

## THE SUBFAMILIES OF PROTONEURIDAE (ZYGOPTERA)

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The subfamilial classification of the Protoneuridae is reviewed. No clear-cut divisions are apparent between the 3 currently recognised subfamilies (the Caconeurinae, Disparoneurinae and Protoneurinae), based on an examination of adult morphology in representatives of 20 of the 23 genera. The Protoneuridae should be regarded as comprising a single subfamily.

### INTRODUCTION

FRASER (1957) divided the family Protoneuridae into four subfamilies: Proto-*neurinae* (New World); *Caconeurinae* (Indian subcontinent); *Disparoneurinae* (Old World); and *Isostictinae* (Australasian). LIEFTINCK (1975) elevated the *Isostictinae* to family rank, primarily on the basis of larval structure (cf. FRASER, 1955, 1957; WATSON, 1969).

FRASER (1957) defined the other three subfamilies as follows:

– *Caconeurinae*: "More robust build"; "superior anal appendages with a long obtuse ventral process"; "CuP of much greater length, extending to a maximum of 10 to 13 cells distal to the level of the vein descending from the subnodus"; anal vein present in all genera but one, in which it is fused with the wing margin, but "always more or less reduced and never extending beyond the level of the distal end of the discoidal cell".

– *Disparoneurinae*: Superior appendages of male "trigger-shaped in profile, triangular as seen from the dorsal aspect; the inferiors broad at base, extending posteriorly and with the end curled abruptly upwards"; CuP generally "extending beyond the level of the vein descending from the subnodus, often several cells beyond; anal vein nearly always present but much reduced and never longer than 1 or 2 cells beyond the level of the discoidal cell".

– *Protoneurinae*: CuP generally extending "to the level of the vein descending from the subnodus or a short distance distal to it"; anal vein fused with wing margin, or represented by "remnants".

More recent examination of species representing most of the genera of *Protoneuridae* has revealed that Fraser's subfamilial division of the *protoneurids* is inappropriate. WATSON & THEISCHINGER (1984) treated the *Disparoneurinae* plus *Protoneurinae* as a single subfamily, but did not document their arguments for doing so. Those arguments are now presented in full.

#### MATERIAL EXAMINED

Specimens were examined from the Australian National Insect Collection, CSIRO, Canberra; the Florida State Collection of Arthropods, Gainesville, Florida, U.S.A.; and the International Odonata Research Institute, also at Gainesville. Much of the non-Australian material is lodged in the Gainesville collections. Inevitably, some of the series were short; furthermore, I was in no position to verify the identifications of most of the non-Australian specimens. However, these inadequacies and potential inaccuracies could not affect the outcome of the survey.

WATSON & THEISCHINGER (1984) placed the Australian species of *Notoneura* Tillyard (type species *Alloneura solitaria* Tillyard from Australia) in the genus *Nososticta* (type species *Alloneura solida* Hagen in Selys, also from Australia). The status of the many non-Australian species previously placed in *Notoneura* was not resolved. In this paper, such species are placed in "Notoneura".

The genera and species studied are listed below, in alphabetical order in the three relevant subfamilies that FRASER (1957) recognised. Type species are marked with an asterisk.

#### CACONEURINAE

- Caconeura* Kirby  
 \**gomphoides* (Rambur)  
*ramburi* (Fraser)  
*Esme* Fraser  
 \**cyaneovittata* Fraser (male only)  
*mudivensis* Fraser (female only)  
*Melanoneura* Fraser  
 \**bilineata* Fraser (male only)  
*Phylloneura* Fraser  
 \**westermanni* (Selys) (male only)

#### DISPARONEURINAE

- Chlorocnemis* Selys (type species  
*Chlorocnemis elongata* Hagen in  
 Selys)  
*marshalli* Ris (male only)  
*nigripes* Selys  
*Disparoneura* Selys  
*apicalis* (Fraser) (male only)  
 \**quadrifasciata* (Rambur)  
 (male only)  
*ramajana* Lieftinck (male only,  
 from LIEFTINCK, 1971)

