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Establishment of larval pits by *Tachopteryx thoreyi* (Odonata: Petaluridae): habitat modification by a non-burrowing petalurid

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Tachopteryx thoreyi is one of only two species of petalurid dragonflies with a non-fossorial larval stage. In the context of questions related to the phylogenetics, historical biogeography and current distribution of the Petaluridae, the evolution of a burrowing larval stage in petalurids, which is unique in the Odonata, is of considerable interest. This paper reports observation of crypts, or shallow pits or depressions, established by some larvae of *Tachopteryx thoreyi*, and briefly discusses these observations in the context of the more typical burrowing habit in petalurids.

Keywords: Dragonfly; larvae; fossorial; burrowing; evolution; groundwater dependent species

Introduction

The Petaluridae (Odonata) includes 11 currently recognised dragonfly species: Australia (five *Petalura* spp.), Chile and Patagonian Argentina (*Phenes raptor*), Japan (*Tanypteryx pryeri*), New Zealand (*Uropetala carovei*, *U. chiltoni*) and North America (*Tachopteryx thoreyi*, *Tanypteryx hageni*) (Schorr & Paulson, 2018), nine of which have a fossorial larval stage, unique in the Odonata (Baird, 2014a). The phylogenetics of this iconic and relict family, its historical biogeography, and the evolution of a burrowing larval habit are subjects of considerable interest, particularly in the context of the geographic distribution of extant fossorial and non-fossorial species (e.g. Ware et al., 2014).

Fossorial petalurid larvae excavate permanent burrows, with a burrowing habit documented in *Petalura gigantea* Leach (eastern New South Wales [NSW], south-east Queensland [Qld]), *P. hesperia* Watson (Western Australia), *P. ingentissima* Tillyard (north Qld), *P. litorea* Theischinger (north-east NSW, south-east Qld), *T. hageni* (Selys) (California, Oregon, Nevada, Washington [USA], British Columbia [Canada]), *T. pryeri* (Selys) (Japan), *U. carovei* (White) (New Zealand [NZ]) and *U. chiltoni* Tillyard (NZ) (Baird, 2014a). Burrows typically extend below the water table in soft, peaty or organic-rich soils in mires, seepages, or along stream margins, although there is considerable variation in burrow depth and complexity reported among species (Baird, 2014a, 2017; Karube, 2003; Rowe, 1987; Svihla, 1959; Taketo, 1958; Taketo, 1971; Tillyard, 1911, 1921; Watson, 1965; Winstanley, 1981, 1982; Wolfe, 1953). The larval habits of *P. pulcherrima* Tillyard (north Qld) are unknown, although it may be presumed that they are similar to that of the other tropical north Qld petalurid, *P. ingentissima* (Baird, 2014a).

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Maximum depths recorded for petalurid burrows range from up to 15 cm in *T. hageni* (Svihla, 1959) to 75 cm in *P. gigantea* (for review, see Baird, 2014a). Once established, burrows are occupied and maintained throughout the larval stage through to emergence. A very long larval stage of five years has been documented in *T. hageni* (Valley, 2000), at least five years extrapolated for *Uropetala* spp. (Wolfe, 1953), and at least six years extrapolated for *P. gigantea* (Baird, 2012, 2014a). Burrowing petalurids may all be considered groundwater-dependent species, with the burrowing habit potentially conferring various ecological benefits over their long larval stage, including greater environmental stability, increased protection from fire, drought, flooding and above-ground predators, and provision of refugia from which to practice ambush predation (Baird, 2014a; Baird & Burgin, 2016).

In contrast to the burrowing petalurids, larvae of the monotypic *Tachopteryx thoreyi* (Hagen) (eastern USA; Paulson, 2011) and monotypic *Phenes raptor* Rambur (central and southern Chile and Patagonian Argentina; Garrison, von Ellenrieder, & Louton, 2006) are non-burrowing (for review, see Baird, 2013, 2014a). While very long larval stages are now documented for a number of the burrowing species, and of up to 8 years extrapolated for some non-petalurids such as *Epiophlebia superstes* (Odonata: Epiophlebiidae) (Tabaru, 1984), no such information has previously been published for either of the two non-burrowing petalurids. In an unpublished larval rearing study, however, Larry Everett (pers. comm.) raised several early stadia *Tachopteryx* larvae collected in Tennessee (TN) in September 2010 (< 5 mm long at study commencement) that emerged in July 2013, suggesting a long larval stage in TN of at least three to four years. The rearing climate was considered similar to natural conditions (L. Everett, pers. comm.). It is possible that the duration of the larval stage at higher latitudes in northern USA will be longer. In another unpublished study, Günther Fleck maintained a field collected, final stadium *Phenes* larva for 11 months and one week in captivity in a humid and warm environment (∼ 18°C during July and August to simulate austral winter, otherwise 21–24°C) in a terrarium/vivarium (before being preserved for study). The larva was healthy throughout, but exhibited minimal change in length, with wing pads still not inflated at the end of that period (G. Fleck, pers. comm.). With his experience raising larvae of species with long larval stages, and considering the long duration of the final stadium of the larva he had collected, Fleck suggested that larval stage duration in *Phenes* is likely to be at least four to five years and potentially more in colder environments at higher latitudes and elevations. It appears that burrowing and non-burrowing petalurids all have very long larval stages.

