

OBSERVATIONS ON THE PETALURIDAE (ODONATA)

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The distribution of the Petaluridae is discussed. The tunneling behaviour and emergence patterns of the species are compared, and the supra-generic classification of the family is examined and amended.

DISTRIBUTION OF THE LIVING PETALURIDAE

The extant Petaluridae embrace 5 genera comprising 9 relict, archaic species with disjunctive distributions. Four species of *Petalura* occur in Australia: *P. gigantea* Leach in New South Wales and south Queensland (ARTHINGTON & WATSON, 1982), *P. ingentissima* Tillyard and *P. pulcherrima* Tillyard in north Queensland (FRASER, 1960) and *P. hesperia* Watson in Western Australia (WATSON, 1958). *Tanypteryx hageni* (Selys) occurs in western North America from Knight Inlet, British Columbia (CANNINGS, 1978) to California (PAULSON & GARRISON, 1977), and *Tanypteryx pryeri* (Selys) in Honshu and Kyushu, Japan (TAKETO, 1960). The remaining genera are monotypic: *Uropetala carovei* (White) occurs throughout the main islands of New Zealand (WOLFE, 1953); *Phenes raptor* Rambur is known from Santiago to Lago Llanquihue in Chile (SVIHLA, 1960b); and *Tachopteryx thoreyi* (Hagen) ranges from Quebec (FERNET & PILON, 1968) through eastern U.S.A. as far south as Texas and Florida (NEEDHAM & WESTFALL, 1955). Thus petalurid species occur in the northern hemisphere between 50° N and 31° N and in the southern hemisphere between 15° S and 47° S.

Despite their extensive latitudinal ranges, the species show little morphological variability. Slight regional differences have been noted in populations of *P. gigantea* (J.A.L. Watson, pers. comm.) and *T. hageni* (TURNER, 1970), but only in *U. carovei* have subspecies been des-

cribed (TILLYARD, 1921; WOLFE, 1953; WINSTANLEY & ROWE, 1980). The validity of the subspecies in *U. carovei* has been questioned (WOLFE, 1953; PENNIKET, 1966), and needs further investigation (ROWE, 1981).

The Petaluridae have been characterised as a group of montane bog-dwellers (TILLYARD, 1917; WOLFE, 1953), but most of the species are not restricted to high altitudes. *P. gigantea*, *P. hesperia*, *T. thoreyi*, *T. hageni*, and *U. carovei* have all been recorded at or near to sea level (ARTHINGTON & WATSON, 1982; J.A.L. Watson, pers. comm.; BYERS, 1930; CANNINGS, 1977; WINSTANLEY & ROWE, 1980), and *T. pryeri* is a low mountain dweller (TAKETO, 1960; SVIHLA, 1960c) which is found from 50-1300 m above sea level (A. Taketo, pers. comm.). The presence of *T. hageni* at sea level at the boreal extreme of its range (CANNINGS, 1977) might be interpreted as a climatic compensation of altitude for latitude; this cannot apply with *P. gigantea*, *T. thoreyi* and *U. carovei* which occur at low altitude in lower latitudes (ARTHINGTON & WATSON, 1982; BYERS, 1930; WINSTANLEY & ROWE, 1980).

LARVAL HABITAT

The larval habitat of the Petaluridae is unique among Odonata. The larvae of *P. gigantea*, *P. hesperia*, *T. hageni*, *T. pryeri* and *U. carovei* excavate permanent tunnels extending below the water table in boggy areas (TILLYARD, 1909; 1911; WATSON, 1958; SVIHLA, 1959; TAKETO, 1958, 1971a, 1971b; WOLFE, 1953). Exuviae of *P. ingentissima* have been found above tunnels adjacent to streams (J.A.L. Watson, pers. comm.), but the larva of *P. pulcherrima* and its habitat are unknown. WILLIAMSON (1932) located a *T. thoreyi* larva close to a vertical tunnel in mud but DUNKLE (1981) found no evidence of tunnelling in this species. *P. raptor* larvae have been found in slow streams and on the surface in a hillside seepage area (SVIHLA, 1960b). If *T. thoreyi* and *P. raptor* do not tunnel, this represents a marked behavioural departure from the rest of the family.

