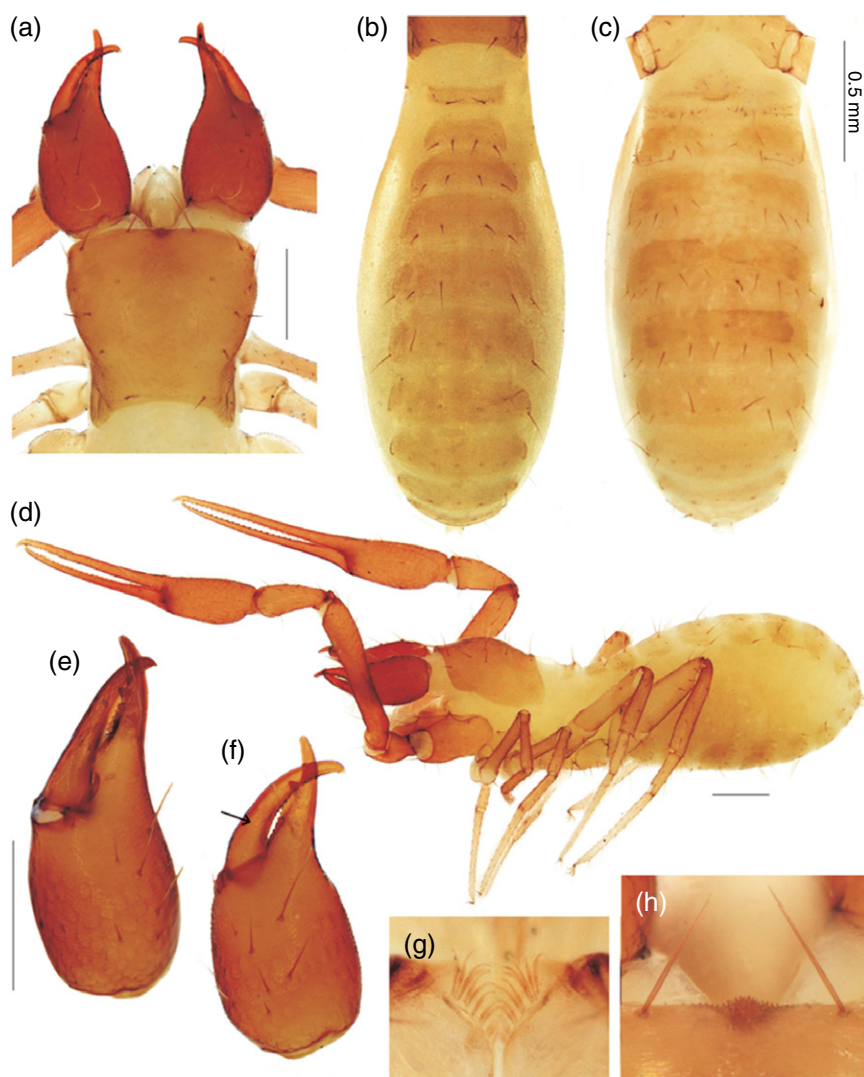


Fig. 4. *Pseudotyrannochthonius eberhardi* sp. n., holotype female (AM KS.118361): (a) cephalothorax and chelicerae, dorsal; (b) abdomen, dorsal; (c) same, ventral; (d) habitus, lateral; (e) left chelicera, ventrolateral; (f) same, lateral (arrow points to position of a lost seta); (g) coxal blades; (h) epistome.

est; *et* subdistal and duplex *xs* distal, distance between *dt* and *et* c. 1.5 times diameter of *dt*, *dt* shorter than other trichobothria; movable finger with 4 trichobothria, *st* subproximal and in medial position on finger, triplet *sb*, *b* and *t* distomedial to distal, distance between *sb* and *b* about $3.5 \times$ distance between *b* and *t*, *sb* situated subventrally, *b* medial and *t* rather subventral; microsetae absent on both fingers. Fixed finger proximally with one or two strong and short setae near *esb*. Both fingers slightly curved in dorsal view (Fig. 3e), almost straight in lateral view; fixed finger with one large lyrifissure at the base; venom apparatus absent in both fingers. Chelal finger homodontate (Fig. 5d), fixed finger with c. 26 small but erect diastemodontate teeth and 6–7 proximal continuous serrations, movable finger with c. 22 small but erect and diastemodontate teeth, proximally with three terminally blunt teeth; intercalary and accessory teeth absent. External and internal chelal condyles small and rounded.

Cephalothorax (Figs 3a,b, 4a): Subquadrate, $1.03 \times$ longer than broad, without furrows; lateral margins constricted posteriorly, eyes absent but eye region bulging and convex in

dorsal view (Fig. 3b); epistome small, rounded and heavily sclerotised, strongly cuspid (Fig. 4h); with 18 setae arranged 6:4:4:2:2, all setae comparably short; with three pairs of lyrifissures, first and second pair between anterior and ocular row of setae, third pair situated posteriolateral to setae of posterior row (Fig. 3b).

Abdomen (Figs 4b–d): Pleural membrane papillostriate. Tergites and sternites undivided; setae uniserrate and acuminate. Tergal chaetotaxy (Fig. 4b): 2:4:4:4:6:6:6:7:5:4:4:0. Sternal chaetotaxy (Fig. 4c): 16–18:16:11:11:9:9:8:6:4:–:2.

