

THE ENIGMATIC AUSTRALIAN ENDEMIC SPECIES *HEMIPHLEBIA MIRABILIS* SELYS (ZYGOPTERA: HEMIPHLEBIOIDEA): FOUR SHORT OBSERVATIONS AND A NEW RECORD

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This paper is dedicated to Philip S. Corbet on the occasion of his 70th birthday.

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Abstract

Four observations relevant to the phylogenetic status of *Hemiphlebia* and a new locality record are reported. The observations concern lack of closure of the forewing arculus, retention of paraglossae in the larvae, the chromosome number, and the morphology of the sperm. The record is for a new site in Tasmania.

Introduction

Hemiphlebia mirabilis Selys shows remarkable features that have been regarded, at different times, as either primitive or secondarily specialised. Selys (1869) and Munz (1919) treated *H. mirabilis* as an advanced coenagrionid. Tillyard (1928b) and Fraser (1955) regarded it as a survivor from the Permian. Fraser (1957) placed it as sister species to the whole remainder of the order, or else as sister to Coenagrionoidea, while for classification purposes he accorded it taxonomic status as superfamily Hemiphleboidea. Belyshev & Karytov (1985) transferred *Hemiphlebia* together with *Chorismagrion risi* Morton, the only other extant zygopteran to have an open discoidal cell in the forewing, to a new suborder, Archeoptera. However, there are no grounds for regarding *Hemiphlebia* and *Chorismagrion* as being closely related, or for separating them from Zygoptera. Bechly (1998) considered *H. mirabilis* "an extant relic type-genus", placing it as sister to a clade Lestiformia, (which includes the family Lestidae). He has Hemiphlebiidae + Lestiformia as the sister group to a clade (Coenagrionomorpha) containing the coenagrionoid families.

In large part the common view that *H. mirabilis* is archaic and phylogenetically isolated from other extant Zygoptera is based on two morphological features. In adults the forewing lacks the lower portion of the arculus such that the discoidal cell is open at its base. This feature is found also in the fossil suborder Protozygoptera and is primitive (plesiomorphic) for modern Odonata according to the Tillyard (1926, 1928a, 1935) system of wing vein nomenclature as used by, e.g., Fraser (1957) or Watson & O'Farrell (1991). Bechly (1998) treated the open discoidal cell of *Hemiphlebia* as a plesiomorphy,

commenting that “a parallel reversal [in *Hemiphlebia* and *Chorismagrion*] is very unlikely!” In larvae the prementum carries two large prongs. Tillyard (1928b) identified these as most probably representing the paraglossae, and he homologised them with a pair of minute teeth observed in some calopterygids (a family which at that time he regarded as among the most primitive in the order). In contrast, Bechly (1998) regarded these prongs as a secondary feature of Hemiphlebiidae alone, not homologous with the glossae or paraglossae of other orders.

Modern odonatologists are aware that uniquely retained, primitive character states afford no basis for determining phylogenetic relationships or for constructing a taxonomic classification (Hennig, 1965). Nevertheless, the concept that *H. mirabilis* is quite likely primitive, archaic, or relictual, based largely on these two characters, persists.

I report here two observations relevant to the interpretation of the wing venation and larval prementum of *H. mirabilis* as primitive or derived, a third observation relevant to the possible placement of *H. mirabilis* as a coenagrionid, a new locality for the species in north-eastern Tasmania, and a peculiar and apparently autapomorphic feature of the spermatozoa. These items except the wing vein observation and locality were previously noted in Trueman (1993) but that document is unpublished and not readily accessible. The wing observation is new to this paper. The locality was previously reported in a research paper (Trueman & Cranston, 1994) commissioned by a department of the Australian federal government, but as that paper, too, is unpublished and not accessible to the majority of odonatologists this record is repeated here.

Observation 1

I have examined 33 pinned specimens of *H. mirabilis* in various Australian museum collections plus approximately 20 field collected specimens (all except essential voucher specimens being subsequently released unharmed) at the newly-found sites near Yea, Victoria (Trueman *et al.* 1992) and in north-eastern Tasmania (Trueman & Cranston, 1994 and this paper). Of these, one female specimen from Tillyard’s series, in the Australian Museum, Sydney, has the forewing arculus closed by a vein in both wings. The venation of the specimen is otherwise as figured for *H. mirabilis* by Fraser (1957).

