

Larval burrow morphology and groundwater dependence in a mire-dwelling dragonfly, *Petalura gigantea* (Odonata: Petaluridae)

Ian R.C. Baird*

College of Health and Science, University of Western Sydney, Penrith South DC, NSW 1797, Australia

(Received 14 December 2013; accepted 3 June 2014)

Most species of petalurid dragonflies have a fossorial larval stage, which is unique in the Odonata. Larvae typically excavate burrows in soft peaty soils in mires, seepages or along stream margins, which are occupied by a single larva throughout the long larval stage. This paper reports on a study of burrow morphology in *Petalura gigantea*, with the objectives of describing their burrows, documenting any variability in burrow morphology across the hydrogeomorphic range of habitats used by the species, identifying factors contributing to any such variability, resolving questions in relation to the single previous illustration of a burrow system and identifying the level of groundwater dependence of larvae. The species was found to be an obligate, groundwater dependent, mire-dwelling species with well-maintained and sometimes complex burrows. Burrow complexity and morphological variation are inferred to be a response by larvae to the hydrogeomorphic characteristics of the habitat and substrate attributes. All burrows were occupied by a single larva, consistent with previous observations of other fossorial petalurids, but in contrast to the previous description of a *P. gigantea* burrow complex occupied by multiple larvae. The functional role of identified burrow features is discussed. Although the fossorial larval habit confers ecological benefits, the species' groundwater dependence and restriction to mire habitats places it at increased risk in the event of any reduction in groundwater availability, more intense fire regimes, and the potential compounding effects of rapid climate change.

Keywords: *Petalura gigantea*; Odonata; Petaluridae; larvae; burrow morphology; fossorial; groundwater dependence; mire; Blue Mountains, Australia

Introduction

The extant Petaluridae consists of five genera (Corbet, 1999; Fleck, 2011) with 11 species currently recognised worldwide, including the endemic Australian genus *Petalura* Leach with five species (Hawking & Theischinger, 2004; Theischinger & Endersby, 2009).

Within the Petaluridae, the majority of species have been described as “pit dwellers” that utilise a ground-dwelling, fossorial (burrowing) larval habit that is unique in the Odonata (Corbet, 1999). Fossorial petalurids excavate permanent burrows, with a burrowing habit documented in *Petalura gigantea* Leach (New South Wales [NSW], south-east Queensland), *P. hesperia* Watson (Western Australia), *Tanypteryx hageni* (Selys) (California, Oregon, Washington [USA], British Columbia [Canada]), *T. pryeri* (Selys) (Japan), and *Uropetala carovei* (White) and *U. chiltonii* Tillyard (New Zealand). These typically extend below the water table in soft peaty soils in mires,

*Current address: 3 Waimea St, Katoomba NSW 2780, Australia. Email: petalurids@gmail.com

seepages, or along stream margins, although there is considerable variation in burrow depth and complexity reported among species (Baird, 2012; Benson & Baird, 2012; Rowe, 1987; Svihla, 1959; Taketo, 1958, 1971; Tillyard, 1911, 1921; Watson, 1965; Winstanley, 1981, 1982; Wolfe, 1949, 1953). Exuviae of the tropical *P. ingentissima* Tillyard (north Queensland) have been found above small tunnels in rainforest stream banks (J.A.L. Watson, cited in Winstanley, 1982), with a burrowing habit confirmed by Karube (2003). Exuviae of *P. pulcherrima* Tillyard (north Queensland) and apparent ovipositing have also been observed in swampy patches adjoining stream banks, and apparent ovipositing along margins of a *Pandanus* swamp has also been reported (Theischinger & Endersby, 2009). The larval habits of this second tropical species are unknown, although it may be presumed that they are similar to *P. ingentissima*. Although previously assumed, a recent study has also confirmed a burrowing habit in *P. litorea* Theischinger (north-eastern coastal NSW, south-eastern coastal Queensland) (I.R.C. Baird, unpublished observations).

In contrast, the North American (eastern USA; Paulson, 2011) *Tachopteryx thoreyi* (Hagen) and South American (central and southern Chile and Patagonian Argentina; Garrison, von Ellenrieder, & Louton, 2006) *Phenes raptor* Rambur have a non-burrowing terrestrial larval habit (for review, see Baird, 2013b; Corbet, 1999).

Fossorial petalurid larvae reportedly commence burrow excavations during early larval instars, with a positive correlation between burrow diameter and larval stadia reported in *Uropetala* spp. (Wolfe, 1953) and *T. pryeri* (Taketo, 1958, 1971). Early stadia larvae of *T. pryeri* (Taketo, 1958) and *T. hageni* (Svihla, 1984) have also been observed in moist sites amongst mosses and decaying leaves prior to burrow development. Once established, burrows are occupied throughout the larval stage, through to emergence. A long larval stage of five years has been documented in *Tanypteryx hageni* (Baird, 2012, pp. 27–28; Valley, 2000), and of at least five years, extrapolated for *Uropetala* spp. (Wolfe, 1953). Based on extrapolations from his observations on the rate of burrow widening in *U. chiltonii* in sub-alpine habitats, Richard Rowe (personal communication, 5 June 2011) has suggested that the larval stage in this species could potentially reach over 20 years in such habitats. Extrapolation from a landscape-scale population study (Baird, 2012, ch. 7) and a partial larval rearing study (J.W.H. Trueman, personal communication, 23 November 2006; Baird, 2012, pp. 26–27) suggest, respectively, a larval stage of at least six years, and possibly 10 or more, in *P. gigantea*.

Maximum depths recorded for petalurid burrows include burrows up to 15 cm deep in *T. hageni* (Svihla, 1959), up to 24 cm (mostly <15 cm) in *T. pryeri* (Taketo, 1971), at least 60 cm in *P. gigantea* (Tillyard, 1911), at least 40 cm in *P. ingentissima* (R. McCormack, personal communication, 1 April 2013), 60 cm in *P. hesperia* (Watson, 1965) and *Uropetala* spp. (Wolfe, 1953), and 64 cm in *P. litorea* (I.R.C. Baird, unpublished observations). The figures for *P. gigantea*, *P. ingentissima*, and possibly *P. hesperia*, are based on single excavations.

Petalura gigantea has been reported as inhabiting permanent seepages, bogs and swamps of the NSW coast and ranges, from near the Victorian border to near the Queensland border, and between near sea level and 1240 m altitude (Baird, 2012; Benson & Baird, 2012; Davies, 1998; Hawking & Theischinger, 2004; Theischinger, 2001; Theischinger & Endersby, 2009; Trueman, 2000). The species has also been recorded in a montane bog in Girraween National Park in south-eastern Queensland (M. Mathieson, personal communication, 19 September 2013). The species is listed as endangered in NSW (NSW Scientific Committee, 1998). All recorded habitats of the species may be considered peat swamps or mires (bogs and fens) and included within the *Coastal Heath Swamps* or *Montane Bogs and Fens* Freshwater Wetland vegetation classes of Keith (2004). The species has been recorded from both vegetation classes in the Blue Mountains region (Baird, 2012, ch. 6). These mires may all be considered groundwater dependent ecosystems (NSW Government, 2002; Serov, Kuginis, & Williams, 2012) with proportional dependence on groundwater (Baird, 2012, ch. 6; *sensu* Clifton & Evans, 2001). In Australia, the term “swamp”, as used in this paper, is a generic term which may refer to a wide range of wetland types, including

peat forming bogs and fens (mires), in contrast to its more specific application in the USA, for example (see Cowardin, Carter, Golet, & LaRoe, 1979). Similarly, the terms “bog” and “fen” are used somewhat differently in Australian mire literature (see Whinam & Hope, 2005 for a discussion of the Australian context). Although mire habitats of *P. gigantea* include bogs and fens in the Australian context, these would generally be considered fens in traditional northern hemisphere mire classifications (see Gore, 1983). However, in terms of our current understanding of the global diversity of mire ecosystems, and their developmental factors and environmental gradients, the validity of applying some of these traditional typologies more universally has been questioned (e.g. Wheeler & Proctor, 2000; Whinam & Hope, 2005). The species has been recorded from six different mire types (differentiated primarily on vegetation characteristics) in the Blue Mountains, with potential habitat identified in an additional four types. These mires have developed on sedimentary, metasedimentary and igneous geologies, with recorded localities of *P. gigantea* across the Blue Mountains region between 180 and 1240 m altitude, and identified potential habitat up to 1270 m (Baird, 2012, ch. 6).

As a result of the complex topography and hydrogeology of the Blue Mountains, these mires are characterised by considerable spatial heterogeneity in the distribution, depth and characteristics of organic-rich peatland soils (e.g. Chalson & Martin, 2009; King, 1993, 1994), and spatio-temporal heterogeneity in hydrology (e.g. Holland, Benson, & McRae, 1992), within and among swamp patches and swamp types (e.g. for Newnes Plateau Shrub Swamps, see Benson & Baird, 2012). These swamps include a range of hydrogeomorphic expressions, including low gradient, valley floor, impeded drainage swamps; hanging swamps associated with relatively impermeable strata (aquitards or aquicludes) on steeper valley sides; and localised fracture-controlled seepage springs. Many include examples of each within mires developed continuously across a complex topographic surface and characterised by a complex piezometric surface (Baird, 2012). Mires develop where the water table is emergent, and may be associated with perched or extensive unconfined aquifers, or as effluent discharge from confined aquifers (Marshall, 2005). An understanding of the hydrological and substrate characteristics of these mire habitats is fundamental to understanding the ecology of the fossorial larvae of *P. gigantea*.