- Elatoneura* Cowley  
*fraenulata* (Hagen)  
 \**glauca* (Selys)  
*tropicalis* Pinhey (male only)  
*Nososticta* Hagen in Selys  
*baroalba* Watson & Theischinger  
*coelestina* (Tillyard)  
*fraterna* (Lieftinck)  
*kalumburu* Watson & Theischinger  
*koolpinyah* Watson & Theischinger  
*koongarra* Watson & Theischinger  
*liveringa* Watson & Theischinger  
*pilbara* Watson  
 \**solida* (Hagen in Selys)  
*solitaria* (Tillyard)  
*taracumbi* Watson & Theischinger  
 "Notoneura"  
*finisterrae* (Förster)  
*insignis* (Selys)  
*nigrofasciata* Lieftinck  
*rangifera* Lieftinck (female only)  
*salomonis* (Selys)  
*thalassina* Lieftinck (female only)  
*xanthe* Lieftinck (female only)

*Prodasineura* Cowley

- autumnalis* Fraser (including  
*a. corvina* Lieftinck, male only)  
*collaris* (Selys)  
*dolorosa* (Needham) (male only)  
*\*dorsalis* (Selys) (male only)  
*hosei* Laidlaw (male only)  
*laidlawi* (Förster)  
*verticalis* (Selys)  
*vittata* (Selys) (male only)

Genus not examined:

*Isomecocnemis* Cowley

## PROTONEURINAE

*Epileoneura* Williamson

- capilliformis* (Selys) (male only)  
*fernandezii* Racenis (male only)  
*fuscaenea* Williamson (male only)  
*incusa* Williamson  
*\*lamina* Williamson  
*machadoi* Racenis (male only)  
*metallica* Racenis (male only)  
*spatulata* Racenis (male only)  
*venezuelensis* Racenis (male only)  
*westfalli* Machado (male only)  
*williamsoni* Santos

*Epiprotoneura* Williamson

- \*nehalennia* Williamson (male only)

*Idioneura* Selys

- \*ancilla* Selys (male only)

*Microneura* Selys

- \*caligata* Selys

*Neoneura* Selys

- aaroni* Calvert  
*amelia* Calvert  
*\*bilinearis* Selys  
*carnatica* Selys (male only)  
*crisrina* Racenis (male only)  
*esthera* Williamson  
*myrthea* Williamson

*Peristicta* Selys (type species

- Peristicta forceps* Selys)

*aeneoviridis* Calvert

*Phasmononeura* Williamson

- ciganae* Santos (male only)  
*ephippigera* (Selys)  
*\*exigua* (Selys) (= *olmyra*  
 Williamson)

*Protoneura* Selys (type species *Agrion*

- capillare* Rambur)  
*ailsa* Donnelly (male only)  
*aurantiaca* Selys  
*cara* Calvert (male only)  
*cupida* Calvert (male only)  
*sanguinipes* Westfall  
*viridis* Westfall

*Psaironeura* Williamson

- \*remissa* (Calvert) (male only)  
*tenuissima* (Selys)

*Ropponeura* Santos

- \*beckeri* Santos (male only)

Genera not examined: *Junix* Racenis,

*Proneura* Selys

## RESULTS

It is best to summarise the results character by character across the three subfamilies.

## ANAL APPENDAGES

In the "Caconeurinae", the superiors are forcipate, elongate or otherwise unlike those of the other subfamilies. In *Caconeura*, *Melanoneura* and *Phylloneura* the inferiors are long, with upturned tips.

Not all "disparoneurines" fit Fraser's diagnosis. All except *Chlorocnemis*, in which they are elongate and slightly forcipate, have triangular superiors but those of *Prodasineura hosei* lack a ventral spine, and *P. laidlawi* has elongate superiors with a rounded to triangular ventral lobe at the tip. According to N. Donnelly

(pers. comm.) other species of *Prodasineura*, while showing the general triangular pattern, have variable ventral spination. The inferior appendages of *Disparoneura* often form truncated pyramids; in some but not all *Prodasineura* they are elongate, with tips turned more inward than upwards; and in *Chlorocnemis* they are elongate and slightly forcipate.

Both superior and inferior appendages vary in the "Protoneurinae". The superiors cannot be characterised readily, but the inferiors are commonly triangular, sometimes elongate; or, in some *Neoneura*, more rounded in section, with a bluntly-pointed tip; or, in *Epipotoneura*, *Peristicta*, *Phasmoneura*, *Psaironeura* and *Roppaneura*, are short or vestigial.