Variation in closure of the forewing arculus has not, to my knowledge, been previously recorded for *H. mirabilis*. It’s closure in this specimen indicates that the more common, open state most probably is not retained from a very distant ancestor of the extant Zygoptera but is derived with respect to the closed condition in all but one other extant species. The open discoidal cell gives no ground for associating *H. mirabilis* with Lower Permian *Kennedyia mirabilis* Till. or Upper Permian *Permagrion falklandicum* Till., as several authors have done. It would be an error to score this wing character as primitively absent for purposes of cladistic analysis, and analyses which have failed to distinguish primary from secondary absence of this vein (e.g., Trueman, 1996) are to this extent misleading.

Observation 2

Tillyard (1928b) illustrated the premental prongs of *H. mirabilis* as projecting forward from a conical base. Examination of preserved specimens in the Australian National Insect Collection (ANIC) shows the prongs take the form of immoveable hooks about 2/3 as long and 1/2 as stout as the hook on the labial palp. Each prong bears a stiff seta at about 1/3 its length from base to tip. The prongs stand upright and the conical bases figured by Tillyard are most likely artifacts created by forcing them to lie flat under a cover slip. Figure 1 (modified from Hawking and Theischinger, 1999) illustrates these prongs in a more natural position. Tillyard (1928b) homologised these prongs with a pair of minute teeth seen in some Calopterygoidea. Examination of species spanning the entire range of zygopteran and anisopteran families (but not the Anisozygoptera) shows that all, regardless of family, carry a pair of minute teeth in approximately the same position as these prongs. In many instances these teeth are so reduced in the final instar as to be readily overlooked but they clearly are present at least in penultimate and earlier (F-1 to F-4) larvae. There are no teeth in addition to the prongs in *Hemiphlebia*. Under high magnification or SEM it can be seen that in any odonate species each tooth carries a single, minute seta, which can be identified with the second pair of ligular setae in second instar larvae as described by Dunkle (1980). In most species which I have examined, those setae in second and third instar larvae are closely associated with a small, tooth-like projection of the cuticle.

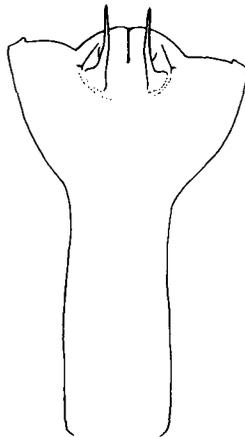


Figure 1. Prementum of *Hemiphlebia mirabilis* Selys, showing the large prongs.

Bechly (1998) argued that the premental prongs of *H. mirabilis* are not homologous with the glossae or paraglossae of other insect orders. I suggest that the premental prongs of *H. mirabilis* are homologous with what Tillyard (1928b) termed the “ligular teeth” of Calopterygoidea, and which are found in all Odonata. This would imply that, if *H. mirabilis* has retained the paraglossae, so too have other species. The argument that *H. mirabilis* is primitive because it alone retains paraglossae is untenable. Whether the extreme size of the prongs in *H. mirabilis* is primitive or derived cannot be determined independently of the phylogeny.

Observation 3

The haploid chromosome complement of *H. mirabilis* is $n=13$. Coenagrionid species almost invariably have a complement of 14 chromosomes, the Gomphidae 12, all remaining odonate families 13 (Kiauta, 1972; Kiauta & Brink, 1975; Kiauta & Kiauta, 1976; Jensen & Mahanty, 1978; Kiauta, 1979; Kiauta & Boon von Ochsee, 1979; Boyes *et al.*, 1980; Jensen, 1980; Kiauta & Kiauta, 1980a, b; Agopian & Mola, 1984, 1988).

I prepared chromosome squashes from a number of Australian species using the following protocol. Field collected males were narcotised with CO_2 and the testes dissected in insect saline. Testes were transferred to 50% saline for 12 minutes and fixed in 3:1 methyl alcohol: glacial acetic acid for 1-2 hours. The preparation was washed in 60% acetic acid, transferred to a drop of 60% acetic acid on a cleaned slide, macerated with a brass rod, spread in a further 2-3 drops of 60% acetic acid and dried for 1-12 hours at 60 deg. C. Slides were stained with giemsa for 4-5 minutes.

The resulting slides for *Hemiphlebia* were not of sufficient quality for publication but six of eight preparations do clearly show a haploid complement of 13 small, telocentric chromosomes. For completeness, I repeat here the results (ex Trueman, 1993) for all species examined. For none of these species has the chromosome complement previously been published. The first figure is the number of specimens, the second the haploid complement: *H. mirabilis* (8, 13), *Austroagrion watsoni* (2, 14), *Ischnura heterosticta* (3, 14), *Rhadinosticta simplex* (3, 13), *Nososticta solida* (3, 13), *Xanthagrion erythronurum* (3, 14), *Argiolestes griseus* (2, 13), *Austroargiolestes icteromelas* (3, 13), *Austrolestes cingulatus* (3, 13), *Synlestes weyersii* (4, 13), *Diphlebia lestoides* (4, 13), *Austropetalia patricia* (5, $2n=26$ from egg preparations), *Austrogomphus guerini* (2, 12), *Cordulephya pygmaea* (4, 13), *Eusynthemis brevistyla* (3, 13), *Hemicordulia tau* (3, 13), *Synthemis eustalacta* (3, 13).