Information on the biology and ecology of *P. gigantea* includes the early publications by Tillyard (1909, 1911, 1917) and results of more recent studies (Baird, 2012, 2013a; Baird & Burgin, 2013; Baird & Ireland, 2006; Benson & Baird, 2012; Dearson, 1999; Theischinger, 1975, 1999, 2001; Trueman, 2000). Tillyard (1911) excavated a single *P. gigantea* burrow system in a montane mire in Medlow Bath, Blue Mountains, providing the only documentation of burrow morphology or information on larval ecology in this species prior to the current study. Tillyard illustrated a complex burrow system with multiple surface openings and anastomosing tunnels (Figure 1a). Most of the burrow system was below the groundwater level. In contrast, in the only other documented *Petalura* burrow, Watson (1965) illustrated a simple, mostly groundwater-filled, descending burrow in *P. hesperia*, with a number of short lateral chambers which increased in length and diameter with increasing burrow depth, putatively associated with increasing larval size (Figure 1b). The Watson (1965) illustration is virtually identical to one variation in *Uropetala* burrow morphology illustrated by Wolfe (1953). Tillyard (1911) found labia of the fully aquatic larvae of *Griseargiolestes griseus* (Hagen) (Odonata: Argiolestidae) in the gut of two *Petalura* larvae; and suggested that the *Petalura* larvae were utilising identified underwater burrow openings on burrow branch tunnels to access underwater habitat in water-filled seepage depressions containing larvae of this prey species. Such underwater burrow openings would provide opportunities for foraging within water-filled depressions and/or ambush predation from within the burrow opening. In the case of burrow openings that are not submerged, the possibility that *Petalura* larvae may leave their burrows to forage above ground under favourable conditions, or practice ambush predation from within their burrow entrances, as reported in *Uropetala* (Rowe, 1987; Wolfe, 1953) and *Tanypteryx* spp. (Svihla, 1959, 1984; Taketo, 1971), and previously suggested for *P. gigantea*, has not been confirmed.

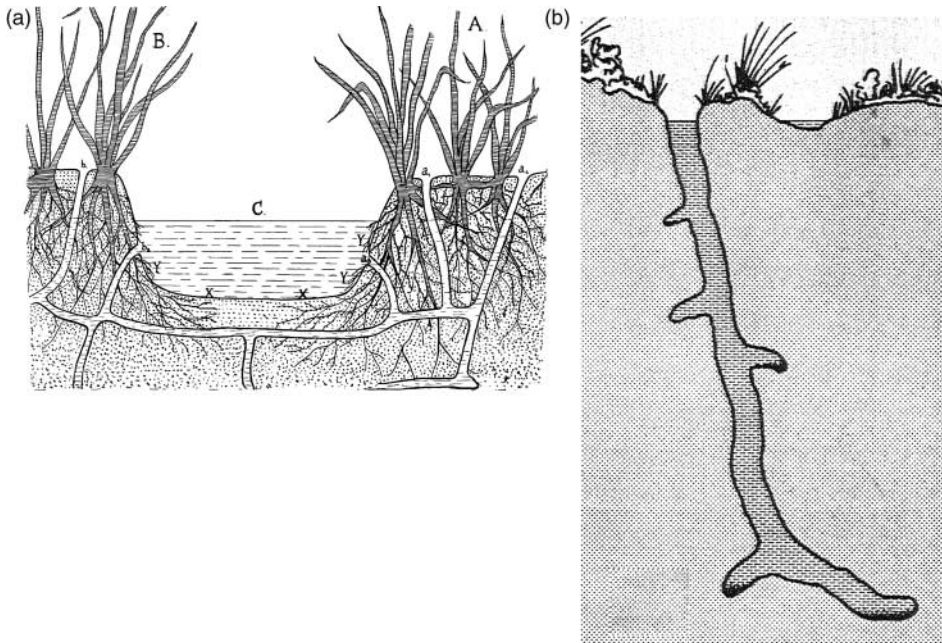


Figure 1. (a) The Tillyard (1911) illustration of a complex anastomosing *Petalura gigantea* burrow system (reproduced courtesy of the Linnean Society of NSW); (b) The Watson (1965) illustration of a simple *P. hesperia* burrow with short lateral chambers (© *Animals* magazine).

With the typical predatory and generally cannibalistic foraging behaviour in odonate larvae (Corbet, 1999), and cannibalism confirmed in *Uropetala* (Harding, 1977; Wolfe, 1953), *T. hageni* (Turner, 1970) and *T. pryeri* (Taketo, 1971), the suggestion by Tillyard (1911) of *P. gigantea* larvae of multiple stadia occupying a single burrow complex with multiple surface openings appears improbable; a point also noted by Winstanley (1982). It is most likely that Tillyard excavated multiple discrete burrows of *P. gigantea* in close proximity that were not clearly differentiated during the excavation process, in what appears to have been highly unstable sediment. In contrast to the complex anastomosing *P. gigantea* burrow illustrated by Tillyard, all other petalurid burrow investigations have revealed simple burrow structures occupied by single larvae.

Burrow investigations offer the opportunity to better understand larval development, behaviour and ecology; and groundwater dependence in fossorial species such as *P. gigantea*. Variation in burrow morphology within a species, in response to substrate variability, has previously been reported in burrowing marine shore crustaceans (Katrak, Dittmann, & Seuront, 2008; Morrisey, DeWitt, Roper, & Williamson, 1999), and considerable variability among burrows has been documented in *Tanypteryx* and *Uropetala* spp. Documenting burrow morphology in *P. gigantea*, across a range of habitats with varying environmental attributes, may thus reveal important aspects of larval ecology and assist in defining its bioclimatic envelope. This may contribute, in time, to understanding the evolutionary divergence in larval lifestyles between the non-fossorial and fossorial petalurids, in conjunction with phylogenetic, morphological and historical biogeographical (palaeoecological) research (e.g. Fleck, 2011; Ware et al., 2014). It will also contribute to better understanding of threats to these species, particularly from habitat loss and degradation, and the potential compounding threats associated with a rapidly changing climate (Baird, 2012, ch. 8). In the context of the lack of knowledge of the larval stage of *P. gigantea*, and questions in relation to the previous single burrow excavation (Tillyard, 1911), detailed burrow investigations were desirable. All previous burrow investigations of fossorial petalurids have involved some form of simple excavation.

In addition to simple excavations, various materials have been used to create casts of burrows of diverse burrowing invertebrates, particularly crustaceans with at least partly water-filled and often complex branching burrows. These materials include plaster of Paris (e.g. [Growth & Richardson, 1988](#)), liquefied cements (e.g. [Morrissey et al., 1999](#)) and polyester resin (e.g. [Shimoda & Tamaki, 2004](#)). These techniques require subsequent excavation of the cast, with the associated substrate disturbance varying greatly in its impact among habitats and species. The use of casts assumes mortality of burrow occupants unless the burrow is unoccupied, and imposes logistical demands when habitats are remote or have difficult access, such as in the topographically complex landscape of the Blue Mountains.

This paper reports on a study of burrow morphology in *P. gigantea*, with the objectives of better understanding larval ecology, habitat requirements and groundwater dependence in the species, and resolving questions in relation to the single previous illustration of a burrow system by [Tillyard \(1911\)](#). A synthesis of some of the results of this study has been published previously ([Baird, 2012](#); [Benson & Baird, 2012](#)).

Methods and materials

This study of *Petalura gigantea* burrow morphology was undertaken in the Blue Mountains region, NSW, Australia (150°20' E, 33°40' S), during November and December 2007; and January, February, March, November and December 2008. Burrows were investigated in four of the six peat swamp types where the species was recorded across the region ([Baird, 2012](#), ch. 6): Blue Mountains Sedge Swamps, Boyd Plateau Bogs, Coxs River Swamps ([Benson & Keith, 1990](#); [Keith & Benson, 1988](#)) and Kurrajong Fault Swamps ([Blue Mountains City Council, 2002](#); [Smith & Smith, 1996](#)). Burrow investigations were undertaken across the range of hydrogeomorphic expressions of swamp types of the region. In addition, hundreds of oviposition sites, burrow openings and emergence locations were observed in a range of habitats across all swamp types where the species was recorded as part of a larger landscape-scale study ([Baird, 2012](#)), providing further information on microhabitat attributes of breeding sites.

Because of the endangered status of *P. gigantea* and its mire habitats, only burrows where emergence had been identified by the presence of an exuvia perched above or near the burrow opening were investigated. For the same reason, this study did not utilise polyester resin or other casts. The presence of groundwater in burrows, and the instability (in some swamps) of the sapric peaty substrate (particularly below the root zone) when disturbed, also precluded the use of full excavations to expose and document burrow architecture, particularly for deeper burrows. A permanent record of burrow architecture was obtained by initial use of a serrated 15 cm knife to cut along the burrow axis through any tough, fibrous, surface root zone to expose the upper burrow section, followed by digital investigation and detailed illustrations based upon direct field measurement. These were at least comparable in detail to the illustrations of burrow morphology for the other petalurids and crustaceans noted above, and they provided sufficient resolution for comparison of burrow morphology and microhabitat attributes, between burrows, and among swamp patches and types.

The initial incision in the substrate was made for a length of *c.*20 cm centred on the burrow opening. Additional vertical incisions were made at each end of and on one side of this initial incision, to form a U-shaped incision. A final angled incision was then made from the ends of the "U" to join the bottom of the initial incision. The resulting block of material was then removed, permitting the upper burrow section to be revealed in cross-section. Depth to water level within the burrow was measured before excavating below this level. Excavated sections, including any small rooted plants, were replaced in sequence following the burrow investigation. Subsequent monitoring confirmed a high level of substrate stability and regeneration of vegetation.

Progressively deeper burrow sections were investigated using an index finger as a probe to identify descending burrow angle and additional morphological features such as lateral chambers, terminal chambers or branch tunnels. Whenever a new feature or change in burrow angle was detected, inserting the steel tape measure and measuring from the surface determined the depth. The length of deeper lateral chambers was estimated using the index finger as a gauge, as they were typically shorter. Pushing the hand down through the burrow was usually reasonably easy due to the nature of the soft organic-rich substrate; however, denser sandy layers sometimes required additional use of the knife. This technique also permitted longer side tunnels to be investigated and measured. Upper burrow and lateral chamber diameters were measured, while diameters of deeper burrow sections were estimated based on the number of specific fingers that would fit in the burrow diameter at that point and amount of movement available.

Soil depth was determined using a 1.8 m long \times 8 mm diameter steel rod probe for most burrows investigated. Depth of sediment was thus only recorded up to 1.8 m, until the probe contacted bedrock, or until it was difficult to push the probe deeper, indicating a dense mineral substrate (e.g. sand, gravel or clay loam) which larvae would have difficulty excavating. Soil depth was not determined for burrows in remote locations or where opportunistic investigations were carried out. Typically, three probes were taken around each burrow location and averaged.

Slope at burrow locations was measured using a Suunto® clinometer (Suunto, Vantaa, Finland) over a distance of 5 m to remove localised irregularities associated with hummock- or tussock-hollow microtopography.

