THE TAXONOMY AND ECOLOGY OF THE EPHEMEROPTERA (MAYFLIES) OF SOUTH AUSTRALIA

by

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ABSTRACT.

Many groups of Australian freshwater invertebrates remain little known taxonomically and ecologically. The Ephemeroptera is no exception; with 72 species of mayflies described, but ecological knowledge restricted to casual observations and one brief publication. In South Australia only three species have previously been recognised. one from Adelaide, and two from the south-east of the State.

The present study has recognised thirteen mayfly species in South Australia. All species have been described from both adult and nymphal material and keys enabling their identification are included. Five new species have been recognised, *Atalophlebia auratus*, *Atalonella pilosa*, *Jappa pipinna*, *Cloeon paradieniensis*, and *Centroptilum elongatum*; one species transferred from the genus *Atalophlebia* to *Atalonella* (*Atalonella inconspicua* (Eaton) comb. nov.); and the first associated nymphal descriptions of five previously described species *Atalonella inconspicua* (Eaton), *A. fuscula* (Tillyard), *Baetis soror* Ulmer , *Cloeon fluviatile* Ulmer , and *Tasmanocoenis tillyardi* (Lestage) made. Three species have been re-described from South Australian material *Atalophlebia australis* (Walker), *A. australasica* (Pictet) and *Tasmanophlebia lacus-coerulei* Tillyard . A brief analysis of interspecific and intraspecific variation is given.

The habitats occupied by the mayfly fauna from a permanent stream (Deep Creek) and an intermittent creek (Spring Creek) were determined by comparison of monthly or fortnightly samples taken from each locality over a twelve month period. Collections were made with a dual net sampler (480 µm and 110 µm mesh) that ensured collection of all nymphal instars. The life cycles of four species from these creeks were determined by analysis of size frequency histograms. All species studied, except *Tasmanocoenis tillyardi* in Deep Creek, had polyvoltine life histories with at least three generations per year. Two species, *Baetis soror* and *T. tillyardi*, had flexible life cycles, with an increased number of generations in the warmer Spring Creek.

Studies of egg development demonstrated two strategies; development directly related to temperature above a threshold, and a cool temperature induced quiescence. Light and/or photoperiod had little effect on incubation period, and eggs of *B. soror* and *Atalonella fuscula* did not survive desiccation. Survival of mayflies in South Australian intermittent streams appeared either to be by entry into the hyporheos during dry periods and/or occupation of residual surface pools, rather than by drought resistant eggs.

The distribution of mayfly species within South Australia and of these species throughout Australia was examined, and three groups defined; two endemic species, nine species now restricted to the Mt. Lofty-Flinders Ranges (including the Fleurieu Peninsula and Kangaroo Island) and eight species probably re-invading from Victoria. The latter two groups have common species suggesting that past distributions were more continuous. The present discontinuity has probably been caused by increased aridity, and eustatic sea level changes which have isolated the two faunas. The Ephemeroptera of South Australia therefore consist of two endemic species, two Victorian species and nine species widely distributed throughout Australia, but relictual in South Australia.

DECLARATION.

Except as stated herein, this thesis contains no material which has been accepted for the award of any other degree or diploma in any University, and to the best of my knowledge and belief, this thesis contains no copy or paraphrase of material published or written by another person, except where due reference is made in the text of the thesis.

P. J. Suter.

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CHAPTER 1

I.1 GENERAL INTRODUCTION

Although abundant and in places diverse, in the aquatic environment, Australian freshwater insects remain little known taxonomically with much of the classification unreliable below the level of family. The Ephemeroptera, or mayflies, are no exception to this generalised condition with only 72 species described, mainly from two States; New South Wales and Tasmania. Of the 72 species described, only 33 have nymphs reliably associated with adults. Edmunds and Allen (1966) noted that less than 20% of the 2,000 described species of Ephemeroptera are known from nymphal material. Needham, Traver and Hsu (1935) recorded 507 North American species of which 218 nymphs were known. Although the ratio of associated nymphs to adults is nearly 50% in Australia, the descriptions are such that classification is unreliable. The existence of numerous undescribed species (Riek (1970a) recorded 124 Australian species) compounds the difficulties in classification, especially in ecological studies.

The first Australian mayfly to be described was *Baetis costalis* by Burmeister in 1839. This species was later placed in the genus *Potamanthus* by Pictet (1843), who also described *B. australasica* from Australia. In 1853 Walker described *Ephemera australis* from Tasmania. However, all three species were later placed in the genus *Leptophlebia* by Eaton (1871). In his monograph, Eaton included three new Australian species in the genus *Leptophlebia*: *L. furcifera* from Melbourne, *L. inconspicua* from Adelaide, and *L. strigata* from "North Australia". He also described *Coloburus haleuticus* from Victoria, the first record of the Siphlonuridae in Australia. In 1881, Eaton described a new genus, *Atalophlebia*, with *A. australis* (Walker) as the genotype and, in his second monograph "A Revisional Monograph of Recent Ephemeridae or Mayflies" (1883-1888), included the six Australian species (excluding *Coloburus haleuticus*) in this new genus. The genus *Coloburus* Eaton was changed by Eaton in 1887 to *Coloburiscus*, and the Australian species was included in this genus.

In 1908, Ulmer redescribed, in greater detail, *Atalophlebia furcifera* (Eaton) and the South Australian species *A. inconspicua* (Eaton); and he recorded the first species in the Family Baetidae, describing *Baetis soror* from Western Australia. A nymph of '*Atalophlebia* sp.' was described but not associated or named. In 1916, Ulmer described a further six species; two in *Atalophlebia*; *A. uncinata* and *A. sexfasciata*, three in *Euphyrus*, *E. mjöbergi*, *E. unguicularis* and *E. bicornis*, and one in *Thraulus*, *T. dentatus*; and he recorded in Australia the presence of two species described from Java by Klapálek (1904), namely, *Cloeon virens* Klapálek (Ulmer incorrectly spelt the specific epithet *viridis*) from the Kimberleys, Western Australia; and *Pseudocloeon kraepelini* from north Queensland. Ulmer (1919) subsequently divided *Thraulus dentatus* into two species and placed them in the genus *Atalophlebia* as *A. lucida* and *A. fusca*. In addition another new species, *A. simillima* Ulmer, was also described (Ulmer, 1919). Needham and Murphy (1924) erected a new genus *Atalonella* to include two species, one from Chile and one from Australia (*A. fusca*).

The most comprehensive work on the Australian mayflies then followed, with four systematic papers by Tillyard. The first, in 1921, recorded a new genus of the Siphlonuridae, *Tasmanophlebia*, with *T. lacustris* from Tasmania as the genotype. His subsequent paper in 1933 included five new species of Siphlonuridae in three genera; *Ameletoides lacus-albinae*, *Tasmanophlebia lacus-coerulei*, and *T. nigrescens*, *Coloburiscus giganteus* and *C. munionga*. All these species were associated with their respective nymphs. Lestage (1935a) placed *C. giganteus* and *C. munionga* in the new *Coloburiscoides* which distinguished the Australian species from the New Zealand *Coloburiscus* species. To Tillyard's extensive work on the Siphlonuridae only three new species have been added, one by Harker (1954) in the new genus *Mirawara*, *M. aapta*, and two by Riek (1955) *M. megaloprepia* and *M. purpurea*.

Following his redescription of the genotype of *Atalophlebia* in 1934, Tillyard (1936) described seven new species of Leptophlebiidae; *A. superba*, *A. hudsoni*, *A. albiterminata*, *A. ida*, *A. brunnea*, *A. fuscula* and *A. delicatula*, two Baetidae; *Baetis frater* and *Cloeon tasmaniae*, and one Caenidae. Lestage (1930) had previously described a new genus, *Tasmanocoenis* to include *T. tonnoiri* from Geeveston, southern Tasmania, but Tillyard placed his caenid in *Caenis* as *C. scotti*. Tillyard (1936) also completed the association of nymphs and adults in the Siphlonuridae by describing the nymph of *Tasmanophlebia lacustris* Tillyard.

With the exception of a short note by Lestage (1938) renaming *C. scotti* Tillyard as *C. tillyardi* (because the former name was occupied), the next contributions to the systematics of Australian Ephemeroptera were by Harker 1950a, 1954 and 1957. In these three papers, she recorded a further 23 species of Leptophlebiidae; six Baetidae; one Caenidae; one Siphlonuridae; and one Heptageniidae.

