

Genetic structure and new occurrence records of the iconic Tasmanian mountain shrimp *Anaspides tasmaniae* (Thomson, 1893) (Anaspidesidae: Anaspidae) reveal relictual distribution in southern Tasmania

Christoph G. Höpel^{id}^{A,C}, Shane T. Ahyong^B and Stefan Richter^A

^AAllgemeine and Spezielle Zoologie, Institut für Biowissenschaften, Universität Rostock, Universitätsplatz 2, 18055 Rostock, Germany.

^BAustralian Museum Research Institute, Australian Museum, 1 William Street, Sydney, NSW 2010, Australia, and School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia.

^CCorresponding author. Email: christoph.hoepel@uni-rostock.de

Abstract. The iconic ‘mountain shrimps’ of the genus *Anaspides* Thomson, 1894, are endemic to Tasmania, inhabiting various freshwater habitats such as mountain tarns and creeks, as well as streams inside caves. They are often labelled as ‘living fossils’ because of their close resemblance to their Triassic relatives. Prior to 2015, only two species were recognised but recent studies have uncovered a total of at least seven species. The type species of *Anaspides*, *A. tasmaniae* (Thomson, 1893), was previously believed to occur throughout Tasmania, but following a review in 2016, this species was confirmed only from a small range on the east and south-east side of Mt Wellington, with *Anaspides* from other parts of Tasmania referable to other species. We herein provide a detailed assessment of the distribution and genetic structure of *A. tasmaniae* based on extensive field surveys throughout the ranges of all species of *Anaspides*. The distribution of *A. tasmaniae* is extended to include four separate localities in and around the Mt Field National Park, 50 km north-west of Mt Wellington. The recovered genetic structure of *A. tasmaniae* based on 48 specimens indicates that the disjunct distribution is unlikely to be the result of artificial translocation but, instead, probably reflects postglacial relictualisation of a formerly continuous range present during Pleistocene glacial maxima. Of particular interest is the record of syntopy in *Anaspides*, observed at the entrance of Khazad Dum cave, where both *A. tasmaniae* and *A. swaini* inhabit the inflow stream.

Keywords: Anaspidae, Anaspidesidae, *Anaspides tasmaniae*, conservation, endemic, genetic structure, glaciation, mountain shrimp, relictual distribution, Tasmania.

Received 23 December 2020, accepted 11 March 2021, published online 9 April 2021

Introduction

The mountain shrimps of the genus *Anaspides* Thomson, 1894 (Anaspidesidae: Ahyong and Alonso-Zarazaga 2017) are endemic to Tasmania and are probably the most iconic freshwater invertebrates of the island (Ahyong 2016; Ahyong and Alonso-Zarazaga 2017). *Anaspides* occurs in a variety of freshwater surface habitats such as mountain tarns, creeks, streams, and pools, as well as subterranean streams in caves all over Tasmania. Although *Anaspides* spp. are found in surface waters between 150 m and approximately 1500 m above sea level (asl), they mainly occur in high-altitude areas above 700–800 m asl. *Anaspides* is often referred to as a ‘living fossil’ because of its close resemblance to Triassic relatives. The first species of *Anaspides* was discovered in 1892 by

G. M. Thomson, who collected specimens on Mt Wellington, which he initially named *Anaspis tasmaniae* Thomson, 1893 (but later corrected to *Anaspides tasmaniae*) (Thomson 1894). In 1908, Smith enlarged the known distribution of *Anaspides*, finding populations on the Hartz Mts, Mt Field and Mt Read. A second species of *Anaspides*, *A. spinulae* Williams, 1965, was described from Lake St Clair (Williams 1965a). In the same year, Williams reported the first records of *Anaspides* from caves (Williams 1965b). Further investigations in caves and surface waters revealed further occurrences and higher morphological variation in *Anaspides*, as well as molecular evidence for undiscovered diversity (Goede 1967; Lake and Coleman 1977; O’Brien 1990; Jarman and Elliott 2000).

Our current taxonomic knowledge is based significantly on the investigations of Ahyong (2015, 2016), which led to recognition of five new species: *A. clarkei* Ahyong, 2015, *A. jarmani* Ahyong, 2015, *A. swaini* Ahyong, 2015, *A. eberhardi* Ahyong, 2016 and *A. richardsoni* Ahyong, 2016. *Anaspides richardsoni* occurs in the northern half of Tasmania from the West Coast Range, east to Cradle Mountain, Gunns Plains and Mole Creek, across the Central Plateau, and south to Mt Field, whereas *A. swaini* has a more central-south-western distribution, being reported from the Wellington Range over the Snowy Range and Arthur Range to the flanks of lakes Pedder and Gordon, and north to the vicinity of Lake St Clair. Moreover, Ahyong (2016) reported morphological differences within these widespread species, especially within *A. swaini*, recognising three subtly different, geographically discrete forms, which might represent separate species (currently under study). The remaining species have narrow ranges and are morphologically rather consistent. *Anaspides spinulae* occurs only within Lake St Clair, *A. eberhardi* is present only in caves of the Junee–Florentine karst and *A. jarmani* and *A. clarkei* are found in just a few localities in south-east Tasmania. Finally, *A. tasmaniae*, formerly believed to be widespread over the whole island in surface waters and caves, now appeared to be limited to a small range on the east and south-east side of Mt Wellington above 450 m asl with no known cave occurrences. Richter *et al.* (2018), using molecular data, largely corroborated the major species clades of Ahyong (2016) and recovered a monophyletic *A. tasmaniae*, with different sister group relationships depending on the gene fragment used.