Results

The swamp patches and swamp types where burrow investigations were undertaken are shown in Table 1. These ranged from low gradient, valley floor, impeded drainage swamps to hanging swamps on valley sides. Thirty-three confirmed *Petalura gigantea* burrows were investigated across 10 swamp sites, representing four swamp types; but due to logistical reasons, not all to their full depth. Ten additional burrows, which were investigated partly, are not included in these results due to uncertainty as to their identification as *Petalura* burrows or the presence of anomalous characteristics. During investigation of some burrows, additional burrows were identified in close proximity, and partly investigated. One final stadium ♂ larva, c.4.5 cm in length (Figure 2), was located in a terminal chamber of a burrow which was investigated in the mistaken belief that it was unoccupied. The depth of the swamp sediments to bedrock or relatively impenetrable material, based on the results of the soil depth probe at burrow locations, and surface slope, are shown in Table 1. Of the 33 *Petalura* burrows that were investigated, and for which data are presented, 27 were investigated to full depth. Burrow depths ranged from 18 to 75 cm, the deepest depth recorded for a petalurid burrow worldwide, with a mean depth of 37 cm (seven burrows <30 cm, seven burrows >39 cm, one burrow >60 cm) (Table 1). Figure 3 illustrates a range of typical burrow morphological features and Figure 4 illustrates a representative selection of burrows investigated.

Substrates varied from relatively dense clay loams, organic sands and peaty loams to soft sapric peat, fibrous peat and sandy peat, with considerable variation in density and organic content, frequently between distinctive strata within a single burrow. Denser and more mineral rich material was generally recorded deeper in the soil profile. Individual burrows also frequently included gravel, sand or fine charcoal layers within more organic-rich soils. Localised areas within some montane bogs, particularly in association with low gradient, braided drainage systems, consisted of small patches of vegetation growing in a shallow peaty root-mat layer “floating” on saturated muck. A positive correlation between burrow diameter and organic content was observed qualitatively, both within and between burrows. Burrows varied in diameter, nominally from 2 to 4.5 cm, although most were 2.5–3.5 cm. Burrow sections in denser organic sands and clay loams, or soils

Table 1. Swamp patch, swamp type, and characteristics and dimensions of *Petalura gigantea* burrows investigated. Read in conjunction with Figures 3 and 4.

Burrow number	Swamp patch code ¹	Swamp type ²	Soil depth (cm)	Slope (°)	Lateral chambers (n)	Terminal chamber (Y/N)	Burrow investigated to full depth (Y/N)	Burrow openings (n)	Branch tunnel (Y/N)	Above-ground chamber (Y/N)	Burrow dimensions (cm)					Total burrow depth
											V	W	X	Y	Z	
1	PBB01	06	170	2	2	Y	Y	1	N	Y	43	14	16	5	—	43
2	PBB01	06	> 180	2	1 ³	Y	Y	1	N	Y	30	8	11	—	—	30
3	PBB01	06	> 180	2	1 ⁴	Y	Y	1	N	Y	28	16	8	—	—	28
4	PBB01	06	> 180	2	1	Y	Y	1	N	N	33	8	5	19	6	39
5	PBB01	06	> 180	2	1 ⁴	Y	Y	1	N	N	28	9	5	—	—	28
6	PBB01	06	> 180	1	5	Y	Y	1	N	N	51	14	10	16	—	51
7	PBB01	06	> 180	2	1 ⁴	Y	Y	1	N	N	35	22	17	—	—	35
8	PBB01	06	> 180	2	0	Y	Y	1	N	N	18	—	2	—	—	18
9	PBB01	06	> 180	2	1	Y	Y	1	N	N	32	12	8	—	—	32
10	PBE01	01	—	—	2	Y	Y	1	N	N	25	15	31	5	50	75
11	PKB05	03	140	1	1	Y	Y	1	N	N	36	19	10	—	—	36
12	PKB05	03	104	1	1 ⁴	Y	Y	1	N	N	20	14	3	—	—	20
13	PKB05	03	60	1	1	Y	Y	1	N	Y	26	7	3	—	—	26
14	PKB05	03	45	2	1	Y	Y	1	N	N	44	23	20	—	—	44
15	PKB05	03	40	3	1 ⁴	Y	Y	1	N	N	35	9	5	—	—	35
16	PKB07	03	60	2	1	N ⁵	Y	1	N	N	39	25	18	—	—	39
17	PKB07	03	74	2	1	Y	Y	1	N	N	25	15	15	—	—	25
18	PKB07	03	52	2	0	Y	Y	1	N	N	35	—	20	—	—	35
19	PKB07	03	52	2	1	Y	Y	1	N	N	33	20	20	—	—	33
20	PKU01	04	> 180	2	2	Y	Y	2	N	Y	32	18	2	—	—	32
21	PMH01	01	180	5	4 ⁴	Y	Y	1	Y	N	38	15	15	13	8	46
22	PMH01	01	95	14	2 ⁶	Y	Y	1	N	N	43	15	5	19	—	43
23	PMH01	01	—	5	1 ⁷	Y	Y	1	N	N	30	—	—	—	—	30
24	PMH01	01	—	5	1	Y	Y	1	N	N	50	13	2	—	—	50
25	PMH01	01	—	3	2 ⁸	—	N	1	N	N	—	12	24	12	—	—
26	PMH01	01	—	1	5 ⁹	—	N	2	Y	N	—	9	6	7	—	—
27	PMH01	01	—	3	4 ¹⁰	—	N	1	N	N	—	14	23	10	—	—
28	PMH01	01	> 180	5	1 ¹¹	—	N	1	N	N	—	10	5	—	—	—

(Continued)

Table 1. Continued.

Burrow number	Swamp patch code ¹	Swamp type ²	Soil depth (cm)	Slope (°)	Lateral chambers (n)	Terminal chamber (Y/N)	Burrow investigated to full depth (Y/N)	Burrow openings (n)	Branch tunnel (Y/N)	Above-ground chamber (Y/N)	Burrow dimensions (cm)					Total burrow depth
											V	W	X	Y	Z	
29	PMH02	01	—	9	1	—	N	1	N	N	—	11	10	—	—	—
30	PMH08	01	—	0	3 ¹²	—	N	1	N	N	—	8	7	—	—	—
31	PMH18	01	—	6	1 ¹¹	Y	Y	1	N	N	55	13	12	—	—	55
32	PMH18	01	—	6	3 ¹³	Y	Y	2	N	N	41	6	5	4	19	60
33	PNN01	01	—	—	1 ¹⁴	Y	Y	2	Y ¹⁵	N	35	9	5	—	—	35

¹Swamp patch location details, see Baird (2012, Appendix 1).²Swamp type (from Baird, 2012): Blue Mountains Sedge Swamps (01), Boyd Plateau Bogs (03), Kurrajong Fault Swamps (04), Coxs River Swamps (06).³Presence of 8 cm deep × 8 cm diameter burrow space at burrow opening in very soft substrate may represent a collapsed upper lateral chamber.⁴Horizontal section of burrow between two offset descending burrow sections treated as a lateral chamber variation (see Figure 4).⁵Due to the soft substrate, it is possible that some terminal burrow expansion had occurred, but that a chamber was not identified.⁶One lateral chamber was small and the other consisted of a swelling of the burrow along the burrow axis.⁷Additional lower chamber consisted of a swelling of the burrow along the burrow axis.⁸Both lateral chambers shorter than typical lateral chambers.⁹Putative primary burrow with two typical length lateral chambers and two short lateral chambers; secondary branch burrow with second surface opening had one typical lateral chamber.¹⁰One typical lateral chamber, one short chamber and one forked chamber.¹¹One typical lateral chamber with burrow section immediately above swollen along burrow axis.¹²Upper lateral chamber typical size, with two short lower lateral chambers.¹³Upper near-surface lateral chamber typical size, with second burrow opening at far end. Second lower lateral chamber small and lowest lateral chamber forming horizontal section between two offset descending burrow sections.¹⁴Near-surface lateral chamber unusually long (20 cm), with indistinct secondary burrow branch and opening to surface.¹⁵15 cm long ascending lower branch tunnel with indistinct terminal chamber. Branch tunnel intersects main burrow at 23 cm deep.



Figure 2. Final stadium ♂ *Petalura gigantea* larva found in the terminal chamber of a burrow in a montane fen in the Blue Mountains, NSW, 2 December 2008. Photo by Ian Baird.

with dense roots and rhizomes were typically narrower in diameter than those in softer peats, generally varying from 2 to 2.5 cm in diameter.

Terminal chambers of some burrows had small deposits of loose material which had either not been removed during burrow maintenance or which had accumulated since emergence and cessation of burrow maintenance. Burrows in Boyd Plateau Bogs, which overlie granite bedrock, had small quantities of granite gravel in terminal chambers, and on occasion in lateral chambers and outside the burrow entrance where it had been deposited (Figure 4[B12, B13, B19]). Two of the nine burrows investigated in Boyd Plateau Bogs terminated in a thin layer (<2 cm) of granite gravel directly overlying granite bedrock, where further burrow deepening was impossible. Particularly in micro-sites with sandier substrate (organic sands) and/or a substrate with a dense fibrous surface mat of roots and rhizomes, the diameter of the burrow opening of final stadia larvae was frequently only about 13 mm, considerably less than the internal burrow diameter. This was consistent with the single description of burrow opening diameter by Tillyard (1911). This clear contraction at the burrow opening was less frequently observed in burrows in more organic-rich substrates, where the opening diameter was often closer to the internal burrow diameter. However, the nature of burrow openings varied depending on the characteristics of the litter layer or ground-layer vegetation cover (e.g. presence of dense low herbs or *Sphagnum*), the extent to which the burrow opening was capped with excavated material, and in response to fire history, particularly a recent fire event. Burrow openings varied from being well-defined circular holes to being irregular in appearance. See Baird (2012, pp. 12–22, 239–240) for photographs of burrow openings and associated features reported here.