Five new genera, *Atalomicria, Jappa, Kirrara* (Leptophlebiidae), *Bungona* (Baetidae) and *Mirawara* (Siphlonuridae) were erected. The genus *Atalomicria* was erected to include *A. uncinata* (Ulmer, 1916) and *A. sexfasciata* (Ulmer, 1916). The first record of the cosmopolitan genus *Centroptilum* was made (Harker, 1957) when *C. collendum* was described from Kuringae Chase, New South Wales. The full list of species described by Harker is given in Table I.1.

Demoulin (1955a) considered that two species described by Ulmer (1916 and 1919) could not be validly placed in an existing genus of the Leptophlebiidae, and therefore erected two new genera, *Thraulophlebia* and *Ulmerophlebia* to include *T. lucida* (Ulmer, 1919) and *U. mjöbergi* (Ulmer, 1916). In the same year Demoulin (1955b) re-described the genotype of *Tasmanocoenis* (Caenidae) and recognised that *Caenis tillyardi* (Lestage) belonged in this genus.

In seven systematic papers published since 1957 only five new species have been added to the known Australian mayfly fauna. In 1955, Riek revised the family Siphlonuridae (as the subfamily Siphlonurinae) adding two new species, *Mirawara megaloprepia* and *M. purpurea;* and in 1963 he recorded the first representative of the family Ephemerellidae, *Austremerella picta* in Australia. Alterations to the generic classification have been made by Thew (1960), Williams (1968) and Riek (1970a). Williams stated that "*Ulmerophlebia, Caenis,* and *Atopopus,* according to Mr. E. F. Riek, C.S.I.R.O., are possibly synonymous with, respectively, the genera *Jappa, Tasmanocoenis* and *Atalonella.* The rejection of *Atopopus* means that the family Heptageniidae, contrary to the earlier indication of Harker, is not present in Australia. *Deleatidium* is now regarded as *Atalophlebioides*". Demoulin (1955b) had previously

TABLE I.1

The Australian Ephemeropteran species described by Harker 1950a, 1954, and 1957. Genera marked (*) were erected by Harker.

Family	Species	Year of Description
Leptophlebiidae	*Atalophlebia longicaudata*	1950
	A. marowana	1950
	A. maculosa	1950
	A. incerta	1950
	A. kokunia	1954
	A. miunga	1954
	A. pierda	1954
	A. tuhla	1954
	A. kala	1954
	A. yugana	1957
	A. darrunga	1957
	Deleatidium annulatum[1]	1950
	D. pusillum[1]	1954
	D. decipiens[1]	1954
	D. manatum[1]	1954
	D. (Atalophlebioides) annulatum[1] *(in Deleatidium)*	1950
	D. (A). bundutum[1]	1954
	D. (A). crassa[1] *(in Leptophlebia)*	1950
	Atalonella parva (in Atalophlebia)	1950
	A. darkara	1957
	**Atalomicria uncinata (Ulmer)*	1954
	**A. sexifasciata (Ulmer)*	1954
	**Jappa kutera*	1954
	**J. tristis*	1954
	**Kirrara procera*	1954
	**K. amenia*	1954
	K. algona	1957

Continued ....

Table I.1 (Cont.)

Family	Species	Year of Description.
Baetidae	*Baetis baddamsae*	1950
	B. confluens	1950
	B. sogeriensis	1954
	Cloeon nandirum	1957
	**Bungona narilla*	1957
	Centroptilum collendum	1957
Caenidae	*Tasmanocoenis jillongi*	1957
Siphlonuridae	**Mirawara aapta*	1954
Heptageniidae	*Atopopus spadix*[2]	1950

[1] Species now placed in the genus *Atalophlebioides*

[2] Species now placed in the genus *Atalonella*

placed the only species described in the genus *Caenis* in *Tasmanocoenis* [*T. tillyardi* (Lestage)] and Thew (1960) accepted this generic change. Although the rejection of *Atopopus* by Williams (1968) was not a formal publication of a synonymy it is accepted by Riek (1970a) who states "The Heptageniidae were incorrectly recorded in the Australian fauna by Harker (1950, 1954)." Riek (1970a) also records the presence of 124 species of Australian mayfly, 52 more than have been described, and although there are probably numerous undescribed species, until descriptions are published they cannot be recognised. In 1978 Soldan described a new genus in the F. Caenidae, and described two new Australian species *Pseudocaenis queenslandica* and *P. rieki*. These descriptions were not available for consideration by Suter (1979) in a revised key to the Australian mayfly nymphs, and consequently *Pseudocaenis* was not mentioned.

Ecological information about Australian mayflies is almost non-existant. Although Tillyard (1933, 1934, 1936); Harker (1954); and Riek (1955, 1970a) record some ecological information in their taxonomic papers, only Harker (1950b) has published a paper on any aspect of the life of Australian Ephemeroptera. Other ecological studies have been limited by the lack of taxonomic information (Leonard and Timms, 1974; Thorpe and Lake, 1973; Lake, Coleman, Mills and Norris, 1977; Knott, Suter and Richardson, 1978).

Taxonomic studies on the Australian mayflies in previous years have tended to treat the ecological aspects superficially, not recognising that ecological information on each species is useful in the final taxonomic product. To attempt a taxonomic revision of the Ephemeroptera of the Australian continent, in the limited period of time available for the present study, was not only logistically impossible (due to the size of the continent, numerous environments involved from alpine to coastal, cool temperate to tropical) but would necessitate the superficial treatment of the ecology of each species, probably to the detriment of the final taxonomic product. For these reasons, only a relatively small geographical region has been treated both taxonomically and ecologically, in an attempt to clarify some of the taxonomic confusion that now exists, and to obtain some ecological understanding of the Ephemeroptera in an Australian environment.

CHAPTER 2.

TAXONOMY OF THE EPHEMEROPTERA OF SOUTH AUSTRALIA.

II.1 Introduction

The first species of mayfly from South Australia was recorded by Eaton in 1871 when *Leptophlebia inconspicua* was described from Adelaide. In subsequent papers, 1883-1888, Eaton placed this species into the new genus *Atalophlebia*. Since that date only two other records of the Ephemeroptera in South Australia have been made. Harker (1954) recorded *Atalophlebia australasica* from Tillyard's 1934 collection near Mt. Gambier; and Timms (1974) recorded a *"Caenis sp."* in Valley Lake, Mt. Gambier, and L. Edward near Millicent. Both Williams (1968) and Riek (1970a) acknowledge the presence of mayflies in South Australia, but neither mention any specific families or genera.

With the exception of the species described by Eaton (1871) the other records of Ephemeroptera are from the wet south-east of South Australia. It appears that because South Australia is the driest State in Australia, the existence of fresh water in regions other than the south-east had been ignored, leaving a large gap in our knowledge of Australian freshwater invertebrates, and zoogeographical relationships of these animals.

Preliminary collections from the Fleurieu Peninsula, the Mount Lofty Ranges and the Flinders Ranges showed that mayflies were abundant in all permanent freshwater streams, waterholes and in many dams and reservoirs. Further collections from the freshwater habitats in South Australia have led to the recognition of 13 species of Ephemeroptera, all,but one,of which have nymph and adult associations confirmed in the laboratory or in the field.

From the onset of this study it was clear that many of the characters used to classify species of Ephemeroptera had not been subjected to rigorous appraisal and analysis to determine the amount of variation that does occur within a particular species. There are certain notable exceptions to this, especially work in the F. Baetidae by Müller-Liebenau (1969, 1973), and Thew (1960) in the F. Caenidae. The revision of the European species of *Baetis* by Müller-Liebenau (1969) included assessment of qualitative characters which are useful in the separation of species, and Thew assessed the characters used to determine the genera of the Caenidae using both qualitative and quantitative characters. Studies of this nature are necessary to enable a rationalization of the Ephemeroptera species' classification, based on characteristics which do not show excessive geographical or environmental modification. The problem is compounded in that characters which distinguish species in one particular genus may be of little use for the determination of species in any other. The only way to determine which characters are useful is to analyse them individually.

In the classification of Australian Ephemeroptera many variable characteristics have been used, and even though variation has been noted, these characters have still been of prime importance in the separation of species (as occurs in the Siphlonuridae, Riek 1963).