Genital region (Fig. 5d): Genital opening slit-like, with five pairs of setae proximal to opening, arranged in two rows 3:2; 3:2; two lyrifissures present anterolateral to genital opening.

Coxae (Fig. 3c,d): Manducatory process with two acuminate distal setae, apical seta straight, about three times longer than subapical seta and extending to about half of the rallum, subapical seta dwarfed and bent towards interior margin; pedipalpal coxa with three setae, two at distal margin and one more medial near interior margin, with one medial lyrifissure. Coxae I with 12–14 coxal blades (Fig. 3d), each terminally trifurcate blades (Fig. 4g), arranged in five distinct groups: 2:2:2:2:5;

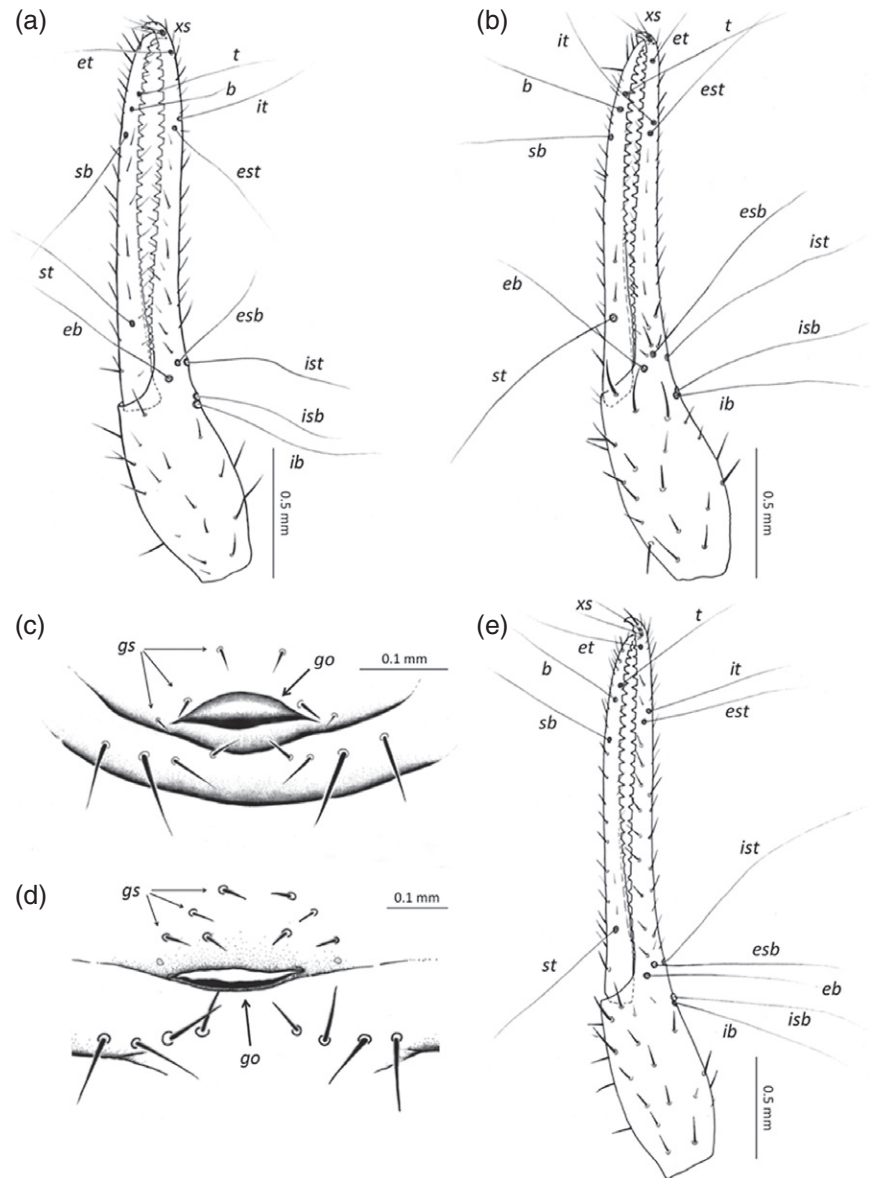


Fig. 5. *Pseudotyrannochthonius jonesi* (Chamberlin 1962), female: (a) left chela (AM KS.17830), (b) same (AM KS.21863), (c) female genital region (AM KS.17830); *P. eberhardi* sp. n., holotype female (AM KS.118361): (d) genital region, (e) left chela. go, genital opening; gs, genital setae.

blades that belong to a common group basally fused, distal blades largest and on a common palm-shaped, spatulate base, all blades arranged in an oblique row; apical process of coxa I broadly rounded; total number of setae on coxae: 1(5):2(5):3(5):4(5), first two setae on coxa I near apical process dwarfed and hard to discern (Fig. 3d, dashed line); each coxa with one small lyrifissure in distoapical position near margin. Intercoxal tubercle pronounced and tear drop-shaped, bisetose (Fig. 3d).

Legs (Figs 3e, 4d): Femora I and II longer than patellae I and II; femur + patella of leg IV $6.3 \times$ longer than broad; metatarsi III and IV with two tactile setae in submedial position, tarsi III and IV with two tactile seta in sub-basal and subterminal position; tarsus III with five terminal setae, tarsi IV and V terminally with five to six long setae; setae on trochantera I–IV: I (5), II (4–5), III (2), IV (2); heterotarsate (Fig. 4d); subterminal tarsal setae not distally serrate, arolium slightly shorter than claws and not divided; all claws simple.