Larvae of *Tachopteryx* have typically been found amongst surface muck under fallen leaves, under *Sphagnum*, and amongst or under wet leaves and other litter (including bark and fallen wood) in wet hillside seepage areas or fens, usually near the uphill edges of seeps and fens (where they transition upslope to drier forest), with minimal surface flow at most, and no sign of burrows (e.g. Dunkle, 1981; Louton, 1982; McPheron & Schiff, 1988). Breeding habitat may occur in forest seeps and forested fens (Barlow, 1991; Dunkle, 1981, 1989; McPheron & Schiff, 1988) and in more open, treeless seepage areas or graminoid fens surrounded by forest (Ferro & Belshe, 1999; Walker & Smentowski, 2003; Williamson, 1932). According to Louton (1982), of five final and many middle instar larvae he collected, none were found in water or mud as stated by Byers (1930) and Needham (1901). The following comments by Louton (1982, pp. 29–30) are of interest:

> Several late and final instar nymphs were kept alive in a tilted aquarium with a soil substrate, a pool at one end and the dry portion covered with sphagnum moss. The nymphs always preferred to remain under the moss. When placed in the water they floated around aimlessly and struggled out of the water as soon as possible. When moving overland, the nymphs were seen to walk on the ends of their tibia in beetle-like fashion, explaining the utility of the apical tibial claws.

Although considered non-burrowers, observations of larvae of *Tachopteryx* indicate that some larvae do modify their environment through establishment of depressions in the substrate. In his

detailed field study of *Tachopteryx*, Dunkle (1981, p. 192) noted that "A few were in depressions in the soil, but none were in burrows, nor were there any burrows present like those described for some other petalurids". Dunkle did not describe the nature of these depressions. Larry Everett (pers. comm.) has similarly observed some larvae under leaves in shallow, circular depressions in the soil in the field (largest depressions being ∼ 3.5 cm in diameter and up to ∼ 1.5 cm deep in the middle) and observed reared larvae establishing such depressions in the soil in their container (unpubl. obs.). No other reported observations have included mention of larvae in such depressions. Dunkle (1981) also described the somewhat flattened and spiny larvae as leaf mimics, well adapted to concealment between and under rotting, fallen deciduous leaves (e.g. *Acer*, *Cornus* and *Quercus* spp.) in seeps or fens in their primarily deciduous forest habitats. Larvae of multiple age classes have also been found in close proximity in Missouri (MO) (M. Ferro, pers. comm.) and TN (L. Everett, pers. comm.), either without obvious depressions or pits, or the presence of such were not identified. Baird (2013, p. 80) noted that an earlier observation by Williamson (1932), of a *Tachopteryx* larva near a vertical tunnel in muddy substrate in MO, "appears anomalous and was presumably either coincidental or the result of shallow tunnelling by the larva in the muddy substrate". It is possible that the tunnel referred to was of a small burrowing crayfish. Eastern USA, including MO (Riggert, 2016), is home to a diversity of burrowing crayfish and a number of these occur in the fen and seepage habitats of *Tachopteryx*. Larvae of *Somatochlora hineana* Williamson (Odonata: Corduliidae), *S. tenebrosa* (Say) and *Tachopteryx* have previously been collected from within crayfish burrows, which they apparently use as refugia, including during dry periods and winter (Pintor & Soluk, 2006; US Fish and Wildlife Service, 2001; Walker & Smentowski, 2003). Such behaviour provides clear evidence of at least some of the benefits associated with the burrowing habit in fossorial petalurids. Burrowing crayfish also frequently occur in the groundwater-dependent mire and stream-side habitats of *P. gigantea*, *P. ingentissima and P. litorea* (Baird, 2014a, 2017; Baird & Benson, 2018; Benson & Baird, 2012), where burrow openings of small crayfish may be confused with those of later stadia petalurid larvae.