Anaspides tasmaniae is readily distinguished from other species of the genus by the combination of well developed eyes, the presence of two antennular clasping spines in adult males, the elongated telson with an evenly rounded posterior margin lined with closely set spinules and a male pleopod I, in which the retinacular lobe is visible in lateral view (Ahyong 2016). In particular, the elongated telson with an evenly rounded posterior margin and the form of the antennular inner flagellum makes it easy to distinguish from other *Anaspides* species.

We herein provide a detailed assessment of distribution and genetic structure of *A. tasmaniae* based on extensive recent field surveys throughout the ranges of all species of *Anaspides*, extend the known distribution of *A. tasmaniae* to an area in the Junee–Florentine Karst, 50 km north-west of Mt Wellington and provide evidence of sympatry of two species of *Anaspides* at the entrance of the Khazad Dum cave.

Material and methods

Specimens were collected during two extensive field surveys in February 2017 and March 2019, sampling widely throughout the range of all species of *Anaspides*. In total, 37 specimens of *A. tasmaniae* were collected and newly sequenced for this study (see Table S1, Supplementary Material). In addition, a total of 9 COI, 11 16S rRNA and one 28S rRNA sequence from the study by Richter *et al.* (2018) were included. The newly sequenced specimens were collected using hand nets and preserved directly in 80–95% ethanol.

Specimens were identified based on morphology following Ahyong (2015, 2016).

Tissue was removed from the 8th thoracopod or from the pleopods of the specimens. The DNA extraction was performed with the innuPrep Forensic Kit (Analytik Jena) and the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's instruction. Three markers were partially sequenced: mitochondrial cytochrome *c* oxidase subunit I (COI) and 16S rRNA as well as the nuclear 28S rDNA. The polymerase chain reaction (PCR) had a total volume of 30 µL containing 3 µL of each primer (each 10 µM), 3 µL 10 × buffer (Sigma Aldrich), 3 µL dNTP mix (2 mM, Biozym), 2.58 µL MgCl₂ (25 mM, Sigma Aldrich), 0.12 µL Taq-polymerase (Sigma Aldrich), 10.71 µL ultrapure water and 4.5 µL of the DNA extract. Primers were LCO2 (5'-TCN ACH AAY CAT AAA GAY ATT GGA AC-3') (Richter *et al.* 2018), HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer *et al.* 1994) for COI, 16Sa (5'-CGC CTG TTT ATC AAA AAC AT-3'), 16Sb (5'-CTC CGG TTT GAA CTC AGA TCA-3') (Xiong and Kocher 1991) for 16S and rd4.8a (5'-ACC TAT TCT CAA ACT TTA AAT GG-3') and rd7b1 (5'-GAC TTC CCT TAC CTA CAT-3') (Richter *et al.* 2007) for 28S rDNA. PCR amplification programs comprised an initial denaturation step at 94°C for 1 min, followed by 40 amplification cycles (94°C for 30 s, 50°C for 30 s, 72°C for 60 s) for COI, 38 amplification cycles (94°C for 30 s, 48°C for 30 s, 72°C for 60 s) for 16S, 35 amplification cycles (94°C for 30 s, 55°C for 30 s, 72°C for 60 s) for 28S, and a final elongation step at 72°C for 5 min. All PCR reactions were performed with a Mastercycler gradient (Eppendorf). PCR products were visualised by gel electrophoresis, using 5 µL of the PCR product with 1.5 µL loading buffer DNA b II (AppliChem) on a 1.2% agarose/TAE gel stained with 5 µL Rotisafe (Carl Roth). PCR products were purified using paramagnetic beads (High Prep PCR, Magbio) following the manufacturer's instruction with a final volume of 25 µL. Sequencing of PCR products was performed in Lightrun96 well plates by the company Eurofins Genomics as well as using the dideoxy chain termination method and cycle sequencing using an ABI Prism® Big Dye® Terminator V.1.1 Cycle Sequencing Kit. Cycle sequencing products were analysed by using capillary separation on an ABI Genetic Analyzer 3130 xl (Applied Biosystems/Hitachi). The resulting chromatograms were manually checked and adjusted with Geneious 2019.1.3 (Biomatters Limited). All sequences were deposited in GenBank (Benson *et al.* 2003) (accession numbers: MW584899–MW584904, MW581074–MW581077, MW581544–MW581580).

The sequences of all three gene fragments were separately aligned using ClustalW (Thompson *et al.* 1994) implemented in Geneious Prime 2019.1.3 (Biomatters Limited). Pairwise distances were calculated using MEGA X (Kumar *et al.* 2018). For pairwise distance analyses the uncorrected p-distances were calculated. Phylogenetic networks were calculated with Network 5.0.1.1 (Fluxus Technologies) separately for COI, 16S, and 28S alignments by using the median-joining method with the parameter epsilon set to 10.