Thus the only extensively distributed pattern in the anal appendages is the "trigger" shape that FRASER (1957) attributed to the superior appendages of "Disparoneurinae", accompanied by inferiors with upturned tips. This pattern occurs in most "disparoneurine" genera, including some species of *Disparoneura* but not the type species, *D. quadrimaculata*.

#### CuP

The length of CuP is variable in the "Caconeurinae", subtending 8 to more than 12 cells in *Caconeura gomphoides* and *C. ramburi*, both large species; 8/8 in *Esme cyaneovittata* but 11-12 in both wings of *E. mudiensis*, again large; 6/7 in the large *Melanoneura*; and 9-12/11 in *Phylloneura westermanni*, another large species. In those large "caconeurines" with CuP very long, CuP extends up to 10 cells beyond the vein descending from the subnodus.

The "disparoneurines" show greater variability. In *Disparoneura quadrimaculata*, the type species and a large one, CuP subtends approximately 10 cells in both wings, extending 6-7 cells beyond the vein below the subnodus, whereas in *D. apicalis* and *D. ramajana* it subtends 6-8 cells, extending 4-6 cells beyond the subnodus. CuP is also long in *Chlorocnemis*, subtending 6-10 cells, and in *Elatoneura*, subtending ca 5 cells, approximately 3 cells beyond the subnodus. At the other extreme, species of *Nososticta* (including "Notoneura") commonly have CuP subtending only one cell and ending well before the level of the subnodus. In some species of this genus CuP descends directly to the wing margin at the distal end of the discoidal cell, and in "Notoneura" *insignis* it subtends 1/2 cells and still ends before the subnodus. *Prodasineura* is intermediate, CuP subtending 0-1/2 to 4-5/5 cells in different species and ending at levels basal to the subnodus in some species to 3 cells beyond it in others.

In the "Protoneurinae" CuP commonly subtends 3 cells in both fore- and hindwings. In *Peristicta* and *Roppaneura* it subtends 4 cells; in *Phasmoneura exigua*, it subtends 1-2/2; and in *Protoneura viridis* and *Psaironeura*, 2/2. In the 3-celled species CuP extends half a cell to 1 cell beyond the vein descending from the subnodus (counted along the cells between R<sub>4+5</sub> and M), but CuP may

not reach the level of the subnodus in species where it subtends less than 3 cells, or may extend 1.5-2 cells beyond the subnodus in species where it subtends 4 cells.

Thus the length of CuP, however assessed, appears to be more closely related to body size than to subfamilial placement. Although fairly uniform in the "Protoneurinae", it varies in the "Caconeurinae" and, more widely, in the "Disparoneurinae", being longer in the larger forms (e.g., *Caconeura gomphoides* and *C. ramburi*; *Esme*; *Melanoneura*; *Disparoneura quadrimaculata*; *Elattonneura*). Indeed, in the "Disparoneurinae" the complete spectrum is shown, including the character-states present in the "Protoneurinae" and "Caconeurinae", from the condition in *Disparoneura quadrimaculata* to that in some species of *Nososticta*, "Notoneura" and *Prodasineura*, where CuP runs diagonally down from the end of the discoidal cell, so that it subtends no cells at the termen.

#### ANAL VEIN

Only one example was found of the anal vein extending beyond the end of the discoidal cell (cf. FRASER, 1957); that was in the "disparoneurine" *Chlorocnemis*.

The anal vein is variable in the "Caconeurinae". *Melanoneura* lacks a separate anal vein, as FRASER (1957) indicated. In *Caconeura* and *Esme*, the anal vein forms a triangular to lunular cell; it leaves the wing margin basal to (or, in some species, almost at) Ac, and returns to it before the end of the discoidal cell, usually well before, in which case the resulting cell tends to be triangular. *Phylloneura*, however, has an anal vein that leaves the wing margin proximal to Ac, then follows a slightly sinuate path to abut on the vein descending from the distal end of the discoidal cell.