In the case of the non-fossorial *Phenes raptor*, Svihla (1960) reported that D. S. Bullock had dredged larvae from mud in shallow "bays" of slow flowing streams in proximity to hillside seepage areas, a larval habitat which he was not able to confirm. Svihla (1960) subsequently collected an immature *Phenes* larva foraging on wet ground in a nearby *Juncus*-dominated, hillslope seepage area above a stream. Svihla (1960, p. 24) also reported a single female disturbed "flying near the ground in the brush close to the mucky side of a small stream", probably investigating ovipositing opportunities in a similar type of habitat (Baird, 2013). Svihla (1960, p. 24) suggested that *Phenes* larval habitat might be similar to that of *T. hageni*, *T. pryeri* and *U. carovei*, "i.e., permanent, spring-fed swampy areas located on hillsides". *Phenes* larvae have subsequently been observed beneath "rotting tree stumps in dry wooded areas" on two occasions (E. Kramer pers. comm.; cited in Jurzitza, 1989), and amongst moist, loose organic debris associated with a decaying log on damp earth in a relatively sunny, anthropogenic rainforest clearing in a very high rainfall zone near Puerto Ramírez, in Patagonian Chile (Garrison & Muzón, 1995). In the latter case, larvae of three or four stadia were observed (J. Muzón, pers. comm.), suggesting a capacity for the species to complete larval development in a permanently moist rainforest-floor environment that would not be considered a fen or seepage habitat. In addition to possible cohort splitting, the presence of multiple stadia suggests the possibility of more than one cohort at the Puerto Ramírez site (Baird, 2013). According to Rosser Garrison (pers. comm.), an additional *Phenes* larva was found amongst rocks in a shallow (mostly 2.5–5 cm deep) riffle area nearby and a seep was also located not far from where the larvae were found in the terrestrial litter habitat. Single larvae of *Phenes* have subsequently been recorded twice in seeps in or adjoining *Nothofagus* forest in the dryer Mediterranean climate zone further north near Vilches Alto, Chile; half submerged in a shallow water-filled pool (< 2 cm deep) under a fallen rotting branch

(Baird, 2013), and amongst muck and decaying plant litter in a small shallow pool less than a few millimetres deep (Fleck, 2011). In habitat, larvae are typically well camouflaged with plant matter and muck adhering to their bodies (Baird, 2013; Fleck, 2011; Garrison & Muzón, 1995). The final stadium *Phenes* larva which Günther Fleck maintained in captivity for 11 months was observed to mostly occupy shallow aquatic microhabitat (generally partly submerged only). The larva occasionally occupied terrestrial microhabitat, but generally in contact with moist substrate. It was also observed on one occasion at night in a surficially dry state (possibly hunting) in the terrestrial part of its enclosure (G. Fleck, pers. comm.). *Phenes* larvae are clearly quite adaptable in their ability to occupy microhabitats ranging from shallow, lotic and lentic aquatic microhabitats, to fully terrestrial ones.

Permanently humid tropical and temperate terrestrial environments such as moist forest-floor litter habitats have previously been recorded as larval habitat for a small number of odonate species (e.g. Watson, 1982; Watson & Theischinger, 1980; Winstanley, 1983), although such non-aquatic habitat use may be restricted to late stadia larvae of some species (Corbet, 2004), e.g. *E. superstes* (Eda, 1964). Larvae of other species which may occur with *Phenes*, such as some *Phyllopetalia* spp. (Odonata: Austropetaliidae), have also been described as semi-terrestrial in habit (e.g. Carle, 1996). In view of the very high rainfall (> 3000 to > 5000 mm/year) in the southern part of the species' range, larvae of *P. raptor* may also be commonly associated with permanently moist or wet terrestrial microhabitats that may not be considered fens or seepage areas (Baird, 2013), although in such a high rainfall area the distinction is perhaps irrelevant. The observation of *Phenes* larvae in moist decomposing organic matter on the rainforest floor at Puerto Ramírez (Garrison & Muzón, 1995) and of oviposition in soil within a dark *Nothofagus* rainforest understorey in Parque Nacional Puyehue in the Los Lagos Region, Chile (J. Muzón, pers. comm.), is consistent with this (Baird, 2013). The observations on two occasions of larvae beneath "rotting tree stumps in dry wooded areas" appears somewhat anomalous, unless the rotting tree stumps were associated with small, and at the time of observation, either inconspicuous or temporarily drying seepages in the otherwise dry wooded areas, or the presence of such a seepage was not noted. Unless larvae are adapted to aestivation during dry periods (a characteristic of some odonates; Corbet, 2004), then presumably, there would be a requirement for at least some permanently moist microhabitat to ensure that early stadia larvae, in particular, do not desiccate, regardless of variation in broader habitat types where the species occurs. It is to be expected that some northerly seepage habitats with a Mediterranean climate are to some extent subject to summer drying, where larvae would require access to suitable refugia during drying conditions (Baird, 2013).