Results

We found *Anaspides tasmaniae* at three different localities east and south-east of Mt Wellington, within the known range of the species: at a small runnel near The Chalet, Mt Wellington (970 m asl); the Browns River at Silver Falls (520 m asl); and Fern Tree Bower (470 m asl) (Figs 1 and 2). Extensive searches of the Mt Wellington plateau in the head waters of North West Bay River, where *Anaspides* has been historically reported to occur (Ahyong 2016), recovered no evidence of *Anaspides*. Also considering the records in Ahyong (2016), true *A. tasmaniae* has been confirmed only from three different drainages in the east and south-east of Mt Wellington: the catchments of the New Town Rivulet, the Guy Fawkes Rivulet and the Browns River (Fig. 2). The neighbouring drainages, all in Wellington Park, i.e. North West Bay River catchment, Knights Creek catchment and Myrtle Forest Creek/Sorell

Creek catchment, are inhabited by *Anaspides swaini* (form 3 of Ahyong 2016) (Figs 1 and 2).

Anaspides tasmaniae, however, was discovered within and near the Mt Field National Park. In Mt Field National Park, we recorded four species of *Anaspides*: *A. richardsoni*, *A. eberhardi*, *A. swaini* (supporting the general distribution shown in Ahyong 2016) as well as *A. tasmaniae*. *Anaspides richardsoni* inhabits the tarns and runnels on the plateau from Wombat Moor and the north side of the Mawson Plateau over the tarn shelf, Newdegate Pass and K Col to the waters of the Mt Field West plateau (Figs 1 and 3). The troglobitic species, *A. eberhardi*, occurs only in caves of the Junee–Florentine Karst at the edges of the Mt Field National Park and Junee Cave State Reserve. We observed *A. eberhardi* in Niggly Cave, Khazad Dum, Porcupine Pot and Junee Cave. Further records of *A. eberhardi* are from cave JF-104, Welcome Stranger Cave, Gormenghast Cave, Pendant Pot, Growling



Fig. 1. Hydrological map of Tasmania showing the Derwent River drainage systems (red outlines), the borders of Mt Field National Park and Wellington Park (black outlines) and collection sites of *Anaspides tasmaniae* (blue dots). Modified after the Tasmanian catchment map, Tasmanian Government, Department of Primary Industries, Parks, Water and Environment, 13.09.2016.