Dimensions (in mm): Body length 3.58. Pedipalps: trochanter 0.46/0.31; femur 1.66/0.27; patella 0.67/0.27; chela 2.50/0.39; fixed finger length 1.72; hand length 0.82; movable finger length 1.73. Chelicera total 1.20/0.46, fixed finger length 0.45, movable finger length 0.46. Cephalothorax 0.97/0.94 (anterior)/0.70 (posterior). Leg I: femur 0.87/0.13; patella 0.55/0.10; tibia 0.51/0.08; tarsus 0.91/0.07. Leg IV: femur 0.35/0.21; patella 0.91/0.19; tibia 0.94/0.13; metatarsus 0.42/0.10; tarsus 0.91/0.08.

Distribution. *P. eberhardi* is currently known from a single cave in the Stockyard Creek karst (Fig. 2). It is almost certainly endemic to the karst area in The Castles Nature Reserve and a short-range endemic species (Harvey 2002; Ponder & Colgan 2002).

Conservation status. The type locality lies in protected forest, and the species is unlikely to be of conservation concern. Protection of *P. eberhardi* is best achieved by restricting access to the caves and preventing unpermitted entry to

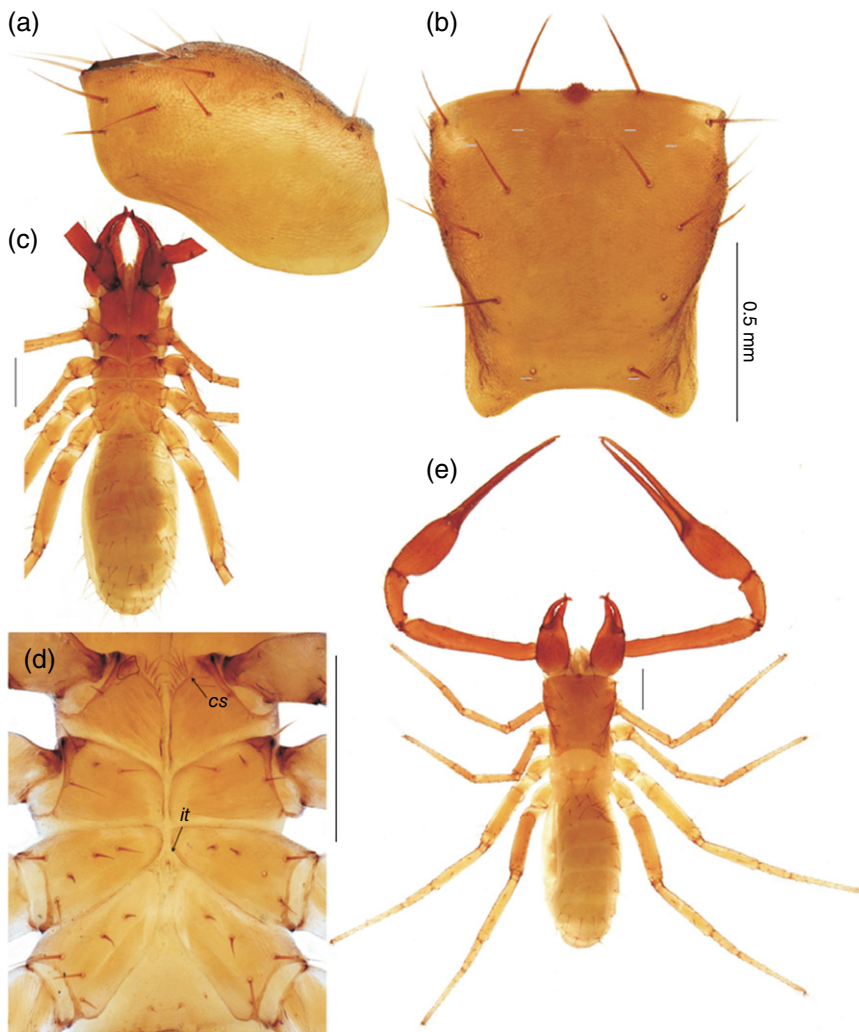


Fig. 6. *Pseudotyrannochthonius jonesi* (Chamberlin 1962) (AM KS.17830): (a) cephalothorax, lateral; (b) same, dorsal, position of lyrifissures indicated by white horizontal bars; (c) habitus, ventral; (d) coxae, ventral; (e) habitus, dorsal. cs, coxal blades; it, intercoxal tubercle. Dashed line, position of dwarfed setae near apical process on coxa I.

avoid damage to the cave environment. Actions that impact on the groundwater table, such as extensive logging in the catchment area of Stockyard Creek, could have a negative impact on this species.

Etymology. The specific epithet is a patronym in honour of Stefan Eberhard, the collector of the holotype, for his outstanding contributions to Australian karst research.

P. jonesi (Chamberlin 1962)

Figures 2, 5a–c, 6, 7.

Tubbichthonius jonesi Chamberlin, 1962: 317–319, figs 5a–j.

P. jonesi (Chamberlin 1962): Beier, 1966: 276, 285.

Type. *Australia: New South Wales:* Holotype ♀ (slide-mounted), in cave ‘probably in Blue Mountains near Sydney’, 1943, W.G. Jones (AMNH JC–2014.01001), examined.