Following initial observation of *Tachopteryx* larvae occupying shallow depressions under fallen leaves in a fen in Big South Fork National River and Recreation Area (TN) in May 2018, and the information from Larry Everett in relation to his unpublished observations of some larvae establishing such depressions, I decided to undertake a survey of some known fen habitats of the species in TN and MO to better understand this behaviour and the extent of its occurrence. This paper reports the results of these larval searches of fen habitats of *Tachopteryx thoreyi* and briefly discusses these observations in the context of the more typical burrowing habit in petalurids.

Methods

Using a predictive microhabitat model, targeted larval searches of a selection of known fen habitats of *Tachopteryx thoreyi* were undertaken in TN and the Ozarks of MO in May and June 2018. Searches involved manual inspection of the soil surface, leaf litter, *Sphagnum* and under woody debris in areas where groundwater seepage was emergent, either in upper fen margins, on or

adjoining forested lower hill-slopes, or along seepage lines or small water tracks in treeless and primarily graminoid fens. Locations of observed ovipositing sites and exuviae were noted to further inform an understanding of microhabitat selection by females for reproduction.

Results

Tachopteryx larvae were found in one fen site in Big South Fork National River and Recreation Area in TN (Figures 1a, 2a, b) and four fen sites in the region surrounding Lake of the Ozarks in MO: Big Buffalo Creek Fen (Big Buffalo Creek Fen Natural Area, Big Buffalo Creek Conservation Area, Missouri Department of Conservation), Mule Shoe fen (Mule Shoe Conservation Area, Missouri Department of Conservation) (Figures 1b, 2c), Lead Mine fen (Niangua River Hills Natural Area, Lead Mine Conservation Area, Missouri Department of Conservation) and Flagmire Hollow fen (Mark Twain National Forest, US Forest Service, Houston District) (Table 1). Larvae were generally well camouflaged with muck and organic material adhered to their spiny bodies. Larvae of various sizes were recorded, including larvae of different sizes in close proximity to each other. The majority of recorded larvae (eight out of 14) were located in crypts, or shallow pits or depressions (hereafter "pits"), which appeared to have been established by the larvae (Table 1). Larval pits were recorded at the TN site and three MO sites and were usually located under a layer of decomposing deciduous leaves and other litter. Although variable in their characteristics, their appearance generally suggested an extended period of larval occupation, with the substrate of the floor of the pit smooth, putatively as a result of larval activity (Figure 2a, c). Association with pits was not limited to the largest larvae although no small larvae were associated with such pits. All larvae were recorded in at least somewhat sloping sites where they would never be subject to inundation, either in treeless and mostly graminoid fens (Figure 1b), or along sloping fen margins where seepage was emergent on adjoining, forested, lower hill-slopes (Figure 1a).

Exuviae were found in the fen in Big South Fork and in Big Buffalo Creek Fen. All exuviae were perched between 20 and 60 cm above ground, but most were < 35 cm above ground. All exuviae recorded were in sites where larvae would never be subject to prolonged inundation. All were perched more or less vertically or hanging slightly backwards, except one which was perched horizontally on a large leaf. Exuviae in the Big South Fork fen were found perched on *Thelypteris noveboracensis* (New York fern) and amongst *Carex intumesum* and *C. crinita*, with extensive *Sphagnum lescurii* ground-layer in a treeless area of graminoid/fern fen, and in

Figure 1. (a) Big South Fork fen (TN) showing transition from drier, forested, lower hill-slope (above) to gently sloping, groundwater-fed, valley-bottom fen (below). *Tachopteryx* larvae were located (arrowed) under fallen deciduous leaves along the upper edges of the fen amongst *Carex*, ferns and *Sphagnum* near this transition (Figures 2a, b). Exuviae were recorded more widely throughout the forested, valley-bottom fen. Photo by Ian Baird (17 May 2018); (b) Mule Shoe fen (MO), a treeless, low gradient, hill-slope, graminoid calcareous fen, where ovipositing was observed and where a larva was recorded in a depression (with "roof") along a small, downslope water track (arrowed) (Figure 2c). Photo by Ian Baird (7 June 2018).