Harker (1950a) claimed that many of the characters previously used in classification of Australian mayflies were "unsatisfactory". Although much of her evaluation of characters was at the generic or family level, a few characters were considered useful for specific determination of adults, viz, genitalia (forceps and penes in males, and the ninth sternite in females), shading and coloration of wings (especially in the subimago) with the understanding that physiological variations in the nymphs especially, may alter the degree of coloration. In the nymphs, Harker (1950a) considered there were more numerous characters useful at the specific level; eye colour, the labrum, relative length of labial palp segments, and the "form of the paraglossae". Colour patterns were considered of importance if precautions were taken, and the patterns were not accepted as being rigid. Harker concluded "it appears that very few characters are stable enough to be used as primary taxonomic characters; however, it is not by single characters that species are separated, but rather by combinations which only become recognisable when a long series is examined" (Harker, 1950a). Although the sentiment of this statement is true, use of many characters which are not consistently expressed within a population, or between populations over the geographical distribution of a species, can only lead to dubious classification, especially if the limits of variability cannot be delineated.

Tsui and Peters (1972) compared the thoracic morphology of some selected Leptophlebiidae genera, and examined three species of *Leptophlebia* to determine which thoracic characters were congeneric. They concluded that "the thoracic characters of the imagos remained constant among the three different species of the genus. However, allometric differences were detected in the mesonotum ... (and) it appears that the diagnostic characters found in the thorax are congeneric, although some minor differences especially in size do occur between species of the same genus" (Tsui and Peters, 1972). The comparison of the mesosternum length, basisternum width and furcasternum width using a triangular scatter diagram suggested that these measurements may be useful in the separation of closely related species.

In a discussion of good taxonomic characters Blackwelder (1967) considered seven criteria:

"1) They are not subject to wide variation among the known specimens,
2) they do not show a high intrinsic genetic variability,
3) they are not readily modified by the environment,
4) they are consistently expressed,
5) they are available in the specimens which must be used,
6) they are visible with reasonable procedures, and
7) they can be effectively recorded.

Of these the ones representing the inherent nature of the animals 1) - 4), are the most important, but failure to consider the others can seriously affect subsequent use of the characters."

The above criteria were considered of fundamental importance in the classification of the South Australian species of Ephemeroptera, and for species which were abundant in the collections, sexual and geographical comparisons of taxonomic characters, both qualitative and quantitative, were made.

Full descriptions of the 13 species of mayfly recorded in South Australia are made, and a discussion of character variation within each abundant species is given. In the genera *Atalophlebia* and *Atalonella* inter-specific comparisons of morphometric characters were also made.

II.2 Materials and Methods

Collection of nymphs was by dip net with mesh pore size of 500µm, or by hand collecting nymphs clinging to the undersurface of rocks or bark in streams. Adults were collected by beating the vegetation along river banks with an Entomological Supplies aerial insect net, or by sweeping the net through a swarm. Specimens were preserved in 70% ethyl alcohol with 5% glycerol added.

Nymphs and adults were associated in the laboratory whenever possible, but some field associations had to be made. In each case, last instar nymphs were placed in plastic containers with detritus, rocks, and water from the place of collection. A mosquito-mesh top was placed over the container to allow free air flow. The rocks were not submerged, allowing a dry platform from which emergence could take place. When the subimago emerged, it was transferred to a dry mesh-covered container, and kept at as near 20°C as possible until the subimaginal skin was shed. The reared imago was allowed to dry and its cuticle to harden for two to three hours before it and its subimaginal skin were preserved in the same vial as the nymphal exuvium.

This method failed for species which live in fast flowing water, e.g. *Baetis*. In these cases, associations were obtained using a model stream similar to that used by Bishop (1969) in his study of drift. Water temperature varied between 20-30°C; the light regime used was long day, short night (16 hours : 8 hours) and the discharge of the system was seven litres per minute. Current was variable, exceeding 15cm sec^{-1} in the shallow "riffle" section and approaching 0cm sec^{-1} in the deeper "pool" section.

Specimens for study were dissected under a Wild M5 Stereoscopic microscope, and the appendages (legs and wings of adults; legs, mouthparts and gills in nymphs) were mounted on glass slides using 'Euparal' or Polyvinylalcohol (P.V.A.) mounting media. The sterna, and nymphal abdominal terga, were prepared using the techniques of Tsui and Peters (1972, 1975), and the nymphal tentoria were studied by the methods given by Hudson (1951). All were mounted in 'Euparal'.

The two mounting media mentioned above were used because both allowed for structures to be mounted directly from an ethanol solution (absolute ethanol for 'Euparal') without necessitating the use of clearing agents or intermediate solutions. Wing structure was not in any way affected by these mountants, and consequently the use of dry mounts (as suggested by Edmunds, Jensen and Berner, 1976) was eliminated.

Genitalia, eggs, and nymphal terga were either mounted on slides or prepared for the Scanning Electron Microscope (S.E.M.). Air drying from absolute ethanol was used for nymphal structures, but shrinkage and distortion occurred in some egg and genitalia preparations. Critical point drying eliminated both shrinkage and distortion. The specimens were passed through an ethanol series to absolute ethanol, and after two changes in this solution were placed into a 1:1 solution of ethanol and amyl acetate. After ½ - 1 hour the specimens were transferred into absolute amyl acetate, in which they remained for one hour. In the Critical Point Dryer (OMAR SPC 900/EX) the amyl acetate in the specimens is replaced with liquid CO_2 by five successive washings, and then at 42°C and 1300psig the CO_2 volatilizes leaving dry, fragile specimens. These were mounted onto stubs with Silver Dag, and then coated with Au/Pd and studied under an E.T.E.C. Autoscan with an operating voltage of 5, 10, or 20 KV.

Illustrations of wings and body colour-patterns were made using a Wild M3 or M5 Stereoscope with an attached drawing head. Legs, mouthparts, gills and high magnification ($\geqslant$ 100x) illustrations were made using a Wild compound microscope and camera lucida. All measurements were made using a Wild M5 Stereoscope with a focussing eyepiece graticule. The redescriptions of previously described species incorporate any observed variations but, in the case of new species, the type specimens only were described.

Wing venation terminology is based on Tillyard's (1932) scheme as illustrated in Figures II.1a and II.1b. This scheme has been used extensively by previous authors subsequent to 1932, including Peters and Edmunds (1964, 1970, 1972) and Edmunds, Jensen and Berner (1976). Each segment of the fore, middle and hind legs of the nymph and male imago is compared to the length of the femur, and is expressed as a ratio. The absolute length of the femur is given last in parentheses. Peters and Edmunds (1964, 1970, 1972) expressed the segment ratios in terms of the tibial length (performed only on the fore leg), but this was not used because of the difficulty of determining the tibial length in specimens in which there is a degree of fusion of the tibia and first tarsal segment. In the case of middle and hind legs in some adults of the Leptophlebiidae, the fusion is complete and the tibial length cannot be determined. The femur does not present this problem as it is always a distinct segment, and it is therefore considered a better standard for comparison. In figures of the labium, the method used by Peters and Edmunds (1964, 1970, 1972) is followed, with the ventral surface shown on the right hand side of the illustration, and the dorsal surface on the left. Comparative measurements of the segments of the labial palpi and maxillary palpi are expressed as ratios, compared with the proximal segment length, which is given in parentheses. All measurements are given in millimetres.

The localities from which material was examined are given at the end of each species' description. Full locality and collecting data is presented in Appendix 1 and discussed in Chapter 6.

For the assessment of morphometric character expression the comparison of absolute values of length were not made because length varies widely, depending on physiological and environmental factors (especially temperature and food supply). A ratio of a dimension to a standard dimension (body length, as measured from the front of the clypeus to the posterior margin of the 10th abdominal tergite for adults, and head width, in nymphs, as measured across the lateral compound eye near the posterior margin of the head) was calculated to eliminate variation in size differences. Ratios of segment lengths and widths were also calculated to validate comparisons between two populations or two species. The ratios calculated for this quantitative analysis are listed in Table II.1. For each character the mean, standard deviation and range were determined and intra-specific and inter-specific comparisons were made using Students' "t" test. The thoracic morphological characteristics of *Atalophlebia* and *Atalonella* were compared using a triangular scatter diagram in which the actual values were not plotted, but rather their percentage contribution to the sum of the characters. Qualitative characters, listed in Table II.2 were not of the correct form to be subjected to statistical analysis, and are discussed separately.

TABLE II.1

Morphometric Characters used in the analysis of character expression of South Australian mayfly species.

Male Imago.