Other material examined. *Australia: New South Wales:* 1 ♀, Glass Cave (J–17), Chevalier extension, Jenolan karst (33.49°S, 150.01°E), 22.iii.1959, unknown collector (AM KS.17267); 1 ♀, same data except Imperial Cave (J–4), Jenolan Caves Fauna Survey, 25.x.1987, M.R. Gray (AM

KS.17830); 1 ♀, same data except Small Cave, 26.ix.1969, Blue Mountains Speleological Club (AM KS.21863); 1 ♀, from ‘Jenolan Caves’, deep zone, no further data (AM KS.5279).

Diagnosis. Adults of *P. jonesi* differ from all epigean species by their troglomorphic features: total lack of eyes (Figs 6a,b, 7f), reduction of body pigment (Fig. 7e), elongate body appendages and high number of chelal teeth (26–30 on fixed and 18–23 on movable finger). They differ from *P. eberhardi*, the only other cave-dwelling species known from New South Wales, in smaller body size (2.98 mm in *P. jonesi*, 3.58 mm in *P. eberhardi*), lower number of cheliceral setae (9 in *P. jonesi*, 11 in *P. eberhardi*, Fig. 7a,b), distal tooth on fixed cheliceral finger larger (Fig. 7a), cephalothorax significantly longer than broad (almost as broad as long in *P. eberhardi*, Figs 6b, 7f), setae of cephalothorax long (Fig. 6b), posterior lyrifissures on cephalothorax situated directly behind posterior setae (shifted laterally in *P. eberhardi*, Fig. 6b), eye region slightly convex or straight in dorsal view (clearly convex in *P. eberhardi*, Fig. 6b), smaller number of coxal blades (9–11 in *P. jonesi*, 12–14 in *P. eberhardi*, Fig. 7g,h), lower number of genital setae (6–8 in *P. jonesi*, 10 in *P. eberhardi*, Fig. 5c), smaller number of setae on coxa II (4 in *P. jonesi*, 5 in *P. eberhardi*,

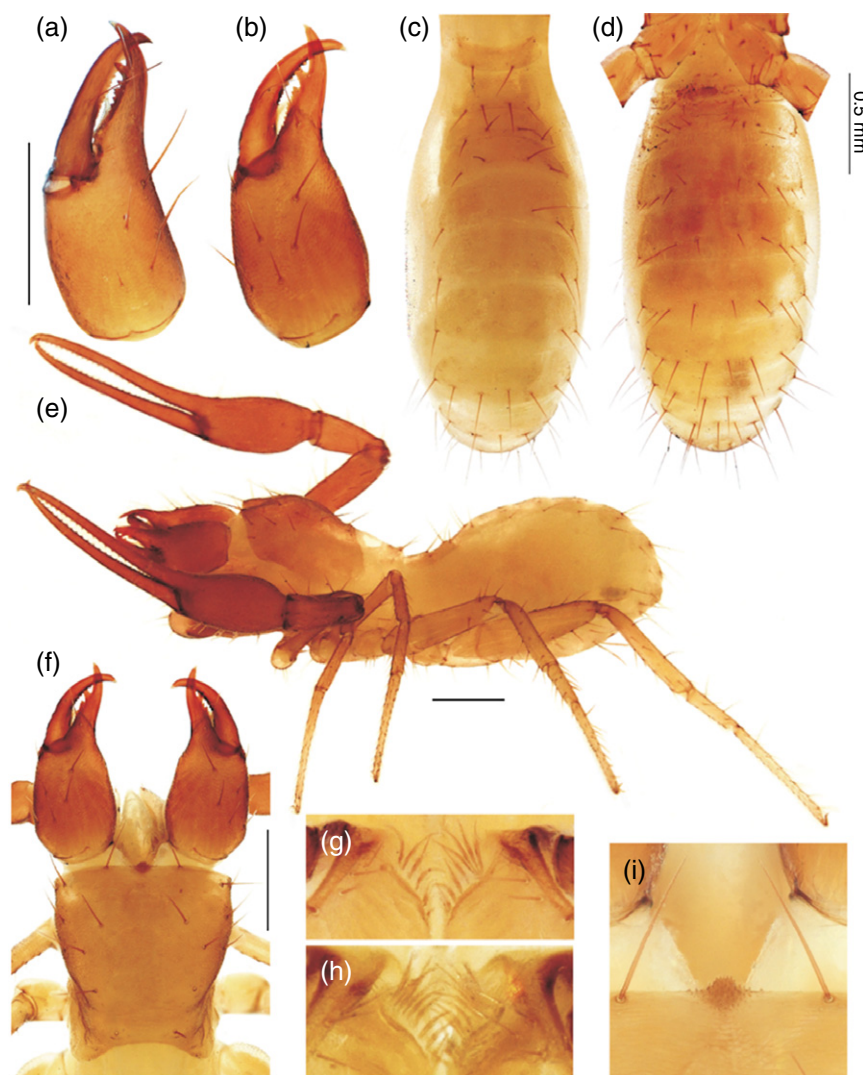


Fig. 7. *Pseudotyrannochthonius jonesi* (Chamberlin 1962) (AM KS.17830): (a) left chelicera, ventrolateral; (b) same, lateral; (c) abdomen, dorsal; (d) abdomen, ventral; (e) habitus, lateral; (f) cephalothorax and chelicerae, dorsal; (g) coxal blades; (h) same (AM KS.21863); (i) epistome.