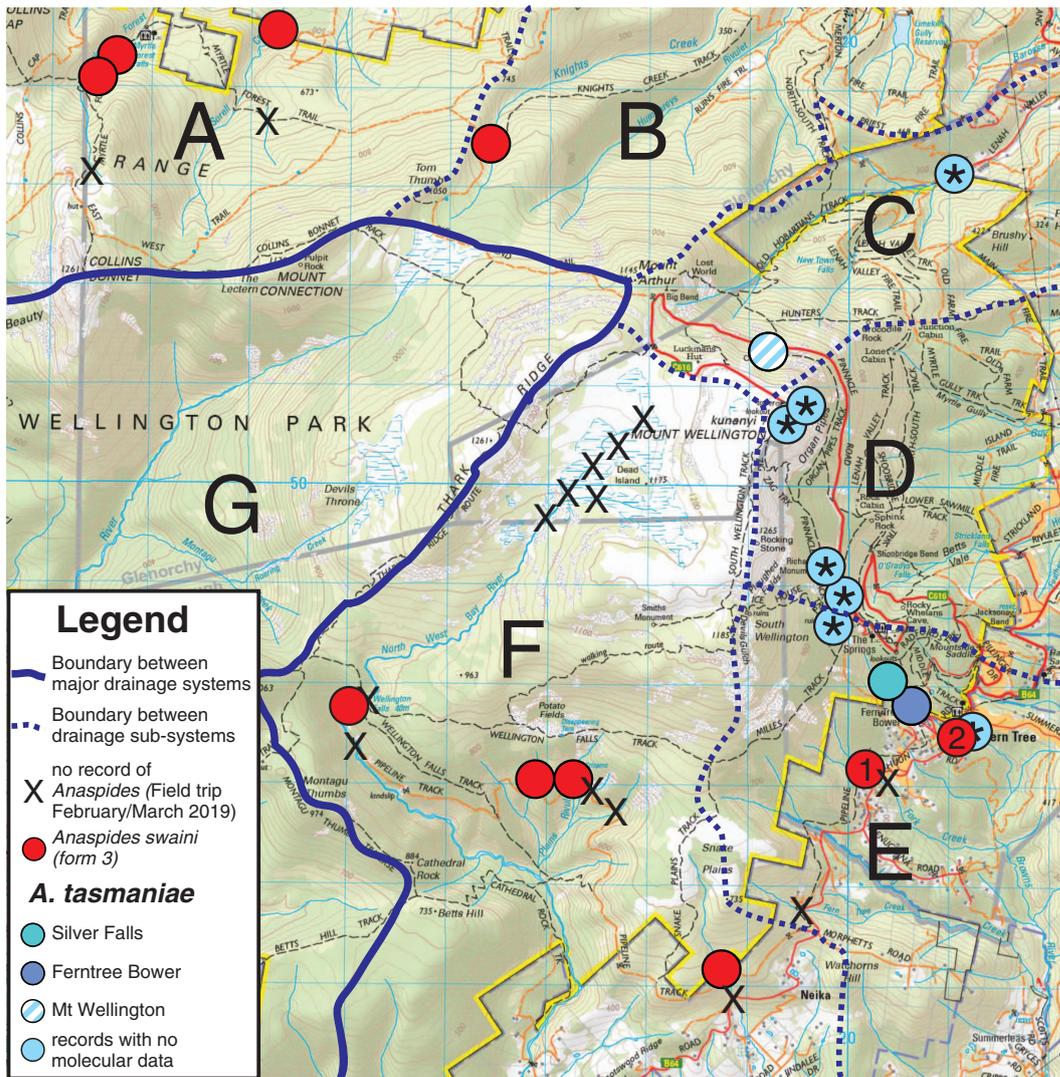


Fig. 2. Topographical map of eastern Wellington Park with drainage and subdrainage systems, as well as known collection sites of *Anaspides* from Ah Yong (2016) and collection sites from this study. Subdrainage systems A–F drain into the Derwent River drainage system: A: Myrtle Forest Creek/Sorell Creek drainage system; B: Knights Creek drainage system; C: New Town Rivulet drainage system; D: Guy Fawkes drainage system; E: Browns River drainage system; F: North West Bay River drainage system, whereas subdrainage system G drains into the Huon River drainage system: G: Mountain River drainage system. Red circles with 1 and 2 refer to two locations that are considered to be accidental translocations of *A. swaini* form 3 by an aqueduct that drew water from the west to the east side of Mt Wellington. Base image by TASMAPP (www.tasmap.tas.gov.au) © State of Tasmania.

Swallet and Settlement Cave (Ahyong 2016). *Anaspides swaini* occurs in the inflow creeks of Growling Swallet (Garths Creek) and Khazad Dum. Although, *A. swaini* has been recorded from Robert Tarn and the Mawson Plateau in the past (1970, 1975; see Ahyong 2016), *Anaspides swaini* is apparently now absent on the plateaus of the Mt Field National Park. Although Robert Tarn is currently inhabited by *A. richardsoni* only, our searches on the Mawson Plateau in March 2019 revealed no signs of any *Anaspides*, with the tarns being completely dried out.

Anaspides tasmaniae was found at four separate localities. Three of these localities lie outside the Mt Field National Park, alongside the Florentine Road, with two creeks draining from Nicholls Spur and one creek draining from Tyenna Peak. All of these three creeks are direct tributaries of the Tyenna River (Fig. 3). These creeks were situated in a tree fern rainforest, with low to no water flow at the time of sampling; *Anaspides* were mainly found in small seemingly isolated pools. All of these sites are in low-altitude areas at 320–340 m asl. The creek drainages (Tributary to Tyenna River I and II) originate