Mire habitats of the species are typically dominated by a hummock- or tussock-hollow microtopography characterised by a distinct elevation and moisture gradient (Baird, 2012, ch. 6). Almost all burrows documented in this study at time of observation had openings above the emergent

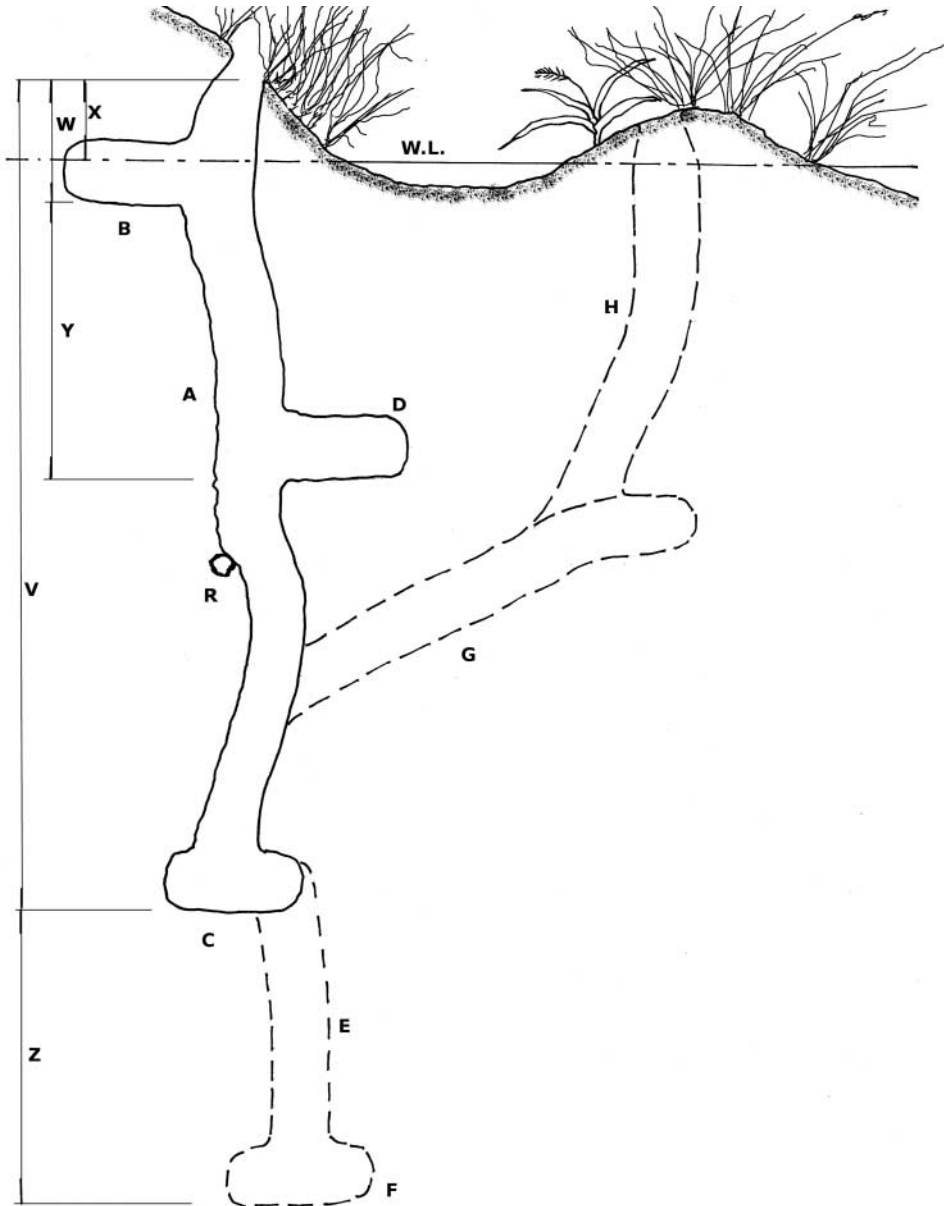


Figure 3. Illustration of a stylised *Petalura gigantea* burrow, showing ground surface (shaded), water level (W.L.), woody shrub root (R), dimensions (V–Z), and a range of possible morphological features (A–H): (A) descending burrow section; (B) upper lateral chamber; (C) terminal chamber; (D) secondary lateral chamber; (E) descending burrow section putatively associated with adaptive burrow deepening during drought; (F) associated second terminal chamber; (G) secondary burrow branch; and (H) associated ascending burrow branch opening to surface. Not all features are present in all burrows and additional anomalous features occur. Read in conjunction with Table 1, Figure 4 and text.

water level and were frequently located amongst vegetation tussocks or *Sphagnum* hummocks. At the time of investigation, all burrows were characterised by the presence of some groundwater, usually within most of the burrow depth, although groundwater depth below the burrow entrance varied (Table 1, Figure 4). No burrows were identified with primary or secondary underwater burrow openings which would have been permanently inundated.

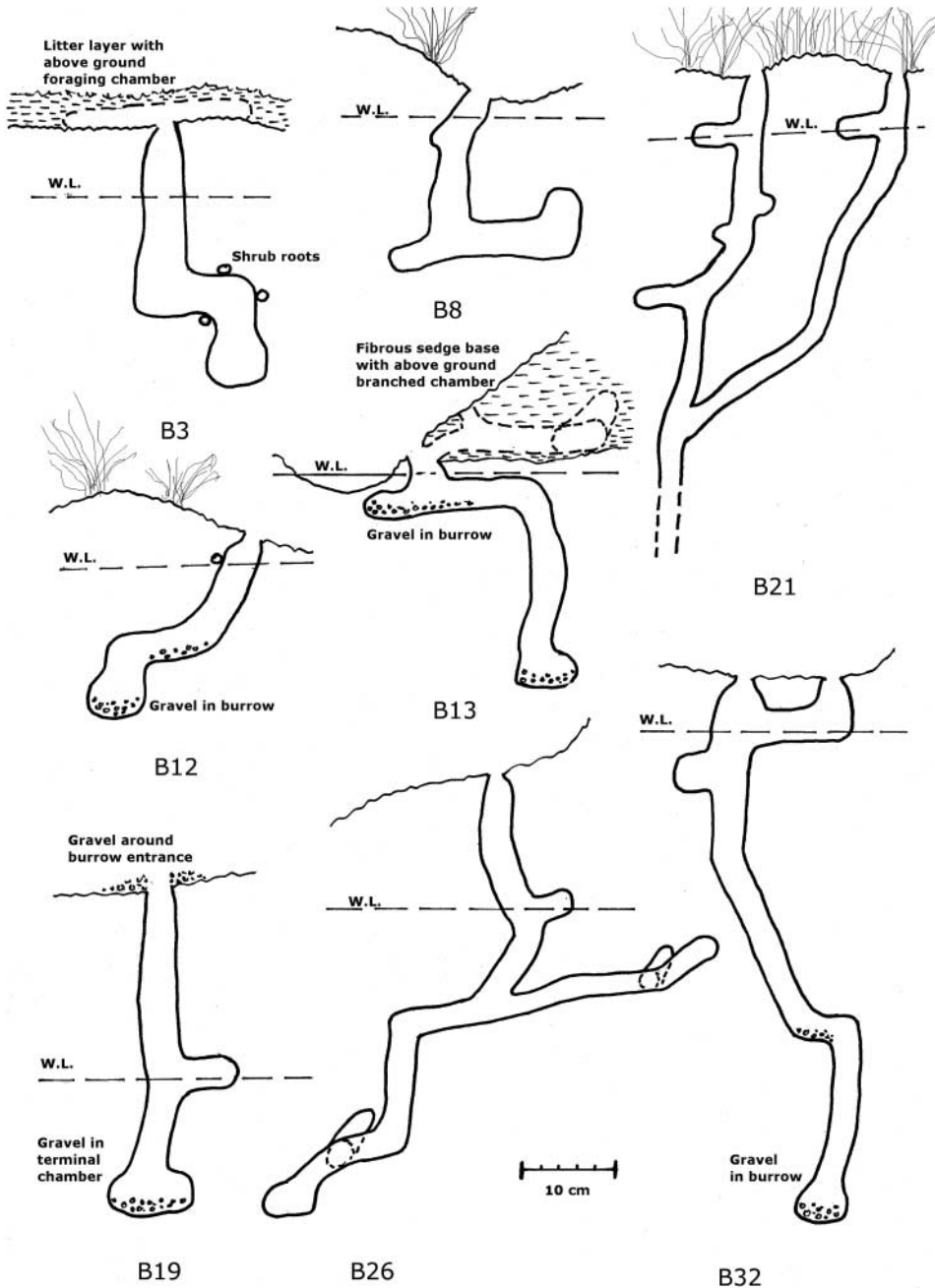


Figure 4. Illustrations (to scale) of selected examples of *Petalura gigantea* burrows investigated, with water level (W.L.) at time of excavation. B3 to B19 occurred in low gradient Montane Bogs and Fens, while the deeper and more morphologically complex burrows, B21 to B32, occurred in Blue Mountains Sedge Swamps, a sandstone-based swamp type with greater hydrogeomorphic complexity. Refer to Table 1 for further details of these burrows.

Most burrows also consisted of a single opening and a single more or less vertically descending burrow (sometimes sloping); with a variable number (often one) of more or less horizontal side chambers (of variable length) and a terminal chamber (Figures 3, 4). In a few cases, burrows did not include lateral chambers, but did include a terminal chamber (Table 1). Terminal chambers were

usually nominally horizontal, and were aligned either to one side of the descending burrow axis, as for typical lateral chambers, or were more or less centred at the end of the burrow. In some cases, terminal chambers were oriented vertically along the burrow axis, consisting of a widening of the burrow diameter over a similar length as that of typical horizontal lateral chambers. In some burrows, in addition to horizontal lateral chambers, additional vertical chambers were located along the descending burrow axis, also having an increased burrow diameter for a short distance, particularly where burrow diameter was otherwise smaller due to a denser substrate. These were most frequently located between the burrow entrance and the upper horizontal lateral chamber. In at least one case, there was a vertically aligned chamber created through expansion of the descending burrow, but no horizontal lateral chamber. Whenever woody roots are encountered by larvae during burrow excavation, the burrow is typically re-aligned around the roots (Figures 3, 4). Such re-alignments generally appear to be the cause of most deviations from a simple, more or less vertical, descending burrow, with the exception of situations where the larva encounters material which is more difficult or impossible to excavate through (e.g. bedrock or dense gravel), and it is forced to either terminate burrow deepening or follow any descending surface of the obstructing layer, where possible (Figure 4[B26]). Lateral chambers most frequently extended for *c.* 5–7 cm, a suitable length to accommodate a late stadium larva (4.5–5 cm length). A number of burrows also included shorter and sometimes smaller diameter lateral chambers (Figure 4[B21]), most frequently above the upper, typical sized, lateral chambers, but also at times below them. There was rarely more than one of these shorter chambers. Some included other morphological features, such as a secondary branch tunnel, and, rarely, an associated burrow opening (Table 1; Figure 4[B21]). In two instances, a secondary branch tunnel also included additional lateral chambers (Figure 4[B26]). All except one of the more morphologically complex branching burrows were located in somewhat steeper sloping patches in Blue Mountains Sedge Swamps, a sandstone-based swamp type (Table 1).