Fig. 6d), and arrangement of trichobothria on the movable chelal finger (sb/b distance 2.0–2.5 times distance b/t ; more in *P. eberhardi*, Fig. 5a,b). Males of *P. jonesi* are unknown.

Description. Adult female (AM KS.17830)

Colour (in ethanol): Cephalothorax, pedipalps and legs orange-brown, chelicerae darker, soft body parts pale yellow (Figs 6e, 7e).

Chelicerae (Figs 7a,b): Distinctively slender. Cuticle of hand gently granulate to squamate. Hand with eight setae, all setae acuminate, movable finger with one seta in medial position (Fig. 7a), with two small lyrifissures in most dorsal row of setae on hand. Fixed finger with one large distal tooth, two to three smaller ones more proximal and eight progressively smaller serrations (Fig. 7a), with one proximal lyrifissure present; movable finger with 12–13 continuous serrations. Galea absent; rallum with 12 blades arising from a slit-shaped depression and distally increasing in size; proximal and distal blades not paired, other blades arranged in pairs, all blades unilaterally pinnate except anterior blade that is slightly serrate; serrula exterior with 25–28 blades, serrula interior present but basal parts hidden.

Pedipalp (Figs 5a,b, 6e, 7e): All setae acuminate. Trochanter, femur 8.3, patella 1.88, chela, 5.85, hand $2.0 \times$ longer than broad; movable finger $1.9\text{--}2.0 \times$ longer than hand; without large basal apodeme. Femur without tactile setae. Palm retrolaterally with c. 14 setae in three loose rows (Figs 5a,b); trichobothria *ib* and *isb* distally on dorsum of palm, fixed finger with eight trichobothria, *esb*, *ist* and *eb* forming an oblique row sublaterally to dorsally at base of fixed chelal finger, *it* and *est* distomedial-distal and forming a pair, *it* slightly more distal than *est*; *et* subdistal and duplex *xs* distal, distance between *dt* and *et* c. 1.5 times diameter of *dt*, *dt* trichobothria shorter than other trichobothria; movable finger with four trichobothria, *st* subproximal and in medial position on finger, triplet *sb*, *b* and *t* distomedial to distal, distance between *sb* and *b* about $2\text{--}2.5 \times$ distance between *b* and *t*, position of *sb* on finger is subventral, *b* medial and *t* situated subventrally; microsetae absent on both fingers. Fixed finger proximally with one or two strong and short setae near *esb* (Fig. 5b). Both fingers slightly curved in dorsal view (Fig. 6e), almost straight in lateral view; fixed finger with one large lyrifissure at the base; venom apparatus absent in both fingers.

Chelal finger homodontate (Figs 5a,b), fixed finger with 28–31 small but erect diastemodontate teeth, proximal four teeth terminally blunt and extended into 6–8 proximal serrations, movable finger with 22–23 small but erect diastemodontate teeth and 6–10 proximal continuous serrations; intercalary and accessory teeth absent. External and internal chelal condyles small and rounded.

Cephalothorax (Figs 6a,b, 7e,f): Subquadrate to elongate, $1.10 \times$ longer than broad, without furrows; lateral margins constricted posteriorly, eyes absent but eye region slightly bulging in dorsal view; epistome small, rounded and heavily sclerotised, strongly cuspid (Figs 7i); with 18 long setae arranged 6:4:4:2:2, all setae long with posterior 2 being the shortest (Fig. 6b); with three pairs of lyrifissures, first and second pair between anterior and ocular row of setae, third pair situated posterior and close to setae of posterior row.

Abdomen (Figs 7c–e): Pleural membrane papillostriae. Tergites and sternites undivided; setae uniserrate and acuminate. Tergal chaetotaxy: 2:4:4:4:6:6:6:7:6:4:4:0 (Fig. 7c). Sternal chaetotaxy: 14–16:14:10:10:9:8:7:6:4:–:2 (Fig. 7d).

Genital region (Fig. 5c): Genital opening slit-like, with three pairs of setae proximal to opening, arranged in two rows 3:3; two lyrifissures present anterolateral to genital opening.

Coxae (Fig. 6c,d): Manducatory process with two acuminate distal setae, apical seta straight, about three times longer than subapical seta and extending to about half of the rallum, subapical seta dwarfed and bent towards inner margin; pedipalpal coxa with three setae, two at distal margin and one more medial near interior margin, with one medial lyrifissure. Coxae I with 9–11 coxal blades (Fig. 7g,h), each terminally trifurcate, arranged in five indistinct groups: 1–2:1:1:1:2–5; blades that belong to a common group basally fused, distal blades largest and basally fused and on a shallow spatulate base, all blades arranged in an oblique row; apical process of coxa I broadly rounded; number of blades on coxae: 1(4):2(4):3(5):4(5), first two setae on coxa I near apical process dwarfed and hard to discern (Fig. 6d, dashed line); each coxa with one small lyrifissure in distoapical position near margin. Intercoxal tubercle pronounced and tear drop-shaped, bisetose (Fig. 6d).