A considerable diversity has been reported in the pattern of excavation followed by larvae of the different species, ranging from the deep anastomosing labyrinths of *P. gigantea* (TILLYARD, 1911), through the elaborate tunnels of *U. carovei* (WOLFE, 1953), to the simple but variable retreats of *T. pryeri* (TAKETO, 1971a, 1971b) and *T. hageni* (SVIHLA, 1959, 1960c, 1967, 1975, 1979). Apart from a greater diameter and depth, the burrows of *U. carovei* resemble those of *T. pryeri* and *T. hageni* (WINSTANLEY, 1981; pers. obs.); the ex-

treme examples illustrated by WOLFE (1953) tend to obscure this similarity. One larva per tunnel is the rule in *U. carovei*, *T. hageni* and *T. pryeri* (WOLFE, 1953; SVIHLA, 1959; TURNER, 1970; TAKETO, 1971a), and cannibalism has been confirmed in *U. carovei* (WOLFE, 1953; HARDING, 1977), *T. hageni* (TURNER, 1970), and *T. pryeri* (TAKETO, 1971a). These observations cast doubt on the interpretation that TILLYARD (1911) placed on the burrows of *P. gigantea*.

CLASSIFICATION OF THE PETALURIDAE

Widely separated eyes, long and very narrow pterostigmata, and, in the female, a complete ovipositor, characterise adult Petaluridae. All final-instar larvae are robust, have stout legs with strong tibial spurs, a slightly concave labium with a spine overlapping the base of the movable hook, and a truncate epiproct; they are unable to propel themselves by expelling water from the rectal chamber.

FRASER (1933) recognised two subfamilies – the Tachopteryginae containing *Tachopteryx thoreyi*, *Tanypteryx hageni* and *T. pryeri*, the morphologically and behaviourally diverse species of the other genera being placed in the Petalurinae. Using colour and antenodal neuration as his criteria, FRASER (1957) erected the “Tanypterictinae”¹ to embrace the species of *Tanypteryx*, and transferred *Tachopteryx thoreyi* to the Petalurinae. The species of the Tanypterictinae were defined as “coloured black and yellow with strongly contrasted, well defined markings as in the Gomphidae; primary antenodal nervures separated by only 3 secondaries in the forewing and by only 2 in the hind”. He defined the species of the Petalurinae as “coloured brown or blackish brown, with poorly contrasted and ill-defined markings of yellow; primary antenodal nervures separated by not less than 4 or 5 secondaries in fore and hindwings”. Colour is not a valid criterion for the separation of the subfamilies: several species in the Petalurinae are conspicuously coloured (TILLYARD, 1912); and colour is inapplicable with fossil genera. With slight modification to conform with the generic specification for *Tanypteryx*, antenodal neuration alone provides a satisfactory basis for the recognition of the Tanypteryginae; KENNEDY (1917) recorded the third, fourth, or rarely the fifth antenodal developed as a brace in *Tanypteryx* species

¹ It is perfectly true that FRASER in 1957 erected a subfamily which he called “Tanypterictinae”, but this was wrong and he should have written “Tanypterygidae”. If any present-day author were to write the similarly derived Calopterygidae as “Calopterictinae” it would doubtless cause an outcry! –Ed.

and he illustrated specimens of *T. hageni* and *T. pryeri* which would not fall within the prescription of FRASER (1957).

EMERGENCE BEHAVIOUR

Emergence behaviour in *P. gigantea* and *U. carovei* has been portrayed as having a mixture of gomphid and aeshnid characteristics, and a unique element – the expansion of the abdomen preceding that of the wings (TILLYARD, 1917; WOLFE, 1953). SVIHLA (1960a) noted that the unique element is lacking in *T. hageni*; and *T. pryeri*, *T. thoreyi* and *U. carovei* are now known to have a gomphid-like emergence (EDA, 1959; TAKETO, 1971a; DUNKLE, 1981; WINSTANLEY *et al.*, 1981). The emergence behaviour of the Calopterygidae and of *Epiophlebia superstes* Selys is similar to that of the higher Anisoptera (EDA, 1963) which may have phylogenetic implications concerning the level at which the Calopterygidae and Anisozygoptera branched from the zygopterous stem.

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Since this paper was presented, ROWE (1981) has argued for the recognition of *Uropetala chiltoni* Tillyard as a species distinct from *U. carovei* (White). (R.J. Rowe, 1981. An annotated key to the New Zealand Odonata. *Mauri Ora* 9: 71-81.