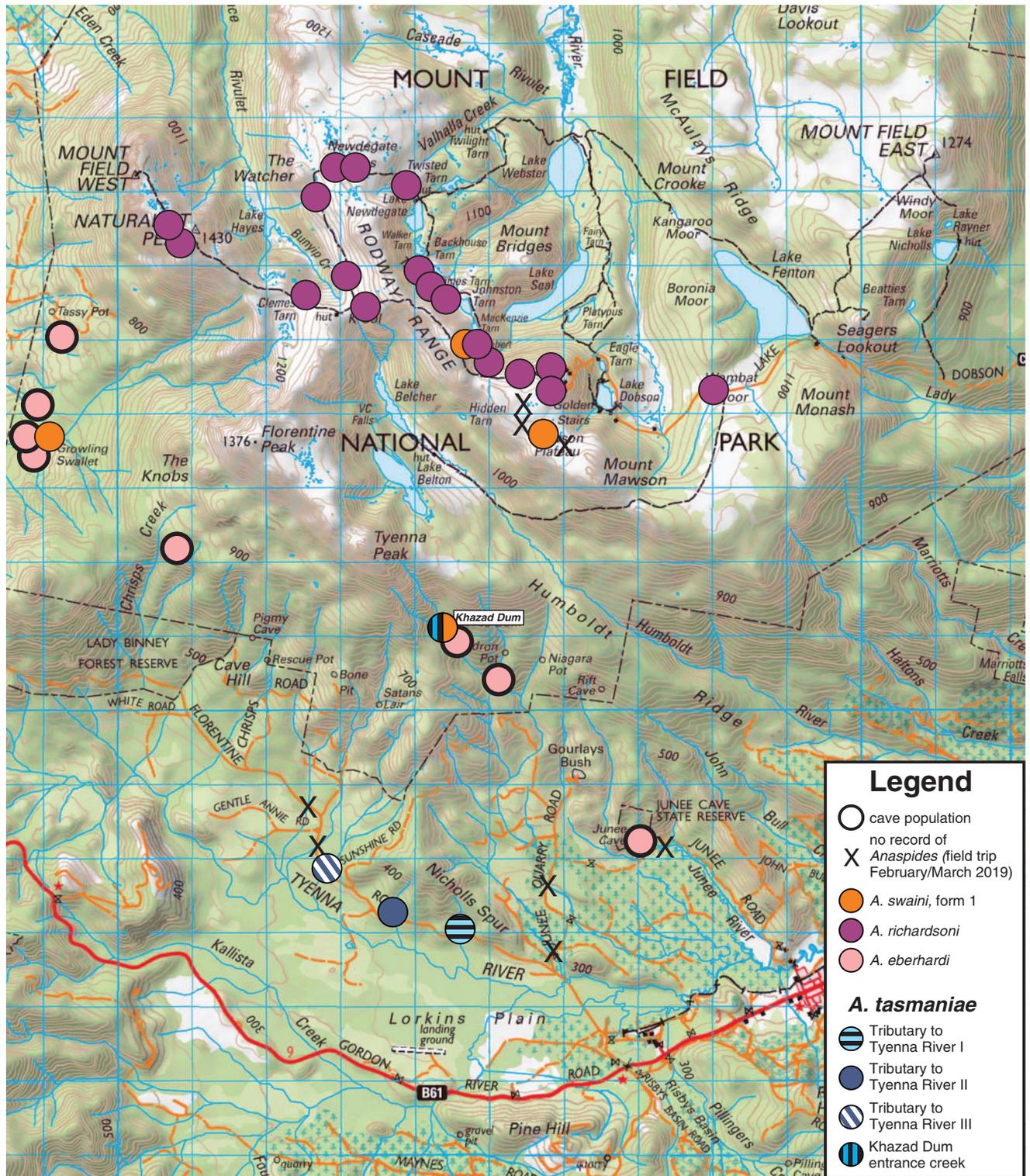


Fig. 3. Topographical map of Mt Field National Park to Gordon River Road with known collection sites of *Anaspides* from Ah Yong (2016) and collection sites from this study. Base image by TASMAM (www.tasmap.tas.gov.au) © State of Tasmania.

Table 1. Water quality parameters for four different collection sites of *A. tasmaniae*

Locality	Date	Water temperature (°C)	pH	Conductivity (µS/cm)	Salinity (psu)
The Chalet, Mt Wellington	19.02.2019	6.6	8.8	39.6	0.0
Khazad Dum entrance	22.02.2019	–	7.75	74.9	0.0
Tributary to Tyenna River I	22.02.2019	10.5	7.6	365.0	0.1
Tributary to Tyenna River III	01.03.2019	11.1	6.47	90.5	0.0

at Nichols Spur with a maximum altitude of 515 m asl, but how far upstream *Anaspides* occurs is unknown. The neighbouring two tributaries to the Tyenna River crossing the Florentine Road as well as two tributaries to the Tyenna River crossing the June Quarry Road had no *A. tasmaniae* (see Fig. 3). The fourth locality is within the Mt Field National Park, where *A. tasmaniae* occurs in the inflow creek to the Khazad Dum cave (760 m asl) (Fig. 3). Here, *A. tasmaniae* was found sympatrically with *A. swaini* (form 1) and although *A. tasmaniae* and *A. swaini* were found outside the cave entrance, as well as in the twilight zone (up to 30 m inside the cave), both species showed no signs of cave adaptation.

Water quality parameters were taken from four different collection sites of *A. tasmaniae*: The Chalet, Mt Wellington; Khazad Dum cave; Tributary to the Tyenna River I and III (Table 1). The water temperatures ranged from 6.6°C at Mt Wellington to 10.5–11.1°C at the other collection sites. The pH ranged from slightly acidic (6.47 at Tributary to the Tyenna River III) to alkaline (8.8 at Mt Wellington, 7.75 at Khazad Dum and 7.6 at Tributary to the Tyenna River I). The conductivity within the localities was always low, ranging from 39.6 µS/cm at Mt Wellington over 74.9 µS/cm at Khazad Dum and 90.5 µS/cm at Tributary to the Tyenna River I to 365 µS/cm at Tributary to the Tyenna River III. The salinity ranged in all localities between 0.0 and 0.1 psu.

Analyses of COI and 16S sequences of *Anaspides tasmaniae* from each of the studied localities recovered three haplotype lineages with six different haplotypes in COI and three haplotypes in 16S (Fig. 4). The first lineage comprises specimens found on the east and south-east side of Mt Wellington, whereas the specimens of the remaining two lineages are from within and adjacent to the Mt Field National Park. Specimens of the second lineage are from the entrance creek of Khazad Dum and specimens of the third lineage are from tributaries of the Tyenna River I, II and III draining from Nicholls Spur and Tyenna Peak (Fig. 3). Between the lineages we found only slight genetic differentiation (uncorrected p-distances: COI: 1.1–1.6%, 16S: 0.3–0.6%). In 28S, individuals of all three lineages share the same haplotype (Fig. 4).