Figure 2.   (a) Well camouflaged late or final stadium *Tachopteryx* larva (arrowed) in shallow, type 'a' circular pit (*denotes edges of pit) in the upper edge (Figure 1a) of Big South Fork fen (TN). Covering leaves temporarily removed. Note lack of free surface water and smooth saturated substrate in pit. Photo by Ian Baird (17 May 2018); (b) Muck covered *Tachopteryx* larva (arrowed; earlier stadia larva than larva in Figure 2a) next to presumed, natural seepage-filled depression amongst surface muck and decaying plant litter along upper edge of Big South Fork fen (TN) (Figure 1a). This seepage-filled depression was considerably wider and more irregular than the type 'b' pit where one larva was recorded in Big Buffalo Creek fen (no clear image available). Covering leaves temporarily removed. Note abundant seepage, plant litter and complex microhabitat. Photo by Ian Baird (17 May 2018); (c) *Tachopteryx* larva in shallow type 'c' pit in Mule Shoe fen (MO) (Figure 1b). Covering "roof" (arrowed) of matted plant litter, sediment and moss temporarily peeled back. No other covering leaves or other litter was present. Note lack of free surface water and smooth, moist substrate in the pit. Photo by Ian Baird (7 June 2018).

Table 1.   Results of *Tachopteryx thoreyi* observations and targeted larval searches in fens in Tennessee (TN) and Missouri (MO). Only includes sites where *Tachopteryx* larvae, exuviae or adults were recorded.

Site name	Survey date	Ovipositing observed	Exuviae recorded (n)	Total larvae (n)	Larvae (n) with pits	Pit type[1]
Big South Fork fen, TN	17 May 2018	No	15	4	2	a
Shut-in Mountain Fens, MO	2 June 2018	Yes	No	-	-	-
Blair Creek Raised Fen, MO	3 June 2018	Yes	No	-	-	-
Big Buffalo Creek Fen, MO	7 June 2018	Yes	7	3	3	a (2), b (1)
Mule Shoe fen, MO	7 June 2018	Yes	No	1	1	c
Lead Mine fen, MO	7 June 2018	Yes	No	3	0	-
Flagmire Hollow fen, MO	8 June 2018	No	No	3	2	a

[1] Pit type:

a = typical, shallow, saucer-shaped, depression-type pit ($\sim$ 2.5–4 cm diameter, 0.5–1.5 cm deep) in the substrate, under deciduous leaf pack or woody debris (Figure 2a). One larva was in a depression on a short $\sim$ 45° slope under the edge of a rotting fallen log near a crayfish burrow. Depressions varied from having moist to saturated substrate, but no standing water at time of observation, to having shallow seepage water;

b = pit (possibly natural) deeper than wide ($\sim$ 3 cm deep), mostly seepage-filled, under deciduous leaf pack. Larva was positioned semi-vertically, with head and upper thorax above water level in possible ambush posture under the leaves (Figure 2b shows a larva next to a larger and more irregular, natural seepage-filled pit);

c = slightly elongated, saucer-shaped depression or crypt ($\sim$ 3.5 cm diameter, $\sim$ 1.5 cm deep) similar to typical type "a" but with a thin and very slightly domed roof of what appeared to be a thin layer of decomposing plant litter, consolidated with silt and early moss establishment (due to light reaching the substrate), with several cracks in the roof which the larva may have used for access, and/or possibly for positioning for ambush predation. The elongated end of the depression also had what appeared to be a short ramp extension which the larva could have used for access or as an ambush position. The larva reacted rapidly to movement when the roof of its pit was disturbed. Minimal ground cover for larval concealment was otherwise available along the narrow water-track and seepage line in this sloping, treeless, seepage-fed, graminoid, calcareous fen (Figure 1b). Pit substrate surface was very smooth, suggesting a long period of occupation. Moist substrate but no free seepage water in crypt at time of observation (Figure 2c).

the adjoining low gradient, valley-bottom, forested fen or swamp forest (dominated by *Acer rubra* and *Nyssa sylvatica*) in the same fen complex. Larvae observed at this site were on the upper margins of the forested fen where seepage was emergent on the adjoining lower hill-slope amongst leaf litter, graminoids, herbs, ferns and *Sphagnum* (Figure 1a). Exuviae observed at Big Buffalo Creek Fen were also along the upper margins of the fen where seepage was emergent on the adjoining lower hill-slope, in a similar position to where larvae were recorded at this site. At this site exuviae were recorded on graminoids, ferns, tall herbs and *Equisetum*.