In some cases burrow density was high, and it was not possible to even partially excavate one burrow without disturbing an adjacent, but discrete burrow. Several burrow openings were recorded within 15 cm on various occasions. In several cases, while excavating a burrow with an exuvia perched outside, and only one burrow opening evident, up to three additional burrows of what were assumed to be late stadia larvae (based on burrow diameter) were identified incidentally in a closely spaced burrow aggregation. These additional burrows, without obvious surface openings, terminated <1.5 cm below the surface, had otherwise typical morphologies, including the presence of upper lateral chambers. In two such cases, loose excavated peaty soil or coarse sand had been pushed into small voids amongst fibrous peat and roots at the top of the burrow, immediately below the surface. In one case, a late stadium larva was identified in one such burrow, <10 cm from a second burrow where emergence had recently occurred.

All burrows investigated were well maintained by larvae through removal of debris and sediment, which was usually deposited outside the burrow opening, as reported in *Uropetala* (Rowe, 1987; Wolfe, 1953) and *T. hageni* (Svihla, 1975, 1981), and putatively by chewing off roots of surface plants as they grew through the burrow walls, also reported in *Uropetala* (Wolfe, 1953). Many burrows, however, did not have mounds of excavated material outside their openings at the time of observation following emergence. Burrows where emergence had occurred earlier in the season were often characterised by roots and root hairs of swamp plants such as *Empodisma minus* (Restionaceae) beginning to grow through burrow walls, presumably following cessation of burrow maintenance. In some burrows located amongst *Sphagnum* and/or *E. minus* hummocks, particularly in Boyd Plateau Bogs, upper burrow sections occurred within live plant material. In these cases, burrow walls were often composed of excavated soft peaty soils which had been packed in amongst the plant fibres, creating more clearly defined tubular burrow structures. Similar features were reported in *Uropetala* burrows which had the upper section in a moss layer (Wolfe, 1953). Occasionally, burrows were capped with excavated material in the same manner as

the burrows of the burrowing crayfish (Decapoda: Parastacidae: *Euastacus australasiensis*) with which they share these habitats in the Blue Mountains. Similar capping has also been reported in *Uropetala* (Rowe, 1987). Excavated material included the full range of swamp soil types, and at times, vegetation fragments. Where it occurred, burrow capping was either complete, or in some cases, a small opening was evident. Burrow capping was observed more frequently in swamp types included within the Montane Bogs and Fens vegetation class (Boyd Plateau Bogs, Coxs River Swamps) with infrequent partial capping only in those swamp types included within the Coastal Heath Swamps vegetation class (e.g. Blue Mountains Sedge Swamps). Where burrow capping was observed, it was frequently associated with particular vegetation and litter characteristics, including the presence of *Sphagnum*. In some cases, excavated material formed small mounds, which may also provide suitable open germination sites for swamp herbs.

Regardless of substrate type and variation in the proportion of organic matter within a mineral soil matrix, burrows were generally characterised by a level of structural integrity that maintained burrow morphology, although this was more pronounced in the fibrous peats, organic sands or other relatively heavier substrates. The least structural integrity was observed in a few burrows in the more highly decomposed and less stable sapric (muck) peats, with substrate characteristics apparently similar to the single burrow excavation by Tillyard (1911). However, these also retained a defined burrow structure. The few exceptions were some burrows in localised patches of quaking bog, where it was not possible to identify any burrow section within the saturated muck which lay beneath the “floating” peaty root-mats. The presence of crayfish burrow complexes in these areas also confounded clear identification of *Petalura* burrows. No burrows were excavated where there was evidence of a burrow complex occupied by, or established by more than one larva.

A small number of burrows in sites with soft organic-rich substrates, with high water tables, in lower gradient sites (e.g. *Carex-Poa* fens), were characterised by an unusual expanded “chamber” above the substrate (Table 1). This chamber was outside the burrow opening and under the dense litter/thatch layer, or occasionally partly within a *Sphagnum* hummock or a mound of dense decomposing plant material associated with an old vegetation tussock (Figure 4[B3, B13]). These chambers were up to 18 cm long, usually more or less horizontal, or they followed the substrate surface. In two instances, ascending chambers were also recorded either within a *Sphagnum* or fibrous peaty hummock associated with a vegetation tussock outside the burrow opening (Figure 4[B13]). These chambers were of variable width (up to *c.*7 cm) and generally had a height a little less than, or similar to the burrow diameter, suggesting that larvae often develop a chamber by pushing through between the peaty soil surface and the overlying litter, which frequently forms a layer that separates from the soil surface. Because of the nature of the slowly decomposing litter layer, these chambers were generally less clearly defined than the actual burrows. They would generally be above water level, except perhaps following heavy rainfall. In several cases excavated material from the burrow had been deposited at one end of these above-ground chambers. These burrow features were recorded in Boyd Plateau Bogs, Coxs River Swamps and Burrell Swamp (a Kurrajong Fault Swamp). In one case, an above-ground chamber was connected to the main descending burrow at one end, but also had a second short descending burrow section near the opposite end. In two cases, above-ground chambers within old sedge tussocks had an additional burrow section rising to the surface of the groundcover vegetation, with a separate burrow opening (Figure 4[B13]).

In a small number of burrows, there was what appeared to be a new descending burrow section with a terminal chamber, that had been excavated below an established terminal chamber (Figures 3, 4[B32]). In the case of the deepest burrow (75 cm), the burrow had been excavated through several layers of contrasting material, below one putative former terminal chamber, and deeply into a relatively dense organic sand layer. In this case, the excavation followed a recent return to wetter conditions after a long drought period and the water table was 31 cm below the surface and just above the dense sand layer.

Discussion

This study has identified a number of features of *Petalura gigantea* burrow morphology which may assist in better understanding the species' larval behaviour and ecology. These include the frequent presence of one or more, short, nominally horizontal, lateral chambers; an apparent association between water table depth and the depth of one lateral chamber; and the presence of conspicuous terminal chambers, putative adaptive burrow deepening during drought, and of occasional above-ground "foraging chambers".

The purpose of the lateral chambers remains to be determined; however, because they were generally nominally associated with the water table at time of investigation, multiple lateral chambers may reflect a response to changing water levels. There were some exceptions in shallow burrows in low gradient sites with presumably relatively stable groundwater levels which did not have upper lateral chambers. In some cases where the lateral chamber was well below the water level, it was conjectured that this was due to the observation being made shortly after a rainfall period. In contrast to the lateral chambers reported in *P. hesperia* (Watson, 1965), and in some *Uropetala* burrows (Wolfe, 1953), which reportedly increased in length and diameter with increasing burrow depth, putatively associated with increasing larval stadia, there was no evidence of such in this study. However, most *Uropetala* burrow variations illustrated by Wolfe (1953) did not have such side chambers (also see Rowe, 1987) and were similar in appearance to some of those reported here for *P. gigantea*. Although terminal chambers or nominally horizontal terminal burrow sections of varying length have been reported in *Uropetala* (Rowe, 1987; Wolfe, 1953) and both *Tanypteryx* spp. (Svihla, 1959, 1979; Taketo, 1971), no upper lateral burrow chambers have been reported in these species with the exception of the one burrow variant in *Uropetala* noted above. Some *T. pryeri* burrows illustrated by Taketo (1971) had no terminal chambers or branches and consisted of a simple descending or submerged horizontal burrow only. In this study, the presence of some shorter lateral chambers at varying depths, including above and below more typical-sized chambers, is hypothesised to represent chamber excavations that were aborted as a result of either changing water levels or as yet unknown behavioural responses.

The presence of what appeared to be a secondary descending burrow section and associated second terminal chamber in some burrows is hypothesised to be an adaptive response by larvae to a progressive lowering of the water table during an extended drought. No such features have been reported in other burrowing petalurids. These burrows were generally located either near swamp edges or on slopes, where there may be greater temporal variability in groundwater levels. This, and the observations of the microhabitat attributes of hundreds of observed ovipositing sites and burrow locations, supported the premise of obligate groundwater dependence and are consistent with documented observations of groundwater in burrows of other fossorial petalurids. This was reinforced by the observation that in a large proportion of burrows, the depth of one of the lateral chambers effectively coincided with the water level within the burrow at the time of excavation, and suggests a functional relationship between these lateral chambers and the water table. These lateral chambers may serve a number of functions, including provision of resting places with more highly oxygenated groundwater near the water level within the burrow, and provision of other suitable environmental conditions during larval development. They may also provide enhanced opportunities for ambush predation upon epigeaic prey entering the upper burrow space, while still allowing the larvae to remain in contact with burrow groundwater and/or rest in a horizontal rather than vertical position.

The above-ground 'chambers' documented in this study have similarities to the above-ground "sub-niveal runways" in *Tanypteryx hageni* (Svihla, 1971). I also observed a large expanded 'chamber' above a *T. hageni* burrow entrance, and within the litter/thatch layer, in association with a "sub-niveal runway" system in a fen in northern California, with similarities to those noted above for *P. gigantea* (Baird, 2012, pp. 20–23). These Blue Mountains sites, however, do not

experience anything more than very occasional light snow, if at all; in comparison, an often deep and extended period of snow cover may occur in *T. hageni* habitat. Wolfe (1953) also reported that “In winter *Uropetala* larvae may form a chamber in thick moss above the water level at the top of the burrow and so do not go out on to the frozen surface of the moss. The nymphs enter these chambers to feed during the winter months.” In contrast to these reported winter adaptations in *T. hageni* and *Uropetala*, I suggest that the above-ground chambers in *P. gigantea* are developed where sufficient litter or *Sphagnum* depth has accumulated or re-established post-fire, and are used primarily for foraging on epigeic prey above the groundwater level, outside the burrow entrance in an environment with a suitable microclimate, which is largely protected from sunlight, and which provides visual concealment from some potential above-ground vertebrate predators. They may also serve additional functions. They appear to be an opportunistic and adaptive response by larvae to particular microhabitat conditions.