Discussion

After the revision of *Anaspides* by Ah Yong (2016), the type species of the genus, *A. tasmaniae*, was shown not to be widespread throughout Tasmania, as had long been believed. It has a much more restricted range, confirmed by Ah Yong (2016) only from the east and south-east side of Mt Wellington. We now provide the first records of true

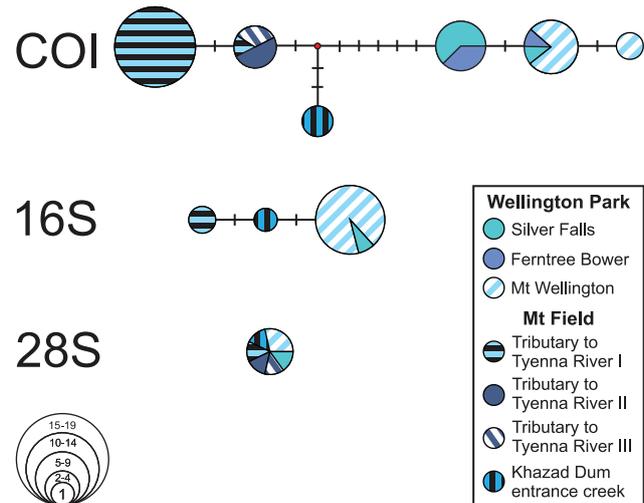


Fig. 4. COI, 16S and 28S median joining haplotype networks of *Anaspides tasmaniae*. Colours correspond to figure legend. The size of each haplotype corresponds to the number of individuals sharing that specific haplotype (see scale). Each dash corresponds to one mutation. The collection sites Silver Falls, Ferntree Bower and Mt Wellington are situated in Wellington Park, and Tributary to Tyenna River I–III and Khazad Dum entrance creek are located in and near Mt Field National Park.

A. tasmaniae from outside of Mt Wellington. *Anaspides tasmaniae* is present in three tributaries of the Tyenna River near Mt Field National Park as well as in the inflow waters of Khazad Dum (Fig. 5b, g). These localities are more than 50 km from the localities at which *A. tasmaniae* occurs at Mt Wellington and the water bodies are connected only via the Tyenna and Derwent rivers, in which *Anaspides*, however, does not occur (Fig. 1). Notably, *A. tasmaniae* occurs together with *A. swaini* (form 1) in the inflow creek of Khazad Dum, which is one of the few documented instances of sympatry in *Anaspides* and the only known locality where two *Anaspides* species actually occur in syntopy. There is no evidence for gene flow between these two species (unpubl. data).

Ah Yong (2016) reported specimens from Khazad Dum cave (Ah Yong 2016, fig. 34E–H) with a more rounded posterior telson margin as in *A. tasmaniae*, armed pleonite 5–6 terga and usually armed pleura as well, but tentatively considered these specimens to be aberrant *A. swaini*. We now reidentify these specimens as *A. tasmaniae*. Our specimens showed no apparent cave adaptations, which was also noted by Ah Yong



Fig. 5. Typical habitats and appearance of *A. tasmaniae*: (a) small residual pool of a runnel near Florentine Road (Tributary to Tyenna River III), Markus Grams measuring water parameters; (b) inflow creek to Khazad Dum cave; (c) small pool in runnel at Mt Wellington; (d) male, Creek on June Florentine Road from Nicholls Spur (Tributary to Tyenna River I); (e) female, creek on June Florentine Road from Nicholls Spur (Tributary to Tyenna River I); (f) female, small pool at Mt Wellington, the Chalet; (g) inflow creek and twilight zone of Khazad Dum cave; (h) adult specimens in a small pool at The Chalet, Mt Wellington.

(2016). Interestingly, Ah Yong (2016) mentioned also anomalous specimens similar to those from Khazad Dum from Risby Basin cave (located at the foot of the Maydena Range south of Gordon River Road, 8 km from Khazad Dum and draining as well into the Tyenna River), which potentially could also represent *A. tasmaniae*.

Furthermore, our searches 'confirmed' the absence of *Anaspides* on the Wellington Plateau. *Anaspides* was historically recorded from tarns on the plateau but has not been recorded there since major bushfires swept the area in the 1930s, permanently altering the habitat, resulting in the loss of tarns and swamp flora (O'Brien 1990). Ah Yong (2016) also mentioned that Manton (1930) observed two colour forms in *Anaspides* on Mt Wellington: a dark brown to olive-green form found on the Mt Wellington plateau, and a light brown form occurring on the slopes. Manton's dark form probably refers to *Anaspides swaini* (form 3), and the light brown form, to *A. tasmaniae*. Our observations support these hypotheses with *A. tasmaniae* ranging from light to medium brown (Fig. 5d–f, h) and *Anaspides swaini* (form 3) being much darker, ranging from dark brown to dark olive green. In the Browns River catchment, we found only *A. tasmaniae*, although specimens of *A. swaini* (form 3) were collected there in the early 20th century, having presumably been translocated from the North-west Bay catchment via a now defunct aqueduct (Ah Yong 2016). Evidently, the translocated *A. swaini* population has not survived.