Ovipositing was observed in Big Buffalo Creek Fen, Mule Shoe fen, Lead Mine fen, Shut-in Mountain Fens (The Nature Conservancy Shut-in Mountain Fens Preserve, Wildcat Hollow, MO) and Blair Creek Raised Fen (Blair Creek Fen Natural Area, Mark Twain National Forest, US

Forest Service, MO) (Table 1). Ovipositing in these sites was observed along upper fen margins where treeless fens transitioned to forest seeps on adjoining lower hill-slopes, and in treeless graminoid fens where suitable seepage was evident and where access to the substrate (amongst fen vegetation) was available to ovipositing females. The female observed ovipositing in Mule Shoe fen was ovipositing into the exposed and more or less vertical surface of a shallow layer (< 15 cm deep) of saturated soil on the open edge of an erosion scald in two separate, but nearby locations, in this sloping calcareous fen, in an area with apparently little cover for larvae. This female investigated nearby ovipositing opportunities, but appeared to find the low graminoid vegetation too dense for her to access the substrate. Such ovipositing access constraints have also been documented in other petalurids (e.g. Baird, 2014b; Wolfe, 1953). In the other sites, ovipositing females also selected less dense openings amongst the low fen vegetation to access the substrate, typically associated with small water tracks or seepage lines.

Most fens surveyed in this study had burrowing crayfish, but not all burrows were characterised by the presence of chimneys at the burrow entrance which would immediately indicate that they were crayfish burrows, although their burrow diameter was typically a good indicator. Exuviae and larvae were frequently found in close proximity to crayfish burrows, further suggesting that the "vertical tunnel" observed by Williamson (1932) near a *Tachopteryx* larva in MO was probably a crayfish burrow.

Discussion

The observations in this study of the majority of recorded *Tachopteryx* larvae inhabiting crypts, pits or shallow depressions is consistent with field observations by Dunkle (1981) and unpublished observations by Larry Everett of some larvae being found in shallow pits in the field, and confirmation that captive raised larvae will also create such pits. Dunkle's (1981) reference to depressions, the only previous published reference, has apparently and surprisingly gone uncommented upon until now in the literature. The actual method of pit development is unknown. In some less-developed examples it could arguably simply be the result of ongoing movement by larvae over an extended period of time in a localised area with very soft saturated soil, but examples documented here, and the larval rearing observations by Larry Everett, indicate habitat modifying behaviour. No such habitat modifications have been reported in any of the relatively few observations of larvae of *Phenes*, although Günther Fleck (pers. comm.) has observed a captive, final stadium *Phenes* larva in a shallow, irregular depression in *Sphagnum* in its container, probably created by the larva incidentally compressing the soft *Sphagnum* with its movements, possibly to maximise body contact with the moist moss. The establishment of pits by some *Tachopteryx* larvae suggests a more sedentary lifestyle with fidelity to their pits (once pits are established) as long as covering plant litter (or other material) is maintained and suitable environmental conditions persist. Larvae without pits are presumably free to forage more widely and seek suitable habitat conditions if necessary. While only larger *Tachopteryx* larvae were observed in association with pits in this study, the smallest larva recorded in such depressions by Larry Everett (pers. comm.) was ∼ 12 mm long, indicating that this behaviour is not restricted to late or final stadia larvae.

In relation to the origins of the burrowing habit in petalurids, the ecological benefits to larvae of modifying their microhabitat to suit changing environmental conditions are obvious, including in response to a changing climate and groundwater levels. These benefits clearly must outweigh the energy costs of burrow excavation and maintenance for these long-lived larvae (Baird, 2014a). Although the number of burrowing (and non-burrowing) petalurid species which are now extinct is unknown, the burrowing habit has nevertheless probably been beneficial in the persistence of

the nine, extant, groundwater-dependent, fossorial petalurids in Australia, New Zealand, Japan and the Pacific North-West of North America, over tens of millions of years of tectonic, climatic and ecosystem change (e.g. see Ware et al., 2014). In the case of *Petalura* spp. in Australia, in addition to other environmental protections, the benefits include protection from fire on this highly fire-prone continent (Baird, 2014a; Baird & Burgin, 2016; Benson & Baird, 2012). In a study of *P. gigantea* burrows, Baird (2014a) also reported evidence of some adaptive burrow deepening by larvae during a long drought. In groundwater-dependent ecosystems, such as those used by burrowing petalurids worldwide, burrowing provides a relatively stable environment, access to groundwater and the potential to follow changing groundwater levels.