The observed complement $n=13$ for *H. mirabilis* is not consistent with its placement as an advanced coenagrionid.

Observation 4

The mature spermatazoa of *H. mirabilis* are extremely unusual, and unique among Odonata, in that they possess two flagella. All other species for which I made chromosome preparations (see above) had typical odonate-type sperm as described by Jamieson (1987). These sperm have a rod-like body approximately 9-10 μm long and 1.0-1.5 μm in diameter with a single flagellum 60-100 μm in length, or else are unflagellated. In contrast, the sperm of *H. mirabilis* were biflagellate, with an approximately 10% incidence of either three or four flagella. Figure 2 shows sperm as they appear in a chromosome spread. Unfortunately, I had no material from which to make sperm preparations as such.

Biflagellate sperm are highly unusual in Insecta. The fowl louse *Menopon gallinae* (Phthiraptera) has sperm with two flagella each with a single axoneme, and the human body-louse *Pediculus humanus corporis* has sperm with two axonemes in a single flagellum (Jamieson, 1987). *Mastotermes darwiniensis* (Isoptera) has multiflagellate sperm and groups of monoflagellate sperm joined to form multiflagellate functional units are known

from Lepismatidae (*Zygentoma*) and some Dytiscidae (Coleoptera) (Jamieson, 1987). The sperm of some Psyllidae (Hemiptera) are binucleate with a single flagellum while those of some Coccoidea (Hemiptera) are filamentous without a distinguishable head (Robison, 1969). Sperm of the *Hemiphlebia* type have not previously been recorded from Insecta. The fine structure of this sperm needs further investigation.

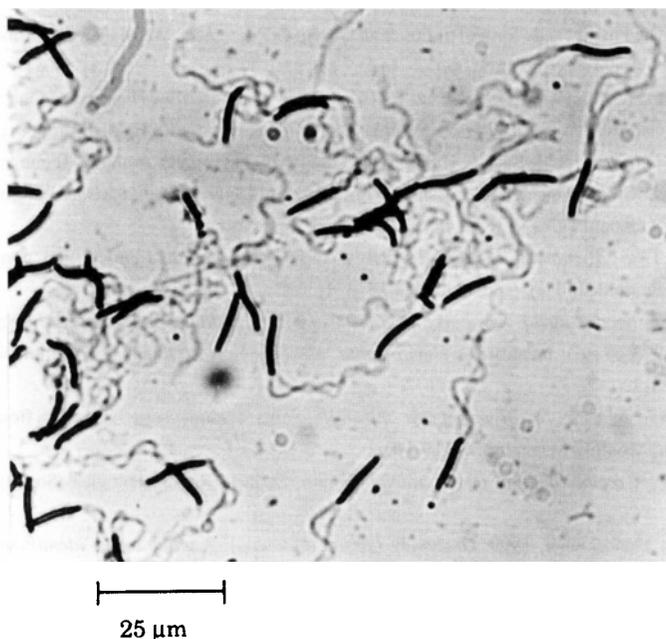


Figure. 2. Mature sperm of *Hemiphlebia mirabilis* Selys as it appears on a chromosome spread.

New locality record

Hemiphlebia is known to survive at four localities: Wilson's Promontory on the southern coast of Victoria (Davies, 1985), at Yea and Alexandria in central Victoria (Trueman *et al.*, 1992), in the Mount William National Park at the far north-eastern tip of mainland Tasmania (Trueman *et al.*, 1992), and in marshes on Flinders Island in Bass Strait (Endersby, 1993). The new locality is at Rattray's Marshes (41 deg 12' S., 148 deg 10' E.), a buttongrass (*Gymnoschoenus* sp.: Cyperaceae) dominated wetland approximately 18 km north of the town of St. Helens on the Tasmanian east coast. *Hemiphlebia* were observed there in February, 1993, as recorded previously by Trueman & Cranston (1994). Searches further south as far as the Wineglass Bay on the Freycinet Peninsular (42 deg 09' S., 148 deg 19' E.; approximately half-way along the eastern coast) failed to reveal any further populations.

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