The discovery of *A. tasmaniae* at independent localities around Mt Field, all distant from Mt Wellington, begs the question of whether the observed distribution is artificial or natural. Although *A. swaini* appears to have been translocated as a result of water-supply engineering in the early 20th century, no similar activities have occurred between Mt Wellington and Mt Field, nor are the localities in question subject to fishery stocking or other plausible interventions. Either way, if the Mt Field populations of *A. tasmaniae* were the result of artificial translocation from Mt Wellington, shared haplotypes would be expected. However, the genetic divergence between Mt Wellington and Mt Field populations indicates that the disjunct distribution is more likely to be natural, and we hypothesise that it relates to glacial events. The main limiting factor for the distribution of *Anaspides* appears to be water temperature (Williams 1965a; Swain and Reid 1983; O'Brien 1990). The species prefer cold water, although they are able to temporarily tolerate elevated water temperatures (Williams 1965a; Swain and Reid 1983). Also, the concentration of dissolved solids and turbidity could play a role in their distribution (Williams 1965a; Swain and Reid 1983; O'Brien 1990). Smith (1908) described the waters in which *Anaspides* occurs as 'ice-cold waters of absolute clarity', which is consistent with our field observations. Considering this, and that temperatures during glacial periods in the Pleistocene were 6–10°C lower than today, in combination with a lowered snowline (~1000–1500 m lower than current) and a lowered sea level (~120 m, 25 000 years ago) (Colhoun 1985; Lambeck and Chappell 2001; Thrush 2008; Colhoun *et al.* 2010), the Tyenna and Derwent rivers were potentially favourable habitats at that time. Thus, during

glacial periods, *A. tasmaniae* may have occupied a wider range including lower altitudes that encompassed the Tyenna and Derwent River catchments during the Pleistocene glaciations. The top of the mountains might not have been inhabited during glaciations although it is not clear whether the plateau of Mt Wellington had an ice cap (Davies 1958) whereas the plateaus of the Mt Field National Park were glaciated several times (Kiernan 1990; Mackintosh *et al.* 2006; Colhoun *et al.* 2010). The increasing interglacial temperatures would have led to contractions of suitable *Anaspides* habitat throughout Tasmania. In the case of *A. tasmaniae*, we suggest it occupied a wider continuous range during the Pleistocene glacials, and with postglacial warming became restricted to the higher and colder areas at Mt Wellington and in the Mt Field area, where they are relictual today.

Conservation

Although our research extends the known distribution (four new collection sites) of *A. tasmaniae* as well as its known genetic diversity through discovery of three distinct haplotype clusters in COI and 16S, the overall geographic range is still limited and the populations are vulnerable. This is especially the case for the three tributaries of the Tyenna River, which are outside the protected area of the Mt Field National Park in low-altitude areas. Additionally, the presence of *Anaspides swaini* (form 3) in adjacent drainages at Mt Wellington suggests that *A. tasmaniae* is indeed limited to the three water catchments at the east and south-east side of Mt Wellington. As Ah Yong (2016) stated, its conservation status requires reassessment to precisely determine its current distribution and population size, especially within the Mt Field National Park.

The Mt Field National Park and the Junee–Florentine Karst area can be considered as a hotspot of *Anaspides* diversity, with four species and several different genetic lineages occurring in that area. Furthermore, Mt Field National Park and the adjacent landscapes have great importance for the populations of *A. tasmaniae*, which is found only in a small range at the east and south-east of Mt Wellington and in four different localities in and alongside the Mt Field National Park. Current climatic trends will probably see further contraction of suitable habitats of *Anaspides* to higher altitudes in the future, making conservation planning even more poignant. It is uncertain if the Mawson Plateau or Mount Wellington Plateau will again become suitable habitats for *Anaspides* in the future. For the protection of this iconic species we suggest formal protection of the habitat of *A. tasmaniae* in the Mt Field area, perhaps by extension of the Mt Field National Park south over the Nicholls Spur to the Florentine Road between Junee Quarry Road and Drewhurst Road.

Conflicts of interest

The authors declare no conflicts of interest.

Declaration of funding

Collection of specimens in 2017 was funded by the German Science Foundation (DFG RI 837/22-1) and in 2019 was partly funded by the DAAD (Nr. 57438025, Kurzstipendien für

Doktoranden, 2019/2020) and the University of Rostock (Promotionsstipendienprogramm, 'Unsere Besten promovieren in Rostock'). The present project is funded by the German Science Foundation (DFG RI 837/22-2).

Acknowledgements

We are grateful to Alastair Richardson, Michael Driessen, Arthur Clarke, Cathy Plowman, David Butler, and Stefan Eberhard for enthusiastic support of our *Anaspides* research. We further thank the University of Tasmania, Institute for Zoology, especially David Green, for providing us with scientific equipment for our field trips. We are thankful to Markus Grams and Marian Reinhardt for assistance in the field and to Andrew Palfreyman for providing a new record on Mt Wellington. Specimens were collected under Tasmanian Department of Primary Industries, Parks, Water and Environment permit nos TFA16347 and FA18250. Ralf Bastrop (University of Rostock) provided the infrastructure for sequencing some of the data. We are grateful to the reviewers for their comments and suggestions.