In the absence of burrowing, larvae of *Phenes* and *Tachopteryx* are reliant on persistence of suitable moisture conditions to avoid desiccation. Although Günther Fleck (unpubl. obs.) has observed a captive final stadium *Phenes* larva remain healthy in a surficially dry state for two days with moss (green, but not wet) in a closed box, and observed a surficially dry larva (apparently foraging) in terrestrial habitat at night, the desiccation resistance of *Phenes* and *Tachopteryx* when exposed to prolonged dry conditions is unknown. In the high rainfall, cool temperate rainforest habitats of *Phenes* in the southern part of its range in Patagonia, environmental stability is more assured as long as suitable climatic conditions persist for those widespread ecosystems. Further north in its patchy, groundwater-dependent fen and seepage habitats in the drier, fire-prone, Mediterranean climate zone the species will be more vulnerable to climate variability, and potentially fire (see Baird, 2013). In these areas, unless they have direct access to streams adjoining their seepage habitats, as they sometimes do, suitable refugia during temporarily drying conditions may depend upon at least some groundwater influence and the availability of soft, moist substrates where larvae can bury themselves, or access to other microrefugia such as voids in the substrate, under rocks, logs or tree stumps, or amongst the roots of fen and seep vegetation.

Tachopteryx larvae must benefit from similar means of avoiding unsuitable climatic conditions, as evidenced by the use of crayfish burrows during drought and winter by some larvae, although this presumably involves some risk of predation by their crayfish hosts. The establishment of shallow pits by some *Tachopteryx* larvae must provide benefits to larvae, potentially with some similarity to the benefits realised by fossorial petalurids, such as maintaining access to groundwater or contact with moist substrates. In the case of burrowing petalurids, these benefits include provision of resting places from which to practice ambush predation from within burrow openings, while maintaining ready access to groundwater; behaviour which has been confirmed in *Tanypteryx hageni* (Svihla, 1959, 1984), *T. pryeri* (Taketo, 1971) and *Uropetala* spp. (Rowe, 1987; Wolfe, 1953). The use or establishment of a type "b" pit by one larva observed in this study arguably could demonstrate a potential transitional stage between simple shallow depressions (typical type "a" pit) and the well-defined and sometimes complex burrows established by fossorial petalurids. The larva in this case, however, may well have been occupying an existing, natural water-filled pit. Similarly to *Phenes*, *Tachopteryx* larvae appear to be quite adaptable in occupying microhabitats ranging from those with no free surface water to water-filled pits and shallow pools. Better understanding the desiccation resistance of larvae, the circumstances where pit establishment by larvae occurs, at what stage of larval development it occurs, and the means by which that occurs, across the biogeographic range of the species in eastern USA, may contribute to our understanding of the benefits of pit establishment in *Tachopteryx*, and potentially, the evolution of a burrowing habit in petalurids more broadly.

The internal phylogenetic classification of the Petaluridae has been, and continues to be, of some controversy (e.g. see Fleck, 2011), with obvious implications for how we may understand the evolution of the larval burrowing habit in the context of the distribution of extant burrowing and non-burrowing species. Following on from various previous treatments of the family (e.g. Fraser, 1933, 1957; Winstanley, 1982) (e.g. using wing venation or other morphological

characters), Nel, Bechly, Jarzembowski, and Martínez-Delclòs (1998) split the Petaluridae into the subfamilies Petalurinae and Tachopteryginae; the latter including the tribes Tanypterygini (comprising *Tanypteryx*) and Tachopterygini (comprising *Phenes* and *Tachopteryx*). Using morphological characters, Fleck (2011), however, considered that *Phenes* was a sister group to all remaining modern petalurids and proposed the new subfamily Pheninae for *Phenes*. In a more recent phylogenetic and historical biogeographic study, Ware et al. (2014) found the Petaluridae to be monophyletic with a Pangaean origin in the mid-Jurassic ($\sim$ 157 Ma), with *Tachopteryx* and *Tanypteryx* forming a monophyletic Laurasian clade and the remaining three genera a monophyletic Gondwanan clade. Their molecular clock analysis suggested that these clades separated $\sim$ 146 Ma, consistent with estimated times of break-up of Pangaea between 140 and 180 Ma, with species ages of the extant species ranging from $\sim$ 100 to $\sim$ 30 million years (Ware et al., 2014). They suggested that during the Jurassic, New Zealand was near the origin point of the family, and "that Antarctica was at the centre of the petalurid distribution" (Ware et al., 2014, p. 1291), with subsequent dispersal to other Gondwanan remnants as well as Laurasia, and then from western North America to Japan (*Tanypteryx*). Belyshev (1974) considered the relict distributions of the Petaluridae to represent the circumference of Pangaea (cited in Louton, 1982). Ware et al. (2014) noted that early Cretaceous petalurid fossils have been described from Argentina, Brazil and England (see Coram & Nel, 2009; Nel & Bechly, 2009; Petrulevičius & Nel, 2003), and fossils of "stem group Petalurida, which includes Petaluridae and at least three other now extinct families, are known from the upper Jurassic from Asia, Europe and South America" (see Nel et al., 1998, p. 1294). The fossil record confirms the widespread distribution of a diverse petalurid fauna during that period, with the extant petalurid fauna being reduced by comparison.