Legs (Fig. 6e, 7e): Femora I and II longer than patellae I and II; femur and patella of leg IV $5.9 \times$ longer than broad; metatarsi III and IV with two tactile setae in submedial position, tarsi III and IV with one tactile seta in sub-basal position; tarsi IV and V terminally with five to six long setae; setae on trochantera I–IV: I (5), II (3), III (2), IV (2); heterotarsate (Fig. 7e); subterminal tarsal setae not distally serrate, arolium slightly shorter than claws and not divided; all claws simple.

Dimensions (in mm): Body length 2.98. Pedipalps: trochanter 0.43/0.29; femur 1.66/0.2; patella 0.47/0.25; chela 2.40/0.41; fixed finger length 1.58, hand length 0.80; movable finger length 1.56. Chelicera total 0.94/0.37, fixed finger length 0.44, movable finger length 0.47. Cephalothorax 0.90/0.82 anterior/posterior. Leg I: femur 0.85/0.13; patella 0.54/0.09; tibia 0.43/0.09; tarsus 0.87/0.07. Leg IV: femur 0.30/0.20, patella 0.88/0.20, tibia 0.89/0.125, metatarsus 0.42/0.11, tarsus 1.05/0.08.

Variation. There is some variation in the number of diastemodontate teeth on both fixed (26–32) and movable (18–23) chelal fingers and the number of proximal serrations (4–8 per finger). The transition between teeth and serrations may be continuous. Additional variation is present in the number of coxal blades (8–11 blades in 5–6 groups) and genital setae (an additional pair of dwarf setae is present laterally in some specimens).

Distribution. This species is known from a number of caves in the Jenolan Karst Conservation Reserve (Fig. 2) but has not been collected frequently. It is almost certainly endemic to the Jenolan karst area and a short-range endemic species (Harvey 2002; Ponder & Colgan 2002).

Conservation status. The type locality lies in a karst reserve and the species is unlikely to be of conservation concern. Effective conservation may be best achieved by restricting access to some of the smaller (non-tourist) caves to avoid habitat destruction by trampling. The designation of faunal protection areas in tourist caves, preferably in areas with constant humidity and a diversity of microhabitats, is a second step to assure the long-term protection of this species.

Etymology. The specific epithet was chosen by Chamberlin (1962) as a patronym in honour of Walter B. Jones, the collector of the holotype.

Fixation of type locality. *P. jonesi* was originally described from an unspecified locality ‘probably in the Blue Mountains near Sydney’ (Chamberlin 1962). The re-examination of all Australian Museum collections of *Pseudotyrannochthonius* revealed several specimens from the Jenolan Caves in the Blue Mountains that strikingly matched Chamberlin’s description and illustrations. We hence re-examined the holotype in the collection of the AMNH and were able to match our specimens with the holotype of *P. jonesi*: the very slender carapace that is much longer than broad, generally slender body, the low number of setae near the genital opening, high number of teeth of the chelal fingers, the arrangement of the trichobothria on the fixed finger (distance between trichobothria *sb* and *b* about 2.0 times the distance between *b* and *t*) and the relatively small number of coxal blades render *P. jonesi* unmistakable. The type locality of *P. jonesi* is therefore fixed to the Jenolan karst in the Blue Mountains near Sydney. The most recently collected specimen (AM KS.17830) is from Imperial Cave (J–4), one of the larger tourist caves, and this specimen was used to re-illustrate and redescribe the species.

DISCUSSION

Extent of troglomorphism in *P. eberhardi* and *P. jonesi*

The two species described here do not show strong troglomorphic features recorded for other pseudoscorpion groups such as Chthoniidae and some families of Neobisioidea (e.g. Vachon 1947; Muchmore 1969, 1972, 1984, 1996; Heurtault 1986; Muchmore & Pape 1999; Carabajal Márquez *et al.* 2000; Hendrickx & Vets 2000; Andrade & Mahnert 2003; Reboleira