Notal Length/Body Length	NL/BL
Mesonotal Length/Body Length	MNL/BL
Pronotal Length/Body Length	PNL/BL
Mesonotal Width/Pronotal Width	MNW/PNW
Notal Length/Mesonotal Width	NL/MNW
Fore Wing Length/Body Length	FWL/BL
Hind Wing Length/Body Length	HWL/BL
Fore Wing Length/Fore Wing Width	FWL/FWW
Hind Wing Length/Hind Wing Width	HWL/HWW
Appendix Dorsalis Length/Body Length	ADL/BL
Cercus Length/Body Length	CL/BL
Appendix Dorsalis Length/Cercus Length	ADL/CL
Fore Femur Length/Body Length	FFL/BL
Fore Tibia Length/Femur Length	FT_iL/FFL
Fore Tarsus 1 Length/Femur Length	FT_1L/FFL
" Tarsus 2 " / " "	FT_2L/FFL
" Tarsus 3 " / " "	FT_3L/FFL
" Tarsus 4 " / " "	FT_4L/FFL
" Tarsus 5 " / " "	FT_5L/FFL
Middle Femur Length/Body Length	MFL/BL
Middle Tibia Length/Femur Length	MT_iL/MFL
Middle Tarsus 1 Length/Femur Length	MT_1L/MFL
" Tarsus 2 " / " "	MT_2L/MFL
" Tarsus 3 " / " "	MT_3L/MFL
" Tarsus 4 " / " "	MT_4L/MFL
" Tarsus 5 " / " "	MT_5L/MFL
Hind Femur Length/Body Length	HFL/BL
Hind Tibia Length/Femur Length	HT_iL/BL
Hind Tarsus 1 Length/Femur Length	HT_1L/HFL
" Tarsus 2 " / " "	HT_2L/HFL
" Tarsus 3 " / " "	HT_3L/HFL

Continued ....

Table II.1 (Cont.)

Male Imago (Cont.)	
Hind Tarsus 4 Length/Femur Length	HT_4L/HFL
" Tarsus 5 " / " "	HT_5L/HFL
Mesobasisternum Length/Width	MBSL/MBSW
Mesofurcasternum Length/Width	MFSL/MFSW
Mesobasisternum Length/Mesofurcasternum Length	MBSL/MFSL
Mature Male and Female Nymphs.	
Notal Length/Head Width	NL/HW
Mesonotal Width/Head Width	MNW/HW
Pronotal Width/Head Width	PNW/HW
Mesonotal Width/Pronotal Width	MNW/PNW
Notal Length/Mesonotal Width	NL/MNW
Appendix Dorsalis Length/Head Width	ADL/HW
Cercus Length/Head Width	CL/HW
Appendix Dorsalis Length/Cercus Length	ADL/CL
Fore Femur Length/Head Width	FFL/HW
Fore Femur Length/Femur Width	FFL/FFW
Fore Tibia Length/Femur Length	FT_iL/FFL
Fore Tarsus Length/Femur Length	FT_aL/FFL
Middle Femur Length/Head Width	MFL/HW
Middle Femur Length/Femur Width	MFL/MFW
Middle Tibia Length/Femur Length	MT_iL/MFL
Middle Tarsus Length/Femur Length	MT_aL/MFL
Hind Femur Length/Head Width	HFL/HW
Hind Femur Length/Femur Width	HFL/HFW
Hind Tibia Length/Femur Length	HT_iL/HFL
Hind Tarsus Length/Femur Length	HT_aL/HFL
Maxillary palpi :	
Basal Segment Length/Width	BL/BW
Middle Segment Length/Width	ML/MW
Apical Segment Length/Width	AL/AW
Middle Segment Length/Basal Segment Length	ML/BL
Apical Segment Length/Basal Segment Length	AL/BL

Continued ...

Table II.1. (Cont.)

Labial palpi :

Basal Segment Length/Width	BL/BW
Middle Segment Length/Width	ML/MW
Apical Segment Length/Width	AL/AW
Middle Segment Length/Basal Segment Length	ML/BL
Apical Segment Length/Basal Segment Length	AL/BL
Paraglossae Length/Width	PL/PW
Labrum Length/Labrum Width	LL/LW

TABLE II.2.

Qualitative characters assessed for variation of expression in mayfly species in South Australia.

Male Imago.

Genitalia : Forceps shape
Penes shape
Wings; cross-venation, colour
Legs; markings, tarsal fusion
Tarsal claw structure
Colour; dorsal and ventral colour patterns

Female Imago.

Ovipositor structure
Egg morphology (in a few species only).

Mature Nymphs.

Sex
Colour pattern : dorsal and ventral
Eye colour
Leg markings
Tarsal claw structure
Abdominal Tergite spination
Postero- lateral abdominal spination
Gill structure
Mouthpart structure;
  Labial palpi, shape and spination
  Hypopharynx shape
  Labrum, shape and dentition
  Maxillary palpi, shape and spination
  Mandibles, incisors and prostheca structure

Two species of *Atalophlebia*, *A. australis* and *A. australasica* and two species of *Atalonella*, *A. fuscula* and *A. inconspicua* were subjected to intra- and inter-specific comparisons. *Baetis* and *Tasmanocoenis* (each monospecific genera in South Australia) were only assessed for intra-specific variation. The other seven species recorded from South Australia were infrequent in collections and suitable material was not available to perform the quantitative comparative analysis.

II.3 Keys to the South Australian Ephemeroptera

The following keys will serve to distinguish the male imagos and mature nymphs of the species of Ephemeroptera recorded in South Australia. Figures are included with each couplet to give illustrated examples of the key characters, although occasionally these are not required (e.g. "appendix dorsalis present" as compared with "appendix dorsalis absent").

The key to the imagos is primarily for male specimens because species identification of the female imagos is often very difficult as external morphological characteristics of the female show generic, rather than specific affinities. Only direct association with nymphs can allow accurate identification of females, using external characters. However, with the limited South Australian mayfly fauna the females have also been included in the key, and can be distinguished by external morphological characters in all genera with the exception of *Atalonella*. The external characteristics are useful to distinguish this genus, but species separation is difficult without direct nymphal association, or a study of the morphology of fertilized eggs. Identification of subimagos is not as successful. Generic segregating characters are present in subimagos, and generic identification can be made using the imago key. For specific identification it is necessary to refer to the subimago characteristics listed in the description of each species.

II.3.1 Key to South Australian Adult Ephemeroptera

1a Hind wings comparatively large, about half as long as the fore wing (Figs. II.29a, b). Male penes long and tubular (Figs. II.31a, b).

Siphlonuridae

Only one representative in South Australia : *Tasmanophlebia lacus-coerulei*

1b Hind wings small or entirely absent 2

2a(1) Fore wings with many cross veins; hind wings small, also with many cross veins (Figs. II.1a, b; 3a, b; 5a, b; 8a, b; 10a, b; 12a, b, c; 18a, b).

Leptophlebiidae 3

2b Fore wings with few cross veins, clear open appearance, hind wings present or absent, if present reduced, with cross veins few or absent (Figs. II.22a, b; 24a, b; 26a; 32a). 9

3a(2) Tarsal claws of each pair similar, elongate, slender, hooked distally (Figs. II.1g; 3g; 5h; 8g; 10g; 12f; fore wings<3 x longer than wide (Figs. II.1a; 3a; 5a; 8a; 10a; 12a). 4

3b Tarsal claws of each pair dissimilar, one elongate, slender, hooked distally, one blunt with a distal tooth, club shaped (Fig. II.18g); fore wings > 3 x longer than wide. Male genitalia (Figs.II.18c; 20a, b).

Jappa

Only one sp. in South Australia *J. pipinna* sp. nov.

4a(3) Large species, body length > 8mm; fore wing 9 - 13mm; Sc of hind wing reaches wing margin at 9/10 wing length (Figs. II.1b; 3b; 5b).

Atalophlebia 5

4b Small species, body length < 7mm, fore wing 5 - 7.5mm; Sc of hind wing reaches wing margin at 3/4 of wing length (Figs. II.8b; 10b; 12b).

Atalonella 7

5a(4) Males and females with appendix dorsalis (central caudal filament); body colour yellow/brown (orange). 6

5b Males without appendix dorsalis (present in females); body colour black. Male genitalia (Figs. II.3c, d; 7c, d).

Atalophlebia australasica

6a(5) Fore wings with darker pterostigmatic region, cross veins of costal and subcostal spaces shaded with black, hind wings and rest of fore wings hyaline (Fig. II.1a, b); body yellow with black thorax. Apices of penes widely separate and divergent (Figs. II.1c, d; 7a, b).

A. australis

6b Fore wings tinged entirely with yellow, pterostigmatic region darker than rest of wing; hind wing grey-brown, darker than fore wing (Fig. II.5a, b). Apices of penes convergent (Figs. II.5c, d; 7e, f).

A. auratus sp. nov.

7a(4) Two halves of penes distinctly separated forming a U shape (Figs. II.10c, d; 15c, d); with a small triangular spine on inner margin (visible using transmitted light, Fig. II.10c).