This study has confirmed that burrows are established and occupied by a single larva throughout its long larval stage, consistent with previous studies of *Tanypteryx* and *Uropetala* spp. These results suggest that the previous illustration by Tillyard (1911), of a complex burrow system occupied by multiple larvae, probably involved a misinterpretation of what were most likely a number of closely spaced burrows. Based upon my observation of the presence of short lateral chambers at varying depths in this study, I suggest that the illustration by Tillyard (1911), of long horizontal burrow sections beneath a pool, and connecting a series of vertical burrow sections, resulted from extrapolation of what were either lateral chambers or short burrow branch sections. This is understandable considering the difficulty in identifying burrow morphology in what was apparently very unstable substrate, and in being able to identify the location of larvae prior to excavation. In contrast, extensive investigations during this current study indicated that some level of burrow structural integrity is generally maintained, usually a high level. Even where burrows or burrow sections occurred in muck peat, there was still some sense of a defined burrow, with the few exceptions observed in localised areas of quaking bog. This is consistent with observations of the more clearly defined and well-maintained burrows reported in other petalurids.

The presence of groups of closely spaced burrows identified on numerous occasions in this study is consistent with observed ovipositing patterns of individual females, and in conjunction with at times relatively synchronous emergence patterns from these closely spaced burrows, strongly suggests the presence of larval cohorts (see Baird & Burgin, 2013). Similar patterns have been reported in *Uropetala* and *Tanypteryx* spp. The observation on several occasions in this study of a number of full-sized burrows with no apparent connection to the surface, in close proximity to a typical burrow where emergence had recently occurred, remains to be explained. I presumed that the opening had been closed for some time in response to larval inactivity, and that the surface material had consolidated enough to obscure evidence of a burrow opening. There was no evidence of any burrow connection between any closely spaced burrows, although it may be presumed that on occasion, larvae developing their burrow system may break through into the burrow of an adjoining larva, with one larva subsequently being attacked by the other. A similar dynamic was postulated by Wolfe (1953) in the case of U-shaped *Uropetala* burrows.

Burrow establishment in *P. gigantea* probably commences in early larval instars; initially involving the creation of a small pit within the substrate, as reported for *Uropetala* (Wolfe, 1953) and *T. pryeri* (Taketo, 1958, 1971). In addition to variables such as groundwater regime (water table fluctuations over time) and water quality parameters, soil particle size and density (penetrability) are all attributes that are expected to affect the ability of fossorial larvae to excavate burrows (for marine shore crustaceans, also see Katrak et al., 2008; Morrisey et al., 1999). Burrowing ability will be limited by the physiology of the species, its physical ability to dislodge and move particles and/or chew through plant material such as roots and rhizomes, and the metabolic requirements of burrowing activity and burrow maintenance. Other potentially limiting metabolic factors include temperature and oxygen availability.

In addition to burrows providing access to groundwater, they may provide protection from predators, a favourable site for ambush predation of epigeic invertebrate fauna (e.g. crickets, cockroaches and spiders) or aquatic fauna in seepage-filled depressions (e.g. frog and odonate larvae), and access to specialised groundwater dependent mire prey (e.g. pholoterans, stygofauna and oligochaetes). Once established, the burrow will also provide a relatively stable temperature regime, as reported for *Uropetala* (Wolfe, 1953). The observations of successful emergence following bushfire during drought during this study confirm that burrows provide some protection from the effects of drought and bushfire. Similar advantages have been suggested for Australian burrowing crayfish (e.g. Horwitz & Knott, 1983; Johnston & Robson, 2009a, 2009b; Lake & Newcombe, 1975), particularly those that are dependent on burrows which connect to the water table (Type 2 burrowers; Horwitz & Richardson, 1986). The benefit of such a strategy is obvious in a country such as Australia, with a highly variable climate and frequently fire-prone ecosystems.

Contrasting strata within individual burrows reflect the complex developmental history of these mires over thousands of years, providing evidence of erosion and deposition during intense rainfall events (often after fire), in particular (e.g. Black & Mooney, 2006; Chalson & Martin, 2009; Freidman, 2011). Individual mire patches are characterised by considerable spatial heterogeneity in the distribution of suitable peaty soils, and by areas with contrasting substrate and hydrological characteristics (Baird, 2012; Benson & Baird, 2012; Holland et al., 1992), and thus potential breeding microhabitat for the species. This heterogeneity is most pronounced in those mires developed on sandstones. Burrows or burrow sections in denser gravel, sand and clay-rich substrates are likely to be more difficult for larvae to excavate due to physiological constraints and higher energy demands than in softer and more organic-rich peatier substrates. Consequently, they will be more likely to be smaller in diameter, as identified in this study. Burrow sections in denser and less organic-rich material may also be more stable over time than burrow sections in softer sapric peats, where burrow walls may shed material in response to ongoing movement by larvae and as a result of groundwater movement, particularly below the fibrous root zone. These burrows or burrow sections may thus increase naturally in diameter over time.

Although this study has documented the deepest petalurid burrow to date at 75 cm, it is reasonable to assume that *P. gigantea* may excavate deeper burrows under some circumstances. However, considering the duration of the recent drought and available depths of suitable substrates for excavation, it may be assumed that the range of burrow depths reported here is broadly representative of their range under contemporary climatic, and thus hydrological, conditions.

Apart from burrows where emergence had occurred, no smaller burrows were investigated and confirmed as belonging to early stadia larvae of *P. gigantea*. In the context of the endangered status of the species the author was reluctant to engage in opportunistic burrow excavations in the hope of identifying burrows of earlier stadia larvae. Identifying burrows of the species is at times problematic in the absence of exuviae above the burrow opening, which are readily confused with those of juveniles of the burrowing crayfish which they share these habitats with. Small burrows and other voids within the substrate may be abundant in these mires and may be associated with other invertebrates with underground larval stages, such as crane-flies (Diptera: Tipulidae).

With few exceptions, all burrow openings observed in this study were located above water level at time of observation, and often within elevated vegetation tussocks or *Sphagnum* hummocks. Locations of observed burrow openings are consistent with observed ovipositing locations under particular hydrological conditions. Females do not appear to oviposit into substrates which are covered by more than 1–2 mm of water; however, larvae may subsequently develop burrows at locations which are later inundated during a higher rainfall period. Ovipositing may occur almost anywhere along the hummock- or tussock-hollow elevation gradient, depending on the extent of inundation of any hollows at the time of oviposition, and upon accessibility of the substrate. Thus, in wetter cycles, oviposition and burrow establishment tends to occur at higher elevation than

during drier cycles when oviposition may be restricted to moist substrate in hollows, or peripheral to shallow seepage pools or seepage-fed streamlets which drain these mires. In the early years post-fire and with suitable moisture conditions, dense vegetation tussocks which are re-sprouting also provide ovipositing sites which become less accessible to ovipositing females with increasing time since fire (see Baird, 2012, ch. 6).

Although no burrow openings were identified which would have been permanently inundated, in some low gradient ($<4^\circ$) valley floor mires some burrows were observed which would have been inundated for extended periods with shallow water during above average rainfall periods, particularly burrows at lower elevation on the tussock-hollow gradient which may have been established during a drier period. Such inundation may provide temporary and opportunistic foraging opportunities for larvae in water-filled inter-tussock depressions or for ambush predation from within their submerged burrows. In the case of the occasional burrows with a branch tunnel and second burrow opening documented in this study, it is possible that burrow branches may open under water. These scenarios are consistent with Tillyard's (1911) observation of some burrow openings in water-filled depressions, and evidence of predation upon aquatic odonate larvae by *Petalura* larvae.

With the exception of one burrow in Burrelaw Swamp, all burrows with more complex morphology such as branch tunnels and multiple chambers occurred in valley-side mire patches in Blue Mountains Sedge Swamps, a sandstone-based mire type. This suggests the possibility that the morphological complexity was a response to greater temporal variability in water table depth as a result of slope and hydrogeology in those sloping mire patches. Burrows in lower gradient valley floor mires, such as Boyd Plateau Bogs and Cocks River Swamps, were generally simple in structure, with a descending burrow section, a terminal chamber and perhaps one or two lateral chambers. Burrows in these mire types were also more likely to include above-ground chambers and some level of burrow capping. The presence of above-ground chambers is inferred to be largely a response to less frequent fires, thus allowing accumulation of litter layers and/or more extensive *Sphagnum* cover, within which they may be established. The greater frequency of fire in the more fire-prone, sandstone-based mire systems (e.g. Blue Mountains Sedge Swamps, Newnes Plateau Shrub Swamps), with associated potential combustion of any organic-rich excavated material, is also conjectured to be largely responsible for the relative lack of evident burrow capping in these mire types, compared to the mire types within the Montane Bogs and Fens vegetation class (e.g. Boyd Plateau Bogs). Excavated material, however, may also be eroded away during rainfall events and as a result of increased surface flows along drainage lines. Many burrows at time of emergence did not have conspicuous mounds of excavated material outside their burrow openings, suggesting that it had been eroded, combusted and/or progressively assimilated into the substrate surface over the long period of burrow occupation. One effect of more frequent fire is to simplify the structure of the live and dead ground-layer vegetation cover, and thus, the environment where ovipositing and burrow establishment occurs. Such a reduction in groundcover may also be assumed to result in a temporary reduction in the abundance of potential epigeic invertebrate prey (see Greenslade & Driessen, 1999; Greenslade & Smith, 2010). More frequent fire also results in a more clearly defined environmental boundary at the burrow entrance and may limit the use of the opening by larvae for ambush predation.

This study has identified considerable variability in *P. gigantea* burrow morphology across the hydrogeomorphic range of the mire types of the Blue Mountains. This variability can be understood as a response by larvae to specific microhabitat attributes encountered during burrow establishment and occupation. It is suggested that substrate characteristics and hydrological regime are the primary drivers of this variability, with both factors directly related to hydrogeology, hydrogeomorphology and climate. Where larvae occur in microhabitat with a relatively stable hydrological regime and high water table, there is presumably no ecological benefit or imperative in excavating deeper or more complex burrows.