Not surprisingly, for such an ancient group with controversial phylogeny, the origin of a burrowing larval habit has been the subject of much conjecture. Fleck (2011, p. 88) considered the non-burrowing character of larvae of *Phenes* and *Tachopteryx* as a plesiomorphy, and a primitive characteristic. Fleck noted that "the larvae of *Phenes* and *Tachopteryx* possess lateral abdominal extensions, a plesiomorphic condition apparently not seen in other Petaluridae, supporting the non-burrowing condition as plesiomorphic too". The presence of only four dental folds in the gizzard of *Phenes*, a unique feature in the Petaluridae (but like other Anisoptera), was also considered plesiomorphic by Fleck, supporting his position that *Phenes* was sister to all other extant petalurids. In determining his proposed phylogenetic classification, however, Fleck (2011, p. 93) also placed "a great evolutionary weight to the unique and complex ability to dig galleries". Ware et al. (2014) suggested, alternatively, that non-burrowing in *Phenes* and *Tachopteryx* is a derived trait, which evolved separately in each lineage after the two major clades (of Ware et al., 2014) separated.

In discussing this subject, the larval habits of some gomphids (Odonata: Gomphidae) deserve mention. Although the Gomphidae, which is often considered phylogenetically to be a sister group to petalurids, includes genera which are frequently referred to as burrowers (e.g. Corbet, 2004), these are perhaps more accurately referred to as "buryers". They do not excavate burrows *per se* (in the sense that petalurids do) but instead bury themselves, in a concealment strategy, just below the surface of the bottom sediments of their typical aquatic habitats; in some species with their eyes and caudal appendages protruding above the sediment surface. At the extreme of this behaviour, larvae of several species which have been found up to several centimetres below the substrate surface have developed unique morphological adaptations, including long respiratory "siphons" (see Corbet, 2004). While this burying behaviour provides concealment, and possibly other benefits, with some similarity to burrowing in petalurids, it represents a distinctly different evolutionary trajectory.

Considering the distribution of extant fossorial petalurids and the unlikely scenario of multiple independent origins of a burrowing behaviour which is restricted to petalurids (in the Odonata),

it is reasonable to suggest that the burrowing habit has an ancient origin in the Petaluridae (and potentially other now extinct Petalurida) and pre-dates the break-up of Pangaea. The question remains, however, of whether the non-burrowing habit of *Phenes* and *Tachopteryx* (and potentially other extinct petalurids) is plesiomorphic (Fleck, 2011), or a derived trait (Ware et al., 2014). If the extant species do represent two distinct clades as outlined by Ware et al. (2014), and non-burrowing is not plesiomorphic (as proposed by Ware et al., 2014), then when and why did the non-burrowing habit develop in *Tachopteryx* (part of Ware et al.'s Laurasian clade which includes fossorial *Tanypteryx*) and *Phenes* (part of Ware et al.'s Gondwanan clade, with all other extant species being fossorial)? If it is a derived trait, then the cost of excavating and maintaining permanent burrows (over a long larval period) may have become greater than the fitness benefits, presumably in response to changing environmental conditions across at least part of a species' range.

The larvae of the fossorial petalurids, particularly *Petalura* and *Uropetala* spp. (the largest larvae with the deepest and most complex burrows), show morphological adaptations apparently suited to a burrowing lifestyle, compared to those of *Phenes* and *Tachopteryx* (see Corbet, 2004; Fleck, 2011), both of which appear to have evolved a camouflage strategy of mimicking leaves and other plant litter (Dunkle, 1981; Fleck, 2011), and morphologically adapted to an above ground lifestyle (Fleck, 2011). Interestingly, from an ecological perspective, the burrows of some *Tanypteryx* larvae (the smallest petalurids with the simplest and shallowest burrows) are no more than10 cm deep and little more than pits. The establishment of shallow pits by some *Tachopteryx* larvae might simply represent adaptive behaviour and indicate some behavioural plasticity, but it may also provide some insight into the evolution of the ancestral burrowing habit in petalurids.

The phylogenetics of extant petalurids is still a subject of uncertainty with obvious implications for understanding the origin of burrowing and the phylogenetic relationships among extant fossorial and non-fossorial species. Following on from Ware et al. (2014), further phylogenetic and historical biogeographic studies, supported by morphological comparisons of larvae of these species (e.g. Fleck, 2011), in conjunction with a better understanding of the occurrence of pit establishment in *Tachopteryx*, will hopefully contribute to resolving these questions.

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