Atalonella fuscula

7b Two halves of penes held close together, without spine. 8

8a(7) Penes with two ventral lobes near apex (Figs. II.8a; 15a, b).
A. inconspicua comb.nov.

8b Penes without ventral lobes (Figs. II.12d, e; 15e, f). *A. pilosa* sp. nov.

9a(2) Males with turbinate eyes (females without dorsal compound eyes); marginal intercalaries short, developed between the ends of the main veins (Figs. II.22a; 24a; 26a, g); hind wings present or absent. Baetidae 10

9b Males and females with small lateral eyes, dorsal compound eyes absent; no marginal intercalaries present (Fig. II.32a); hind wings absent. Penes fused with apical indentation, forceps strongly bowed (Figs. II.31c; 32d).
Caenidae

Only 1 species in South Australia *Tasmanocoenis tillyardi*.

10a(9) Hind wings present 11

10b Hind wings absent *Cloeon* 12

11a(10) Marginal intercalaries of fore wing paired (Fig. II.22a). Male genitalia (Fig. II.20c; 22d)
Baetis

Only 1 species in South Australia; *B. soror*

11b Marginal intercalaries of fore wing single (Fig. II.24a). Male genitalia (Figs. II.20d; 24d).

Centroptilum

Only 1 species in South Australia *C. elongatum* sp.nov.

12a(10) Males with turbinate eyes, yellow; terminal segment of forceps triangular (Figs. II.20f; 26i); females with costal and subcostal spaces of wings shaded red/brown; body length > 8mm.

Cloeon paradieniensis sp.nov.

12b Males with turbinate eyes, sepia; terminal segment of forceps small and globular (Figs. II.20e; 26d); females with costal and subcostal spaces of wings opaque, milky; body length < 5mm.

C. fluviatile

II.3.2 Key to the Nymphs of South Australian Ephemeroptera

1a Head prognathous; tail filaments with whorls of setae at apex of each segment, body dorso-ventrally flattened. Families Leptophlebiidae; Caenidae 2

1b Head hypognathous; tail filaments fringed laterally with long fine setae, body usually cylindrical. Families Baetidae; Siphlonuridae 9

2a(1) Seven pairs of gills inserted laterally on abdomen, each gill consisting of a pair of lamellae. 3

2b Six pairs of gills, 1st very small mono-filament, 2nd enlarged to form an elytriform gill cover, remaining pairs bearing long tracheal filaments (Fig. II. 33b, c, d). Caenidae : *Tasmanocoenis* Only one species in South Australia *T. tillyardi*.

3a(2) Gill base broad with one apical filament, lined with fine setae (Fig. II.19c), legs and body covered with long fine setae (Fig. II.21). *Jappa*

Only one species in South Australia, *J. pipinna* sp.nov.

3b Gills lanceolate or linear, with one apical filament (Figs. II.9c; 11c; 13c), apex with multiple tracheal filaments (Figs. II.2c; 4c), body not covered with long fine setae. 4

4a(3) Gills lanceolate or linear, not branched at apex into tracheal filaments (Figs. II.9c; 11c; 13c). *Atalonella* 5

4b Gills broad at apex, with each lamella subdivided into tracheal filaments (Figs. II.2c; 4c). *Atalophlebia* 7

5a(4) Gills lanceolate (Figs. II.9c; 13c); proximal segment of labial palpi narrow, > 2.2 × longer than wide (Figs. II.9g; 13g). 6

5b Gills linear (Fig. II.11c); proximal segment of labial palpi broad, 1.67 × longer than wide (Fig. II.11g); prostheca of left mandible robust with serrated apex (Fig. II.11i); dorsal abdominal markings irregular black and white (Fig. II.14e). *A. fuscula*

6a(5) Dorsal abdominal marking with a broad median light stripe (Fig. II.14d); labrum rectangular, 2 × wider than long (Fig. II.9d); femora with few fine setae (Fig. II.9a). *A. inconspicua* comb.nov.

6b Dorsal abdominal marking with narrow light regions on segments 4 - 10 (Fig. II.14f); labrum almost square 1.5 × wider than long (Fig. II.13d); femora lined with numerous long fine setae (Fig. II.13a).

A. pilosa sp.nov.

7a(4) Apex of gills with each lamella trifurcate (Fig. II.2c). *Atalophlebia australis*

7b Apex of gills multifurcate with more than three tracheal filaments (Fig. II.4c). 8

8a(7) Ninth abdominal segment with only one backward pointing spine (Fig. II.14c); no dark markings on legs (Fig. II.6a).

A. auratus sp.nov.

8b Ninth abdominal segment with two backward pointing spines (Fig. II.14b); femur and tibia with broad bands of black (Fig. II.4a).

A. australasica

9a(1) Four pairs of gills present, first pair elytriform, covering last three pairs. Postero-lateral margins of abdominal segments produced into backward pointing spines (Fig. II.29g).

Siphlonuridae: *Tasmanophlebia*

Only one species in South Australia, *T. lacus-coerulei*.

9b Seven pairs of gills present, postero-lateral margins of abdominal segments not produced into backward pointing spines. Baetidae 9

10a(9) Gill lamellae double on abdominal segments 1 - 6, single on 7th (Figs. II.27e; 28e); hind wing sheaths absent. *Cloeon* 11

10b Gill lamellae single on abdominal segments 1 - 7 (Figs. II.22i; 25d); hind wing sheaths present. 12

11a(10) Paraprocts with 27 - 30 spines (Fig. II.28d); maxillary palpi with terminal spines on distal segment (Fig. II.28f); without definite abdominal colour pattern.

Cloeon paradieniensis sp.nov.

11b Paraprocts with 17 - 22 spines (Fig. II.27d); maxillary palpi without terminal spines on distal segment (Fig. II.27i); abdominal pattern as in Fig. II.27c. *C. fluviatile*

12a(10) Labrum with deep median V-shaped concavity with a tooth on each side of the lateral margins of the concavity, near the apex (Fig. II.25e); tarsal claws very long and slender (Fig. II.25a). *Centroptilum elongatum* sp.nov.

12b Labrum rounded, with shallow U-shaped concavity (Fig. II.22j); tarsal claw short (Fig. II.22f). *Baetis soror*

II.4 Systematics : Family LEPTOPHLEBIIDAE

Peters and Edmunds (1964, 1970) recorded the systematic history of the family and listed characterizations based on Ethiopian and Eastern Hemisphere material. The following characterization is a condensed version given by Peters and Edmunds (1970) to include characters expressed by all representatives in the family; special references to Australian material are made in square brackets.

Male Imago Characteristics. Eyes of male divided into large upper portions with large facets and smaller lower portion with smaller facets; eyes of female not divided, composed entirely of small facets. Median and lateral ocelli well developed. Fore wing veins C and Sc well developed; vein MA_2 attached at base to vein MA_1, one intercalary present between veins MA_1 and MA_2; one intercalary between MP, and MP_2, no intercalaries between MP_2 and CuA; vein CuP strongly bowed; 2 - 3 anal veins present all bowed. Hind wings present or absent [Present in Australian species], costal projection well developed or absent [well developed]. Tarsus of fore leg of male five segmented, segment one short, tarsus of mid and hind legs of male four segmented (T_1 fused to tibia), tarsus of legs of female four segmented. Male genitalia; forceps two or three segmented [three segmented] segments two and three shorter than one. Caudal filaments well developed, usually three present, but the appendix dorsalis may be reduced or absent.

Mature Nymph Characteristics. Nymph dorso-ventrally depressed, head hypognathous to prognathous [usually hypognathous]. Hypopharynx well developed usually with well developed lateral processes. Maxillary palpi three segmented, a rake-like spine usually present on inner anterior margin of maxillae; anterior margin of galeo-lacinia lined with a dense "brush" of setae. Labial palpi three segmented; glossae and paraglossae well developed. Gills on abdominal segments 1 - 7, 1 - 6 or 2 - 7 [1 - 7]. Three well developed caudal filaments present.