References

- Ahyong, S. T. (2015). Preliminary diagnoses of three new species of Tasmanian mountain shrimps, *Anaspides* Thomson, 1894 (Syncarida, Anaspidae, Anaspidae). *Zootaxa* **3957**, 596–599. doi:10.11646/zootaxa.3957.5.8
- Ahyong, S. T. (2016). The Tasmanian mountain shrimps, *Anaspides* Thomson, 1894 (Crustacea, Syncarida, Anaspidae). *Records of the Australian Museum* **68**, 313–364. doi:10.3853/j.2201-4349.68.2016.1669
- Ahyong, S. T., and Alonso-Zarazaga, M. A. (2017). Anaspidesidae, a new family for syncarid crustaceans formerly placed in Anaspidae Thomson, 1893. *Records of the Australian Museum* **69**, 257–258. doi:10.3853/j.2201-4349.69.2017.1680
- Benson, D. A., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., and Wheeler, D. L. (2003). GenBank. *Nucleic Acids Research* **31**, 23–27. doi:10.1093/nar/gkg057
- Colhoun, E. A. (1985). Glaciations of the west coast range, Tasmania. *Quaternary Research* **24**, 39–59. doi:10.1016/0033-5894(85)90082-1
- Colhoun, E. A., Kiernan, K., Barrows, T. T., and Goede, A. (2010). Advances in Quaternary studies in Tasmania. In 'Australian Landscapes'. (Eds P. Bishop, and B. Pillans.) pp. 165–183. (Geological Society: London.)
- Davies, J. L. (1958). The cryoplanation of Mount Wellington. *Papers and Proceedings of the Royal Society of Tasmania* **92**, 151–154.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.
- Goede, A. (1967). Tasmanian cave fauna: character and distribution. *Helictite* **5**, 71–86.
- Jarman, S. N., and Elliott, N. G. (2000). DNA evidence for morphological and cryptic Cenozoic speciations in the Anaspidae, 'living fossils' from the Triassic. *Journal of Evolutionary Biology* **13**, 624–633. doi:10.1046/j.1420-9101.2000.00207.x
- Kiernan, K. (1990). The extent of late Cenozoic glaciation in the Central Highlands of Tasmania, Australia. *Arctic and Alpine Research* **22**, 341–354. doi:10.2307/1551459
- Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K. (2018). MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35**, 1547–1549. doi:10.1093/molbev/msy096
- Lake, P. S., and Coleman, D. J. (1977). On the subterranean syncarids of Tasmania. *Helictite* **15**, 12–17.
- Lambeck, K., and Chappell, J. (2001). Sea level change through the last glacial cycle. *Science* **292**, 679–686. doi:10.1126/science.1059549
- Mackintosh, A. N., Barrows, T. T., Colhoun, E. A., and Fifield, L. K. (2006). Exposure dating and glacial reconstruction at Mt. Field, Tasmania, Australia, identifies MIS 3 and MIS 2 glacial advances and climatic variability. *Journal of Quaternary Science* **21**, 363–376. doi:10.1002/jqs.989
- Manton, S. M. (1930). 36. Notes on the habits and feeding mechanisms of *Anaspides* and *Paranaspides* (Crustacea, Syncarida). *Proceedings of the Zoological Society of London* **100**, 791–800. doi:10.1111/j.1096-3642.1930.tb00998.x
- O'Brien, D. P. (1990). The conservation status of the mountain shrimp (*Anaspides tasmaniae* and *Anaspides spinulae*): a report on its distribution, ecology and taxonomy, including recommendations for management. Department of Parks, Wildlife and Heritage, Hobart.
- Richter, S., Olesen, J., and Wheeler, W. C. (2007). Phylogeny of Branchiopoda (Crustacea) based on a combined analysis of morphological data and six molecular loci. *Cladistics* **23**, 301–336. doi:10.1111/j.1096-0031.2007.00148.x
- Richter, S., Schwentner, M., Wirkner, C. S., and Ahyong, S. T. (2018). Phylogeny and species diversity of Tasmanian mountain shrimps and their relatives (Crustacea, Anaspidesidae). *Zoologica Scripta* **47**, 84–105. doi:10.1111/zsc.12263
- Smith, G. W. (1908). Preliminary account of the habits and structure of the Anaspidae, with remarks on some other fresh-water Crustacea from Tasmania. *Proceedings of the Royal Society of London* **80**, 465–473.
- Swain, R., and Reid, C. I. (1983). Observations on the life history and ecology of *Anaspides tasmaniae* (Thomson) (Syncarida: Anaspidae). *Journal of Crustacean Biology* **3**, 163–172. doi:10.2307/1548252
- Thompson, J. D., Higgins, D. G., and Gibson, T. J. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22**, 4673–4680. doi:10.1093/nar/22.22.4673
- Thomson, G. M. (1893). Notes on Tasmanian Crustacea, with descriptions of new species. *Papers & Proceedings of the Royal Society of Tasmania* 45–76.
- Thomson, G. M. (1894). III. On a freshwater schizopod from Tasmania. *Transactions of the Linnean Society of London, 2nd Series. Zoology* **6**, 285–303.
- Thrush, M. N. (2008). The Pleistocene glaciations of the Cradle Mountain region, Tasmania. Ph.D. Thesis, University of Newcastle, Newcastle.
- Williams, W. D. (1965a). Ecological notes on Tasmanian Syncarida (Crustacea: Malacostraca), with a description of a new species of *Anaspides*. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* **50**, 95–126. doi:10.1002/iroh.19650500109
- Williams, W. D. (1965b). Subterranean occurrence of *Anaspides tasmaniae* (Thomson) (Crustacea, Syncarida). *International Journal of Speleology* **1**, 333–337. doi:10.5038/1827-806X.1.3.7
- Xiong, B., and Kocher, T. D. (1991). Comparison of mitochondrial DNA sequences of seven morphospecies of black flies (Diptera: Simuliidae). *Genome* **34**, 306–311. doi:10.1139/g91-050

Handling Editor: Steven Cooper