In conjunction with extensive observations of the species' dependence upon a moist or saturated substrate for ovipositing, and the microhabitat characteristics of burrow sites, the presence of groundwater throughout most of the burrow depth documented in this study confirms *P. gigantea* as an obligate, groundwater dependent, mire-dwelling species. Putative evidence of adaptive burrow deepening associated with drought during the study further supports this conclusion. It also suggests that at least later stadia larvae in established burrows are capable of persisting under a range of hydrological conditions, ranging from periods of burrow inundation to protracted lowering of the water table. On a number of occasions, emergence was also recorded from burrows in superficially dry substrate (also see Theischinger, 2001), including following fire, although these burrows all still contained groundwater, generally throughout most of their depth. This confirms the capacity of later stadia larvae, at least, to persist through periods of lowered water tables and fire events, and undergo emergence in a post-fire environment. Based upon observations from this study, this capacity is presumed to be limited to situations where larvae have access to groundwater within their burrows. The potential for adaptive burrow deepening at such times will be limited by the depth of suitable burrowing substrate and the energy demands of such activity.

Although the desiccation resistance of eggs and early stadia larvae is unknown, it is reasonable to assume, based on the restriction of the species to particular microhabitat within these mires, that prior to burrow establishment eggs and early stadia larvae may be vulnerable to desiccation during drought or otherwise lowered water tables which result in drying of the surface peat layer. These dry periods are also the times when these peat swamps are most vulnerable to the effects of fire (Horwitz, Pemberton, & Ryder, 1999; Keith, Rodoreda, Holman, & Lemmon, 2006; Pemberton, 2005). Eggs and early stadia larvae are likely to be vulnerable to mortality during any fire events that occur before burrow establishment, either through direct heat effects or combustion of the peaty substrate during periods of reduced surface moisture. However, the long larval stage, its fossorial habit, and access to groundwater provide some potential buffering against above-ground environmental perturbations, such as climate and fire. The effectiveness of this buffering in maintaining viable populations will be dependent upon the spatial and temporal scales at which these exogenous perturbations occur. Nevertheless, reproduction and persistence of populations will be dependent upon the availability of suitable saturated substrate for ovipositing and larval establishment.

In addition to the more widely recognised threats to these groundwater dependent mire ecosystems (NSW Scientific Committee, 2004, 2005, 2007; Threatened Species Scientific Committee, 2005), Baird (2012, ch. 8) and Benson and Baird (2012) highlighted the potential negative effects, individually and cumulatively, upon these mire habitats and their groundwater dependent species, such as *P. gigantea*, as a result of lowering water tables (e.g. due to groundwater abstraction and longwall coal mining), more intense fire regimes and rapid climate change.

Acknowledgements

Haruki Karube, Robert McCormack, Richard Rowe, Harry Hines, Michael Mathieson, John Trueman, Steve Valley and Gunther Theischinger are thanked for generously sharing their observations of petalurids. Gunther Theischinger and two anonymous reviewers are thanked for their comments, which have much improved the paper. This study was undertaken in conjunction with doctoral research, which was supported by a University of Western Sydney Postgraduate Research Award and an Abel Ecology Study Grant.

References

- Baird, I. R. C. (2012). *The wetland habitats, biogeography and population dynamics of Petalura gigantea (Odonata: Petaluridae) in the Blue Mountains of New South Wales* (PhD thesis). University of Western Sydney, Australia. Retrieved from <http://handle.uws.edu.au:8081/1959.7/509925>.
- Baird, I. R. C. (2013a). Emergence behaviour in *Petalura gigantea* (Odonata: Petaluridae): confirmation of upright emergence. *International Journal of Odonatolgy*, 16, 213–218. doi:10.1080/13887890.2013.798975

- Baird, I. R. C. (2013b). Larval habitat and behaviour of *Phenes raptor* (Odonata: Petaluridae): a review of current knowledge, with new observations. *International Journal of Odonatology*, 16, 79–91. doi:10.1080/13887890.2012.757723
- Baird, I. R. C., & Burgin, S. (2013). An emergence study of *Petalura gigantea* (Odonata: Petaluridae). *International Journal of Odonatology*, 16, 193–211. doi:10.1080/13887890.2013.798580
- Baird, I. R. C., & Ireland, C. (2006). Upright emergence in *Petalura gigantea* (Odonata: Petaluridae). *International Journal of Odonatology*, 9, 45–50. doi:10.1080/13887890.2006.9748262
- Benson, D., & Baird, I. R. C. (2012). Vegetation, fauna and groundwater interrelations in low nutrient temperate montane peat swamps in the upper Blue Mountains, New South Wales. *Cunninghamia*, 12, 267–307. doi:10.7751/cunninghamia.2012.12.021
- Benson, D. H., & Keith, D. A. (1990). Natural vegetation of the Wallerawang 1:100,000 map sheet. *Cunninghamia*, 2, 305–335. Retrieved from http://www.rbgnsyd.nsw.gov.au/_data/assets/pdf_file/0009/97659/Benson_2d.pdf
- Black, M. P., & Mooney, S. D. (2006). Holocene fire history from the Greater Blue Mountains World Heritage Area, New South Wales, Australia: the climate, humans and fire nexus. *Regional Environmental Change*, 6, 41–51. doi:10.1007/s10113-005-0003-8
- Blue Mountains City Council. (2002). *Native vegetation mapping of geographic planning areas 1 to 5. Blue Mountains City local government area*. Katoomba, NSW: Blue Mountains City Council.
- Chalson, J. M., & Martin, H. A. (2009). A Holocene history of the vegetation of the Blue Mountains, New South Wales. *Proceedings of the Linnean Society of NSW*, 130, 77–109.
- Clifton, C., & Evans, R. (2001). *Environmental water requirements of groundwater dependent ecosystems. Environmental Flows Initiative Technical Report Number 2*. Canberra: Commonwealth of Australia.
- Corbet, P. S. (1999). *Dragonflies. Behaviour and Ecology of Odonata*. Ithaca, NY: Cornell University Press.
- Cowardin, L. M., Carter, V., Golet, F. C., & LaRoe, E. T. (1979). *Classification of wetlands and deepwater habitats of the United States*. Washington, DC: US Department of the Interior, Fish and Wildlife Service.
- Davies, D. A. L. (1998). The genus *Petalura*: field observations, habits and conservation status (Anisoptera: Petaluridae). *Odonatologica*, 27, 287–305.
- Dearson, C. K. (1999). Survey for *Petalura gigantea* (Giant Dragonfly), *Prasophyllum fuscum* (Leek Orchid) and *Gentiana wingecarribiensis* (Gentian) at Wingecarribee Swamp. Unpublished report for the NSW National Parks and Wildlife Service and the Sydney Water Corporation.
- Fleck, G. (2011). Phylogenetic placement of Petaluridae and basal Anisoptera families (Insecta: Odonata). *Stuttgarter Beiträge zur Naturkunde A, Neue Series* 4, 83–104.
- Freidman, B. (2011). *The geomorphic character, chronology and evolution of upland swamps in the Blue Mountains, NSW* (B. Env. Mgt. (Honours) thesis). Macquarie University, Australia.
- Garrison, R. W., von Ellenrieder, N., & Louton, J. A. (2006). *Dragonfly genera of the New World: An illustrated and annotated key to the Anisoptera*. Baltimore: John Hopkins University Press.
- Gore, A. J. P. (1983). *Ecosystems of the World 4A. Mires: Swamp, bog, fen and moor*. Amsterdam: Elsevier.
- Greenslade, P., & Driessen, M. (1999). The effect of fire on epigaic arthropods in buttongrass moorland in Tasmania. In: W. Ponder, & D. Lunney (Eds.), *The other 99%. The conservation and biodiversity of invertebrates* (pp. 82–89). Mosman, NSW: Transactions of the Royal Zoological Society of New South Wales.
- Greenslade, P., & Smith, D. (2010). Short term effects of wild fire on invertebrates in coastal heathland in southeastern Australia. *Pacific Conservation Biology*, 16, 123–132.
- Growns, I. O., & Richardson, A. M. M. (1988). Diet and burrowing habits of the freshwater crayfish, *Parastacoides tasmanicus tasmanicus* Clark (Decapoda : Parastacidae). *Marine and Freshwater Research*, 39, 525–534. doi:10.1071/MF9880525
- Harding, D. (1977). *A consideration of some aspects of the feeding behaviour, along with a morphological investigation of the mouthparts and alimentary canal of Uropetala carovei White (Odonata)* (BSc (Honours) thesis). Massey University, NZ.
- Hawking, J. H., & Theischinger, G. (2004). Critical species of Odonata in Australia. *International Journal of Odonatology*, 7, 113–132. doi:10.1080/13887890.2004.9748204
- Holland, W. N., Benson, D. H., & McRae, R. H. D. (1992). Spatial and temporal variation in a perched headwater valley in the Blue Mountains: geology, geomorphology, vegetation, soils and hydrology. *Proceedings of the Linnean Society of NSW*, 113, 271–295.
- Horwitz, P., & Knott, B. (1983). The burrowing habit of the Koonac *Cherax plebejus* (Decapoda: Parastacidae). *West Australian Naturalist*, 15, 113–117.
- Horwitz, P., Pemberton, M., & Ryder, D. (1999). Catastrophic loss of organic carbon from a management fire in a peatland in southwestern Australia. In: A. J. McComb, & J. A. Davis (Eds.), *Wetlands for the Future* (pp. 487–501). Adelaide, South Australia: Gleneagles Publishing.
- Horwitz, P. H. J., & Richardson, A. M. M. (1986). An ecological classification of the burrows of Australian freshwater crayfish. *Marine and Freshwater Research*, 37, 237–242. doi:10.1071/MF9860237
- Johnston, K., & Robson, B. J. (2009a). Commensalism used by freshwater crayfish species to survive drying in seasonal habitats. *Invertebrate Biology*, 128, 269–275. doi:10.1111/j.1744-7410.2009.00169.x
- Johnston, K., & Robson, B. J. (2009b). Habitat use by five sympatric Australian freshwater crayfish species (Parastacidae). *Freshwater Biology*, 54, 1629–1641. doi:10.1111/j.1365-2427.2009.02213.x
- Karube, H. (2003). Occurrence of the larvae of *Petalura ingentissima* Tillyard. Paper presented at the 3rd World-wide Dragonfly Association International Symposium of Odonatology, Beechworth, Australia, 7–13 January 2003.