II.4.1 Genus *Atalophlebia* Eaton 1881

Burmeister, 1839 : 800	(In *Baetis*)
Pictet, 1843 : 189-191	(In *Baetis*) *B. australasica*
Walker, 1853 : 538	(In *Ephemera*) *E. australis*
1853 : 559-561	(In *Baetis*) *B. australasica*, *B. costalis*

Eaton, 1871 : 78-81 (In *Leptophlebia*)
1881 : 193-194
1884 : 83-91
Ulmer, 1908 : 40-46
1916 : 2-17
1919 : 16-23
Needham and Murphy, 1924 : 34-36
Tillyard, 1926 : 63-64
1934 : 1-16
1936 : 30-49
Harker, 1950a : 8-17
1954 : 243-252
1957 : 63-68
Kimmins, 1960 : 294
Penniket, 1961 : 1-11
Riek, 1970a : 239
Tsui and Peters, 1975 : 542-544

Male Imago Characteristics. Relatively large mayflies, body length > 8mm, fore wing length 9 - 13mm. Fore wings with abundant cross veins, those in proximal regions of costal and subcostal spaces well defined, tornus midway between CuA and CuP; CuP curves upward proximally towards CuA (Figs. II.1a; 3a; 5a). Hind wing Sc reaches wing margin at 9/10 of wing length, no intercalaries present between forks of MA (Figs. II.1b; 3b; 5b). Tarsal claws paired, similar, elongated, slender, hooked distally (Figs. II.1g; 3g; 5h).

Mature Nymph Characteristics. Posterior margin of pronotum not fused to mesonotum. Tentorial body width slightly greater than length. Gills each consist of a pair of lamellae with multiple tracheal filaments (Figs. II.2c; 4c). Mandibles stout with convex outer margin lined with setae, incisors large, two separate groups, prosthecae with brush of long setae projecting from basal half (Figs. II.2h - k; 4h - k; 6h - k). Labium with median, anterior indentation. Tarsal claws lined with peg-like denticles (Figs. II.2b; 4b; 6b).

History and Discussion.

This genus contains the largest number of described species in the F. Leptophlebiidae in Australia. The genus was erected in 1881 by Eaton with *A. australis* (Walker) designated as the genotype. Subsequently in 1884 Eaton placed six Australian species in the new genus. Ulmer described a further five species, two in 1916, and three in 1919. In 1924 Needham and Murphy erected a new genus *Atalonella* to include two species, one Chilean species and one Australian species, *Atalonella fusca* (Ulmer, 1919). Tillyard (1936) described a further six species of *Atalophlebia* from Tasmania, noting that there were two distinct groups in the material. The three smaller species were later placed in the genus *Atalonella* by Harker (1954), as were the two other species described by Ulmer (1919). In the same paper Harker transferred specimens described by Ulmer (1916) to a new genus *Atalomicria*. In 1950, she described five species of *Atalophlebia* from New South Wales (one of which she transferred to *Atalonella* in 1954) and subsequently (1954) described a further five species. Two more species were described by Harker in 1957, bringing the complement of Australian species in the genus *Atalophlebia* to eighteen. The genus was characterized in terms of thoracic morphology, tentorium and abdominal terga by Tsui and Peters (1975).

In the present study one of the described species *A. inconspicua*, is transferred to *Atalonella*, and a new species of *Atalophlebia* from South Australia is described.

II.4.1.1 *Atalophlebia australis* (Walker) 1853

Ephemera australis Walker, 1853 : 538
Leptophlebia australis Eaton, 1871 : 78
Atalophlebia [genotype] *australis* Eaton, 1881 : 193-194
1884 : 86
Tillyard, 1934 : 1-16
1936 : 33
Harker, 1950a : 8, 28
1954 : 264
Kimmins, 1960 : 294
Scholes, 1961 : 23-26
Penniket, 1961 : 2, 7

This species was fully described by Tillyard (1934) in a study of the genotype of *Atalophlebia*. A transparency of the genitalia of the lectotype designated by Tillyard (held in the British Museum of Natural History) has been examined, but the actual specimen has not been seen. The following description is based on South Australian representatives.

Male Imago.

	$\bar{x}$	SD	n	Range
Body Length	10.69	1.38	14	8.80 - 12.50
Notal Length	3.65	0.39	15	3.20 - 4.20
Mesonotal Width	1.93	0.27	15	1.52 - 2.28
Pronotal Width	1.50	0.16	5	1.24 - 1.64
Fore Wing Length	11.84	0.87	9	9.92 - 12.48
Hind Wing Length	3.45	0.37	10	2.52 - 3.72
Cerci Length	28.00	2.86	5	25.00 - 32.60
Appendix Dorsalis Length	23.35	1.40	4	22.00 - 25.00

Head : dark brown. Dorsal compound eyes black/brown, lateral eyes slate grey. Ocelli closely grouped, dark brown posteriorly, white anteriorly. Epicranial sutures slightly ridged between lateral ocelli.

Thorax : dark brown, black on mesonotum, yellow-white in unsclerotized lateral regions, two light patches near posterior margin of scutoscutellum. Fore legs long, dark brown, femur with black band midway along length, tibia and tarsal segments not banded, tarsal segments lighter brown, first tarsal segment (T_1) partially fused to tibia. Middle and hind legs shorter, yellow/brown, femur with mid-brown band, tarsal segments with short apical spine, T_1 fused to tibia; fore leg femur length 1.18 x middle leg femur length, and 1.07 x hind leg femur length. Tarsal claws similar, hooked apically (Fig. II.1g). Ratios of leg segments (Note: in middle and hind legs, second ratio is tibia + T_1 length: femur length); fore leg 1.00 : 1.34 : 0.11 : 0.51 : 0.44 : 0.34 : 0.21 (2.34mm) middle leg 1.00 : 1.00 : - : 0.11 : 0.10 : 0.09 : 0.19 (1.99mm)

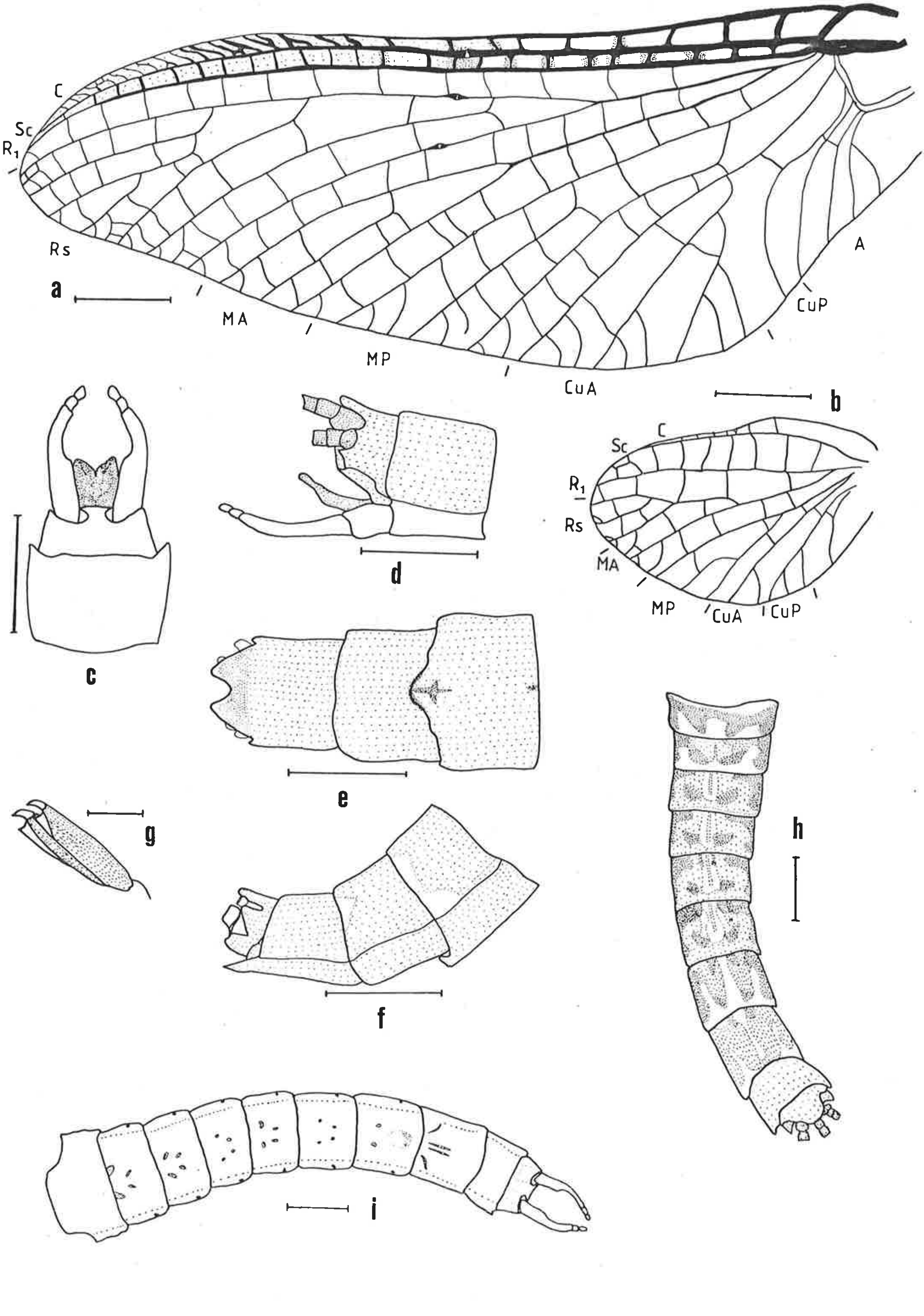
hind leg 1.00 : 1.04 : - : 0.10 : 0.09 : 0.08 : 0.17 (2.18mm).