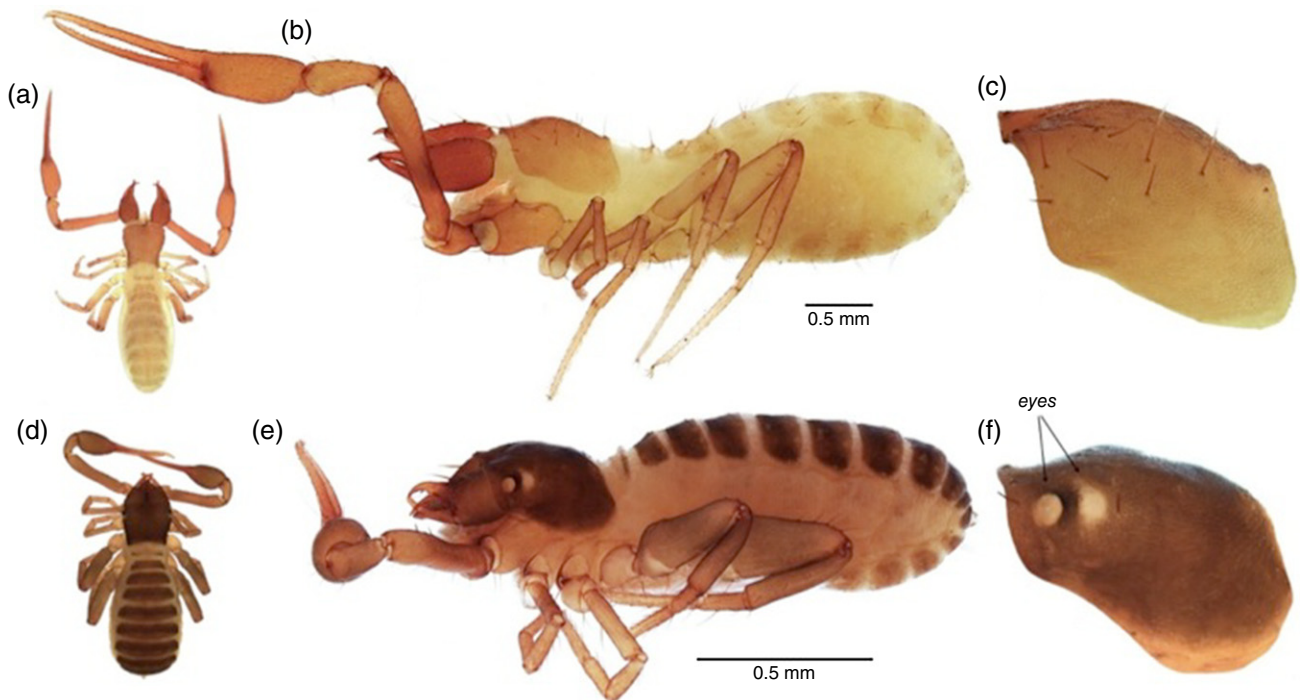


Fig. 8. Comparison of the troglomorphic *Pseudotyranochthonius eberhardi* sp. n. with a putative epigean species from Warrumbungle Range in New South Wales (AM KS.75442): (a) *P. eberhardi* sp. n., habitus, dorsal view; (b) same, lateral view; (c) carapace, lateral view; (d) *Pseudotyranochthonius* sp. from Warrumbungle Range, habitus, dorsal view; (e) same, lateral view; (f) carapace, lateral view. Note the troglomorphic features in *P. eberhardi*, such as the reduction of body pigment, generally slender appearance and lack of eyes.

et al. 2010; Mahnert 2011). Chamberlin (1962) noted that *P. jonesi* 'shows numerous characteristics indicative of a true troglobite (blindness; pallid coloration; and appendicular attenuation which, however, is less pronounced than in some cave-inhabiting forms)'. Indeed, morphological adaptations in the two species described here are rather mild, and the most prominent feature that distinguishes *P. eberhardi* and *P. jonesi* from described epigean forms is the total lack of eyes (Fig. 8). The two species are also larger in body size than many putative epigean species and show a reduction of body pigment so that the cuticle appears to be reddish-brown, whereas the usual colouration of epigean forms is a dark chestnut brown or almost black (Fig. 8). The legs and pedipalps are not strongly elongate and resemble those of described epigean species, although the chelal hand is rather slender and the number of teeth on both the fixed and movable chelal finger is increased: >20 in *P. eberhardi* and *P. jonesi*, 10–15 in described epigean species (Fig. 5). These rather minor adaptive features are shared with other subterranean chthonioid pseudoscorpions in Australia that generally do not have excessively elongate body appendages but are often pallid, lack eyes and have slender chelal hands (Edward & Harvey 2008; Harvey 1989, 1991; Harvey & Mould 2006; Muchmore 1982). This lack of strong troglomorphic features may have a simple biological explanation; chthonioid pseudoscorpions are primarily inhabitants of the topsoil layer and leaf litter (Weygoldt 1969; Benedict & Malcolm 1970) and are pre-adapted for a life in hypogean environments, habitats with often constant levels of humidity and temperature that may

be easy to colonise via cracks and crevices. Although there are some very highly modified chthoniid troglobites including species of *Troglochthonius* Beier, 1939 from Southern Europe (Beier 1939; Helvesen 1968) and *Vulcanochthonius* Muchmore, 2000 from Hawaii (Muchmore 2000), we argue that subterranean habitats are not an evolutionary one-way street for chthonioids but rather fall within the natural ecological range of this group; major morphological adaptations are simply not a prerequisite for a permanent subterranean biology and are therefore rare.

Who is a troglophile and who is a troglomorphic?

Three additional species of *Pseudotyranochthonius* (excluding the two described earlier) from the Australian mainland have originally been described from caves (Table 2). We have recollected these species from their respective type localities and carried out additional fieldwork in adjoining epigean habitats to evaluate their ecomorphological status: troglophilic (cave-loving), a term that indicates the ability of a species to complete its entire life cycle in subterranean habitats and/or epigean habitats with cave specimens generally not showing major morphological derivations from their epigean counterparts or, alternatively, troglobitic (cave-dwelling) for species unable to live in epigean habitats and with morphological adaptations towards life underground (Humphreys 2000; Trajano 2012).