- Katrak, G., Dittmann, S., & Seuront, L. (2008). Spatial variation in burrow morphology of the mud shore crab *Helograpsus haswellianus* (Brachyura, Grapsidae) in South Australian saltmarshes. *Marine and Freshwater Research*, 59, 902–911. doi:10.1071/MF08044
- Keith, D. A. (2004). *Ocean shores to desert dunes: The native vegetation of New South Wales and the ACT*. Hurstville: Department of Environment and Conservation (NSW).
- Keith, D. A., & Benson, D. H. (1988). Natural vegetation of the Katoomba 1:100,000 map sheet. *Cunninghamia*, 2, 107–143. Retrieved from http://www.rbg Syd.nsw.gov.au/_data/assets/pdf_file/0006/97647/Keith_2.pdf
- Keith, D. A., Rodoreda, S., Holman, L., & Lemmon, J. (2006). Monitoring change in upland swamps in Sydney's water catchments: the roles of fire and rain. Sydney Catchment Authority Special Area Strategic Management Research and Data Program. Project number RD07: Long term responses of upland swamps to fire. Final Report. Hurstville, NSW: Department of Environment and Conservation.
- King, D. P. (1993). *Soil landscapes of the Wallerawang 1:100,000 sheet. Report*. Sydney: Department of Conservation and Land Management.
- King, D. P. (1994). *Soil landscapes of the Katoomba 1:100,000 sheet. Report and map*. Sydney: Department of Conservation and Land Management.
- Lake, P. S., & Newcombe, K. J. (1975). Observations on the ecology of the crayfish *Parastacoides tasmanicus* (Decapoda: Parastacidae) from south-western Tasmania. *Australian Zoologist*, 18, 197–214.
- Marshall, B. (2005). *Groundwater: Lifeblood of the environment*. Wentworth Falls, NSW: Blue Mountains Conservation Society.
- Morrisey, D. J., DeWitt, T. H., Roper, D. S., & Williamson, R. B. (1999). Variation in the depth and morphology of burrows of the mud crab *Helice crassa* among different types of intertidal sediments in New Zealand. *Marine Ecology Progress Series*, 182, 231–242.
- NSW Government. (2002). *The NSW State Groundwater Dependent Ecosystems Policy*. Sydney: Department of Land and Water Conservation and the State Groundwater Policy Working Group.
- NSW Scientific Committee. (1998). Giant dragonfly – endangered species listing. NSW Scientific Committee final determination. Retrieved from <http://www.environment.nsw.gov.au/determinations/GiantDragonflyEndSpListing.htm>
- NSW Scientific Committee. (2004). Montane peatlands and swamps of the New England Tableland, NSW North Coast, Sydney Basin, South East Corner, South Eastern Highlands and Australian Alps bioregions – endangered ecological community listing. NSW Scientific Committee final determination. Retrieved from <http://www.environment.nsw.gov.au/determinations/MontanePeatlandsEndSpListing.htm>
- NSW Scientific Committee. (2005). Newnes Plateau Shrub Swamp in the Sydney Basin Bioregion – endangered ecological community listing. NSW Scientific Committee final determination. Retrieved from <http://www.environment.nsw.gov.au/determinations/NewnesPlateauShrubSwampEndSpListing.htm>
- NSW Scientific Committee. (2007). Blue Mountains Swamps in the Sydney Basin Bioregion – vulnerable ecological community listing. NSW Scientific Committee final determination. Retrieved from <http://www.environment.nsw.gov.au/determinations/BlueMountainsSwampsVulnerableEcologicalCommunity.htm>
- Paulson, D. (2011). *Dragonflies and damselflies of the East*. Princeton, NJ: Princeton University Press.
- Pemberton, M. (2005). Australian peatlands: a brief consideration of their origin, distribution, natural values and threats. *Journal of the Royal Society of Western Australia*, 88, 81–89.
- Rowe, R. J. (1987). *The dragonflies of New Zealand*. Auckland, New Zealand: Auckland University Press.
- Serov, P., Kuginis, L., & Williams, J. P. (2012). *Risk assessment guidelines for groundwater dependent ecosystems, Volume 1 – the conceptual framework*. Sydney: Department of Primary Industries, NSW Office of Water.
- Shimoda, K., & Tamaki, A. (2004). Burrow morphology of the ghost shrimp *Nihonotrypaea petalura* (Decapoda: Thalassinidea: Callinassidae) from western Kyushu, Japan. *Marine Biology*, 144, 723–734. doi:10.1007/s00227-003-1237-y
- Smith, P., & Smith, J. (1996). Regionally significant wetlands of the Hawkesbury-Nepean River Catchment for Sydney Regional Environmental Plan 20. Report prepared for the NSW Department of Urban Affairs and Planning. Blaxland, NSW: P & J Smith Ecological Consultants.
- Svihla, A. (1959). The life history of *Tanypteryx hageni* Selys (Odonata). *Transactions of the Entomological Society of America*, 85, 219–232.
- Svihla, A. (1971). Sub-niveal runway of *Tanypteryx hageni* Selys. *Tombo*, 14, 23.
- Svihla, A. (1975). Another locality of the larvae of *Tanypteryx hageni* Selys in Washington. *Tombo*, 18, 43–44.
- Svihla, A. (1979). Notes on *Tanypteryx hageni* (Selys) in the Olympic Peninsular, Washington, U.S.A. *Tombo*, 22, 15–16.
- Svihla, A. (1981). Notes on *Tanypteryx hageni* Selys in the Olympic Peninsular of Washington. *Tombo*, 24, 24.
- Svihla, A. (1984). Notes on the habits of *Tanypteryx hageni* Selys in the Olympic Mountains, Washington, U.S.A. *Tombo*, 27, 23–25.
- Taketo, A. (1958). Discovery of the pit-dwelling larva of *Tanypteryx pryeri* Selys (Petaluridae). *Tombo*, 1, 20–21. (In Japanese, with English summary).
- Taketo, A. (1971). Studies on the life history of *Tanypteryx pryeri* Selys (Odonata: Petaluridae) 2. Habitat and habit of nymph. *Kontyû*, 39, 299–310. (In Japanese, with English summary).
- Theischinger, G. (1975). Ein "Dreigespann" von *Petalura gigantea* Leach. *Tombo*, 18, 45. (In German, with English summary).
- Theischinger, G. (1999). A new species of *Petalura* Leach from south-eastern Queensland (Odonata: Petaluridae). *Linzer biologische Beiträge*, 31, 159–166.

- Theischinger, G. (2001). Habitat mapping and distribution survey for the giant dragonfly (*Petalura gigantea*) in the Blue Mountains Region. Unpublished report to the NSW National Parks and Wildlife Service.
- Theischinger, G. & Endersby, I. (2009). *Identification Guide to the Australian Odonata*. Hurstville, NSW: Department of Environment, Climate Change and Water NSW.
- Threatened Species Scientific Committee. (2005). Commonwealth listing advice on Temperate Highlands Peat Swamps on Sandstone. Retrieved from <http://www.environment.gov.au/biodiversity/threatened/communities/temperate-highland-peat-swamps.html>
- Tillyard, R. J. (1909). Studies in the life-histories of Australian Odonata. 1. The life-history of *Petalura gigantea* Leach. *Proceedings of the Linnean Society of NSW*, 34, 256–267.
- Tillyard, R. J. (1911). Studies in the life-histories of Australian Odonata. 4. Further notes on the life-history of *Petalura gigantea* Leach. *Proceedings of the Linnean Society of NSW*, 36, 86–96.
- Tillyard, R. J. (1917). *The biology of dragonflies*. Cambridge: Cambridge University Press.
- Tillyard, R. J. (1921). Description of a new dragonfly belonging to the genus *Uropetala* Selys. *Transactions and Proceedings of the New Zealand Institute*, 53, 343–346.
- Trueman, J. W. H. (2000). Survey for *Petalura gigantea* Leach (Giant Dragonfly) in New South Wales: 1999–2000 flight season. Unpublished report to NSW National Parks and Wildlife Service.
- Turner, P. E. (1970). *Allusive dragons: functional integration and structural integrity among natural populations of the relict dragonfly Tanypteryx hageni (Selys) (Odonata: Petaluridae)* (PhD thesis). Berkeley: University of California.
- Valley, S. (2000). Some interesting observations of *Tanypteryx hageni*. *Argia*, 12, 9.
- Ware, J. L., Beatty, C. D., Sanchez Herrera, M., Valley, S., Johnson, J., Kerst, C., May, M. L., & Theischinger, G. (2014). The petaltail dragonflies (Odonata: Petaluridae): Mesozoic habitat specialists that survive to the modern day. *Journal of Biogeography*, 41, 1291–1300.
- Watson, J. A. L. (1965). Petalurids: most primitive living dragonflies. *Animals*, 6, 128–131.
- Wheeler, B. D., & Proctor, M. C. F. (2000). Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology*, 88, 187–203. doi:10.1046/j.1365-2745.2000.00455.x
- Whinam, J., & Hope, G. S. (2005). The peatlands of the Australasian region. In: G. M. Steiner (Ed.) *Moore: von Sibirien bis Feuerland – Mires: from Siberia to Tierra del Fuego* (pp. 397–434). Linz, Austria: Biologiezentrum der Oberoesterreichischen Landesmuseen Neue Serie 35.
- Winstanley, W. J. (1981). An emergence study on *Uropetala carovei carovei* (Odonata: Petaluridae) near Wellington, New Zealand, with notes on the behaviour of the subspecies. *Tuatara (Wellington)*, 25, 22–36.
- Winstanley, W. J. (1982). Observations on the Petaluridae (Odonata). *Advances in Odonatology*, 1, 303–308.
- Wolfe, L. S. (1949). *Studies on the genus Uropetala Selys (Odonata: Petaluridae) from New Zealand: with special reference to its life history, ecology and systematics, and including studies on anatomical, histological and biochemical aspects* (MSc thesis). University of Canterbury, New Zealand.
- Wolfe, L. S. (1953). A study of the genus *Uropetala* Selys (Order Odonata) from New Zealand. *Transactions of the Royal Society of New Zealand*, 80, 245–275. Retrieved from http://rsnz.natlib.govt.nz/volume/rsnz_80/rsnz_80_03_003760.html