Sternum yellow brown. Prosternum triangular, posterior width equal to anterior width of mesosternum, longitudinal carinae slightly separated mesally, basal region heavily sclerotized laterally, lighter in middle. Mesosternum; basisternum length 1.13 x width, 0.62 x furcasternum length, furcasternum length 0.77 x width, lateral margin of median longitudinal invagination parallel, diverging slightly both anteriorly and posteriorly, posterior margin concave with a short triangular indentation, lateral margins of furcasternum strongly sclerotized and dark brown.

<u>Wings :</u> hyaline, fore wing (Fig. II.1a) 2.75 x longer than wide, pterostigmal region lightly shaded with yellow/brown, cross veins brown, slightly shaded laterally, in pterostigmal, costal and subcostal spaces, pterostigmal veins may be forked and anastomosed, costal cross veins simple, cross vein system dense except in cubital and anal regions. Variation of the cross vein system is tabulated in Table II.3. Three bullae present, one in Sc, shaded posteriorly by a brown patch, and one in R_2 and $R_{4 \& 5}$. Hind wing (Fig. II.1b) 1.62 x longer than wide, veins light brown, costal margin curved to half its length, proximal region with 1 - 2 faint cross veins, distal region with 7 - 9 cross veins, R_1 straight, Rs joins MA in centre of wing, MA straight, MP forked in proximal half of wing, cubital and anal regions with very few cross veins.

Fig. II.1. *Atalophlebia australis*. a - d, male imago: a, fore wing; b, hind wing; c, genitalia, ventral view; d, genitalia, lateral view. e - f, female imago: e, abdominal segments 7 - 10, ventral view; f, abdominal segments 7 - 10, lateral view. g - i, male imago: g, fore claws; h, dorsal abdominal colour pattern; i, ventral abdominal colour pattern.

Scale lines :	a - f, h - i	1mm.
	g	0.1mm.



C
Sc
R1
Rs
MA
MP
CuA
CuP
A
a
b
Sc
C
R1
Rs
MA
MP
CuA
CuP
c
d
e
f
g
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i

TABLE II.3

Variability of expression of the cross vein system in wings of *Atalophlebia australis* (Walker) from South Australia (n = 8).

Vein Sector	Left wing Range	Right wing Range
Fore wing :		
C/Sc basal half	7 - 8	6 - 8
C/Sc apical half	20 - 25	21 - 26
Sc/R_1 basal half	7 - 10	6 - 12
Sc/R_1 apical half	15 - 17	16 - 18
R_1/R_s	10 - 15	11 - 15
R_s System	33 - 43	28 - 42
R_{4+5}/MA	11 - 13	11 - 13
MA System	7 - 13	9 - 13
MA/MP	10 - 13	11 - 12
Hind wing :		
C/Sc basal half	1 - 2	1 - 2
C/Sc apical half	4 - 8	4 - 8
Sc/R_1	8 - 11	8 - 11
R_1/R_2	3 - 6	3 - 5

Abdomen : yellow with dark brown markings dorsally (Fig. II.1h). Segments 8, 9, 10 yellow brown; ventrally yellow with light brown markings (Fig. II.1i). Cerci long, brown, appendix dorsalis shorter, but well developed.

Genitalia : (Figs. II.1c, d); forceps yellow/brown, first segment longest, broad proximally, narrows half way along length, second segment short and globular, distal segment slightly longer than second, globular. Penes broad, lateral margins parallel extending just beyond narrowing of forceps, apical lobes divergent, giving a V-shaped median indentation, ventral sperm duct openings obvious (Figs. II.7a, b).

Mature Male Nymph. Fig. II.14a

	$\bar{x}$	SD	n	Range
Head width	2.22	0.06	7	2.12 - 2.28
Notal Length	3.21	0.07	7	3.12 - 3.34
Pronotal Width	2.14	0.18	7	1.80 - 2.30
Mesonotal Width	2.42	0.09	7	2.24 - 2.48
Cerci Length	16.03	0.86	4	15.05 - 17.10
Appendix Dorsalis Length	13.54	0.96	5	12.31 - 14.54

Head : prognathous, brown, epicranial sutures light brown. Dorsal compound eyes sepia, lateral eyes black. Ocelli black posteriorly, white anteriorly. Basal segment of antennae brown, flagellum buff, longer than head is wide.

Thorax : brown with light brown markings. Pronotum width 0.96 x head width, lateral margins produced into narrow, curved semi-transparent flanges, antero-lateral margins with short stout setae, lateral margins without setae.

Mesonotum 1.09 x wider than head, brown with light brown markings, wing sheaths black just prior to emergence, (brown otherwise) extending to mid fourth abdominal segment. Legs yellow/brown with brown bands on each segment, femur with two bands (one mid, one distal), tibia with two bands (one faint basally, one mid to 4/5 of tibia length), tarsus with broad band from base to 2/3 of length (Fig. II.2a). Tarsal claws short and curved with 20 - 25 peg like ventral denticles (Fig. II.2b). Femora of fore and middle leg equal in length, hind leg longest, 1.12 x fore femur length.
Ratios of leg segments;

fore leg	1.00 : 1.05 : 0.53 (1.88mm)
middle leg	1.00 : 0.97 : 0.43 (1.90mm)
hind leg	1.00 : 1.02 : 0.43 (2.10mm).

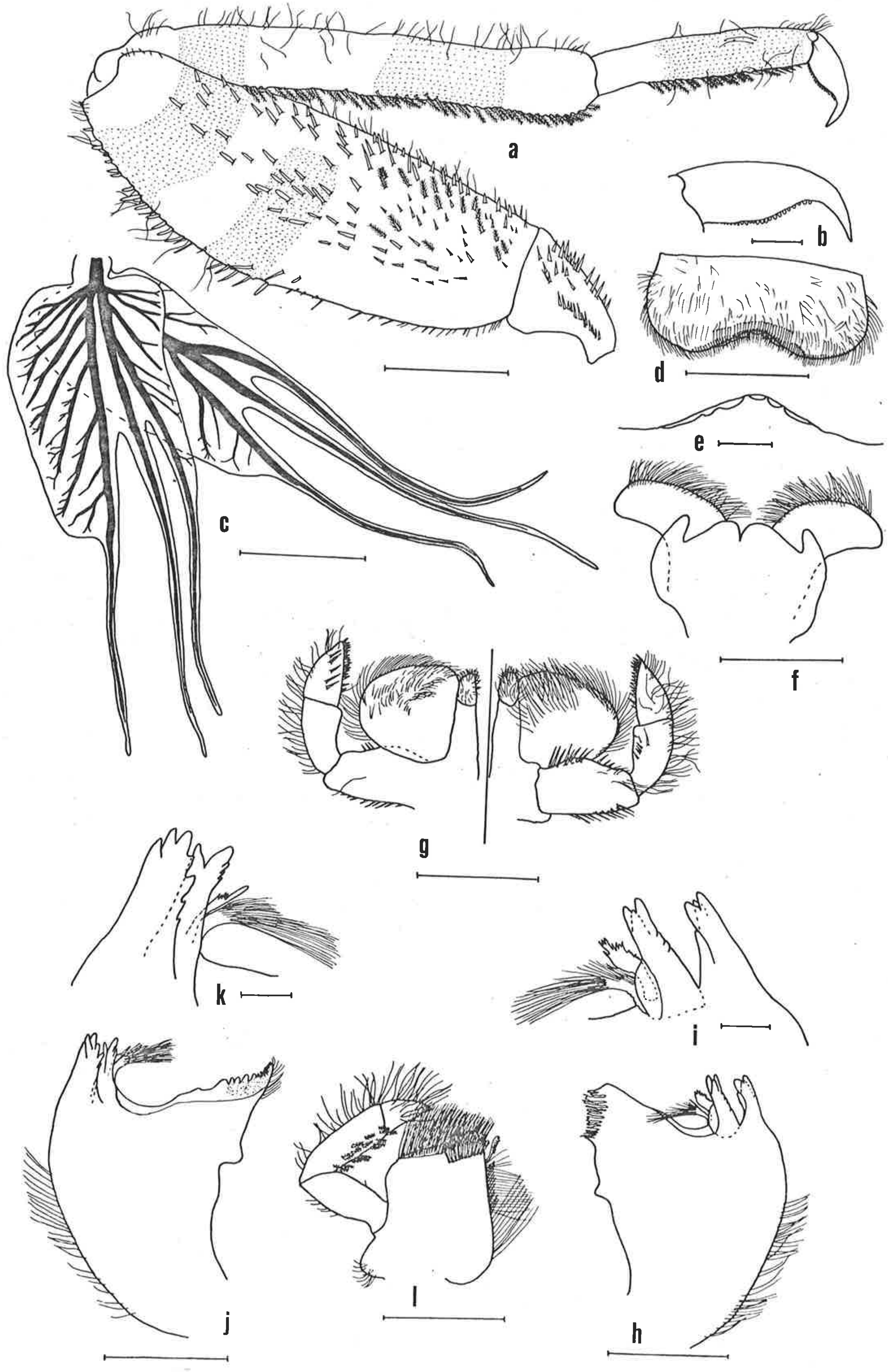
Femur length to width ratios; fore leg 3.16, middle leg 3.26, hind leg 3.54. Sternum; prosternum triangular, width equal to anterior width of mesobasisternum, sterna-costal suture absent, anterior sternal sutures convergent, fused apically. Mesosternum; basisternum length equal to or slightly longer than furcasternum, sterna-costal suture present. Metasternum; basisternum 4 - 5 x wider than long, width slightly less than mesofurcasternum.