The "Disparoneurinae" are similarly variable. *Nososticta* (including "Notoneura") lacks a distinct anal vein, as do *Prodasineura dorsalis*, *P. hosei*, *P. laidlawi* and some *P. collaris*. In *Prodasineura autumnalis*, other *P. collaris*, and *P. verticalis*, the vein forms a triangular cell below the end of Ac (as in *Caconeura* and *Esme*). In contrast, the anal vein of *Disparoneura* and *Elattonneura* is more extensive, of the type shown by the "caconeurine" *Phylloneura*. In *Chlorocnemis*, it continues through the vein descending from the end of the discoidal cell and extends one cell beyond it.

Most of the "protoneurine" genera lack an anal vein, or have it represented by a triangular thickening where Ac meets the wing margin (*Epipleoneura*, *Epipotoneura*, *Microneura*, *Phasmoneura*, *Protoneura*, *Psaironeura*, *Roppa-neura*). Three genera, however, have a substantial anal vein (*Idioneura*, *Neoneura*, *Peristicta*): much as in *Esme* and *Disparoneura*, it leaves the wing margin at Ac and extends to meet the vein descending from the distal end of the discoidal cell, sometimes near the wing margin.

The length of the anal vein thus shows three states: fused with the wing margin;

forming a triangular to rounded cell with its apex at or near Ac; or extending, behind the discoidal cell, from basal to or at Ac to terminate on the vein descending from the end of the discoidal cell. The "Caconeurinae" and "Disparoneurinae" show all three states, and the "Protoneurinae" the first and third.

#### OTHER CHARACTER-STATES

Two other characteristics were documented, the structure of the female pronotum, and the position of Ac with respect to the primary antenodal crossveins Ax<sub>1</sub> and Ax<sub>2</sub>.

In the few "caconeurine" females examined, the posterior lobe of the pronotum is not elaborated. In contrast, it is highly specialised in the disparoneurine genera *Elattonaura*, *Chlorocnemis*, *Nososticta* (cf. WATSON & THEISCHINGER, 1984), "Notoneura" and *Prodasineura*; and in "Notoneura" *xanthe*, the anterior and median lobes are also modified, the anterior lobe bearing a long, slender spine on each side and the median lobe a stout cone behind it. The "Protoneurinae" are variable: in some genera the posterior lobe is low and rounded; in others it is modified; and in *Neoneura* the degree of elaboration varies from, e.g., none in *N. aaroni* to a rounded, bilobed flap in *N. myrthea*.

The position of Ac is very variable within each subfamily. In the "Caconeurinae" and "Protoneurinae" Ac lies between Ax<sub>1</sub> and Ax<sub>2</sub>, sometimes nearer to one or the other, sometimes almost central, or differing between fore- and hind-wing. A more extensive range occurs in the "Disparoneurinae": Ac lies basal to or aligned with Ax<sub>1</sub> in *Nososticta* and "Notoneura", whereas in *Prodasineura* it may lie centrally, or nearer Ax<sub>2</sub>.

Thus although the posterior lobe of the pronotum is more extensively elaborated in female "Disparoneurinae" than in females examined from the other two subfamilies, its elaborated structure is not diagnostic of the "disparoneurines". Nor does the position of the anal crossing provide data useful in corroborating Fraser's subfamilial division of the Protoneuridae.

#### DISCUSSION

The survey has shown that *Caconeura* and the other south Indian genera that FRASER (1957) placed with it tend to stand out as a group of large protoneurids with relatively well-developed cubital and anal venation. However, the great length of CuP in *Caconeura* and these other genera finds a parallel in *Disparoneura*, but in other "disparoneurine" genera CuP is variably reduced, ultimately to a crossvein joining the tip of the discoidal cell to the termen as in some species of *Nososticta*. Anal venation similar to that of the "caconeurines" also occurs in *Disparoneura*, *Elattonaura*, and some *Prodasineura* (placed by Fraser in the "Disparoneurinae"); and in *Idioneura*, *Neoneura* and *Peristicta* of the New World

genera examined.

The anal appendages provide similarly non-diagnostic data. *Caconeura* and some of its allies have the tip of the inferior appendage turned upwards, as in many but not all genera of "Disparoneurinae". There is little resemblance between the anal appendages of either Old World group and those of the New World protoneurids.

Thus the adult characters so far studied do not support the subdivision of the Protoneuridae into three subfamilies. Too little is known of larval structures for them to be used in establishing or confirming subfamilial groupings. It follows that the Protoneuridae should for the present be regarded as including only a single subfamily, the Protoneurinae.

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