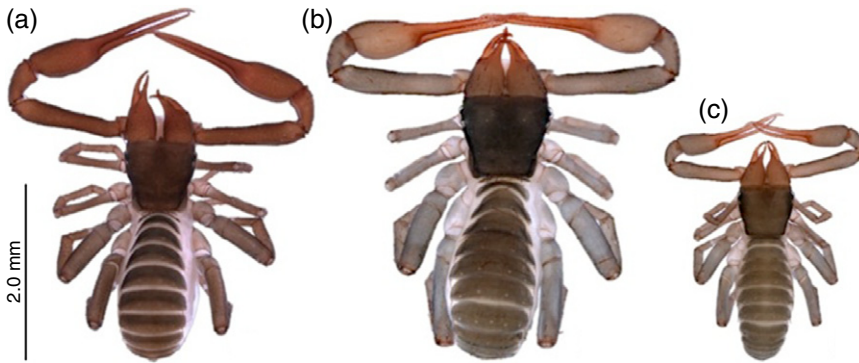


Fig. 9. Females of troglophilic *Pseudotyrannochthonius* species from Australia: (a) *P. giganteus* from Boranup Forest, Leeuwin-Naturaliste National Park in Western Australia (WAM T120400); (b) *P. gigas* from Church Cave, Byaduk Lava Caves in Victoria (WAM T120467); (c) *P. hamiltonsmithi* from Mount Widderrin Caves in Victoria (WAM T120480). Note the dark colouration of the cuticle and the presence of eyes in all specimens.

Pseudotyrannochthonius gigas (Fig. 9b) was described from two caves in the Byaduk Lava caves (western Victoria), but we have collected this species in epigeal habitats close to the cave entrances; the species is widespread and present in the Great Otway National Park some 150 km from the type locality, Mount Eccles National Park and Mount Buangor State Park, all in western Victoria. *Pseudotyrannochthonius giganteus* (Fig. 9a), formerly known from a single cave in the Witchcliffe karst in the extreme south-west of Western Australia, is also widespread and was collected from many localities in the south-western forests during 2008–2012. The species is a frequent cave invader, with specimens collected by the first author from at least nine caves in the Margaret River region. *Pseudotyrannochthonius hamiltonsmithi* (Fig. 9c), previously known only from the type locality, Mount Widderrin Caves near Skipton in western Victoria, has also been collected by us in Mount Buangor State Park, some 50 km north-east of the type locality in open eucalypt forest.

Cave specimens of these species do not show pronounced troglomorphic features, such as the elongation of body appendages or the loss of eyes, although cave specimens are generally a little larger and often (but not always) paler than their epigeal counterparts.

Why only two troglomorphic *Pseudotyrannochthonius* in mainland Australia?

Pseudoscorpions are well known to be frequent inhabitants of subterranean habitats (Beier 1934, 1939, 1953; Chamberlin 1962; Harvey & Volschenk 2007; Judson 2007; Moulds *et al.* 2007; Edward & Harvey 2008; Reboleira *et al.* 2010) and *Pseudotyrannochthonius* is no exception, with diverse karst faunas recorded from eastern Asia (Japan and South Korea) and Tasmania (Morikawa 1960; Dartnall 1970; Eberhard *et al.* 1991; Hong *et al.* 1996; Mallick & Driessen 2005). One of the key outcomes of this study is that in contrast with eastern Asia and Tasmania where species of *Pseudotyrannochthonius* have been recorded from many disparate karst systems, the troglomorphic fauna of this genus in mainland Australia is currently poor. This may be an artefact caused by the lack of subterranean sampling in some regions of Australia (Humphreys 2008), but more likely this pattern is real and potentially linked to mainland Australia's climatic history that, in contrast with the earlier mentioned regions,

has not had Pleistocene glaciation events but widespread post-Miocene aridification instead (Hamilton-Smith 1967; Barr 1973; Byrne *et al.* 2008; Cooper *et al.* 2011). Species of *Pseudotyrannochthonius* are diverse in cool, mesic forest systems throughout eastern and southern Australia, but there are no specimens in research collections from the arid and warmer regions of the continent with less than 600-mL annual rainfall, suggesting that humidity in combination with moderate temperatures is the single limiting factor for the distribution of this genus in Australia. A high proportion of the Australian subterranean fauna is present in the arid and semi-arid western part of the continent with presently subtropical or tropical climates (Guzik *et al.* 2011), habitats that are not suitable for *Pseudotyrannochthonius* and perhaps have not been so for a very long time. This, however, does not explain the low karst diversity of this genus in the temperate south and south-east of the continent, and past climatic events, specifically the lack of significant glaciations, are the most likely hypothesis at this stage.

The epigeal fauna of *Pseudotyrannochthonius* in Australia

A challenge arising from our study is to develop a stable taxonomic framework for the diverse epigeal fauna of *Pseudotyrannochthonius* in continental Australia. Although most species in Australia have been described from a few scattered localities and often single specimens, perhaps suggesting that species belonging to this genus may be rare, our examination of research collections and fieldwork suggest that *Pseudotyrannochthonius* in Australia is in fact a highly diverse group, with many records representing putative species in the mesic forest systems of temperate eastern and southern Australia (Fig. 2). Whereas a taxonomic revision of the troglomorphic fauna of the Australian mainland based on morphology was easy to achieve because of the low number of species, addressing the taxonomy of the epigeal fauna will be challenging because of the high levels of diversity, cryptic nature of species and potential homoplasy in many morphological character systems frequently employed in pseudoscorpion taxonomy (e.g. trichobothrial patterns, number and shape of teeth of the chelal fingers, genitalic characters). Combined approaches, morphology in conjunction with molecular methods and multigene barcoding, such as conducted on Californian trapdoor spiders

of the family Antrodiaetidae (Hedin & Carlson 2011; Satler *et al.* 2011) will be necessary to tackle this complicated yet interesting group of pseudoscorpions.

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