Abdomen : brown, patterned (Fig. II.14a) segments 9, 10 narrowest, segments 2-9 with postero-lateral margins produced into sharp backward pointing projections. Posterior margins of tergites with large singular spines, with smaller spines basally. Cerci well developed, longer than appendix dorsalis. Gills, seven pairs, each consisting of a pair of lamellae with three tracheal filaments per lamella (Fig. II.2c).

Mouthparts : labrum (Fig. II.2d) 2.78 x wider than long, lateral borders rounded with long setae, mid anterior margin indented, rugose, with 4-5 rounded tubercles (Fig. II.2e); two transverse rows of long setae just posterior to indentation. Left mandible (Fig. II.2h); incisors large and separate, outer incisors with four teeth, inner with three, prostheca inserted at base, robust, with enlarged apical region, apical margin with six spines, inner margin with four large and numerous small spines (Fig. II.2i); molar region with 10-12 transverse ridges. Right mandible (Fig. II.2j); outer incisors with three apical teeth, with five serrations on inner margin of third tooth, inner incisors with two teeth, inner lateral margin with up to five spines, prostheca long and slender with four spines along length (Fig. II.2k). Hypopharynx (Fig. II.2f) simple, median lobe divided with lateral processes, fringed with short setae, lateral lobes (paragnaths) large, convex, anterior border fringed with long setae. Maxillae (Fig. II.2*l*); galeo-lacinia rectangular, apical surface with a dense "brush" of curved fine setae, row of 10 - 12 rake setae on ventral surface, rake setae also interspersed within apical brush, mesal corner with a large rake spine, inner margin lined with long fine setae; palpi three segmented, proximal segment 2.24 x longer than wide, segment ratios; 1.00 : 1.22 : 0.66 (0.32mm), middle segment outer margin lined with long fine setae, inner margin with stout pinnate setae, distal segment covered with long fine setae.

Fig. II.2. *Atalophlebia australis*, mature nymph: a, fore leg; b, fore claw; c, third abdominal gill; d, labrum, dorsal view; e, antero-median emargination of labrum, enlarged; f, hypopharynx; g, labium, dorsal (left) and ventral views; h, left mandible, ventral view; i, left incisors and prostheca, enlarged; j, right mandible, ventral view; k, right incisors and prostheca, enlarged; l, right maxilla, ventral view.

Scale lines :	a,c,d,f,g,h,j,l	0.5mm.
	b,e,i,k	0.1mm.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Labium (Fig. II.2g); palpi three segmented, proximal segment 1.81 x longer than wide, segment ratios; 1.00 : 0.80 : 0.60 (0.37mm), middle segment lined with long fine setae; glossae small and oval, lined with short fine setae, paraglossae broad, outer margin convex, dorsal surface densely setose.

Female Imago : colour similar to male, ninth abdominal sternite with deeply incised posterior margin (Fig. II.1e), seventh sternite produced posteriorly, slightly hooked when viewed laterally (Fig. II. 1f). Fore legs shorter than male, with only four distinct tarsal segments, T_1 fused to tibia. Sternum broader than male, mesobasisternum length 0.85 x width, mesofurcasternum 0.65 x width.

Subimago : black to dark brown, wings shaded grey with hyaline lambda (λ) marking complete (see Tillyard, 1934).

Female Nymph : similar to but larger than male, lacking dorsal compound eyes.

Sexual Variation of Nymphs.

Table II.4 shows the sexual variation expressed by *A. australis* nymphs from Mt. Hope Drain, south-east South Australia. Of the 27 characters compared, ten differed at the 5% level of significance (all of which were either leg or thoracic characteristics). The non-significant characters are tabulated in Appendix 2.

TABLE II.4. Morphological characters of *A. australis* nymphs in which males differ from females.

Data refers to last instar nymphs from Mt. Hope Drain South East South Australia. Abbreviations of characters are given in Table II.1. $\bar{x}$ = mean; S.D., = Standard Deviation; Range = Range of observations; d.f., = degrees of freedom; * $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

	Males			Females					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
MNW/HW	1.09	0.03	1.06-1.13	1.18	0.06	1.13-1.29	12	3.77	**
NL/MNW	1.33	0.08	1.26-1.49	1.20	0.04	1.14-1.25	12	4.25	**
FFL/HW	0.85	0.02	0.82-0.89	0.89	0.03	0.84-0.96	25	3.65	**
MFL/HW	0.86	0.02	0.83-0.92	0.91	0.05	0.86-1.00	25	3.56	**
HFL/HW	0.96	0.03	0.92-1.01	1.01	0.04	0.97-1.05	21	4.29	***
FT_iL/FFL	1.05	0.02	1.01-1.08	1.08	0.02	1.04-1.11	24	3.03	**
FT_aL/FFL	0.53	0.02	0.50-0.56	0.47	0.01	0.44-0.49	24	8.84	***
MFL/MFW	3.26	0.11	3.12-3.52	3.39	0.13	3.17-3.58	25	2.74	*
HFL/HFW	3.54	0.13	3.32-3.69	3.66	0.10	3.45-3.81	22	2.66	*
HFL/FFL	1.12	0.02	1.10-1.14	1.15	0.02	1.12-1.18	21	4.10	***

Diagnostic Characteristics.

1. Genitalia of male imago (Fig. II.1c, d and Fig. II.7a, b)
2. Distinctive yellow/brown (orange) colour described by Walker (1853) and Tillyard (1934) as "red", and "rufo-piceous above; venter dull light burnt-umber, approaching rusty brown" by Eaton (1884).
3. Distinctive λ pattern of subimago.
4. Nymphal gills with trifurcate tracheal filaments (Fig. II.2c).
5. Form and shape of mandibles, incisors and prosthecae (Fig. II.2h, i, j, k).

History and Discussion

In 1853 Walker briefly described *Ephemera australis* from Dr. Hooker's 1842 collection from Tasmania. This species was later placed in the genus *Leptophlebia* (Eaton, 1871) and subsequently (Eaton, 1881) was designated the genotype for the new genus *Atalophlebia*. Walker referred to the "red" abdomen, and Eaton referred to rufo-piceous coloration, "an unusual character for this genus" (Tillyard, 1934). Tillyard's extensive descriptions of the male imago, subimago and nymph of *A. australis* enable relatively easy recognition of all stages of this species, but the coloration in the living material differs from that of dry pinned specimens. Newly caught and alcohol preserved adults have a distinctive orange colour, not red, as is the case in dry specimens.

Variation of Character Expression

Tillyard (1934) recorded great variability in the appendix dorsalis in *A. australis*. Eaton (1884) recorded two measurements, suggesting a long appendix dorsalis, but Tillyard recorded variability from of equal length with the cerci, to entirely absent. All material examined from South Australia, Victoria and Tasmania possess a long appendix dorsalis.

Geographical variation was analysed for the male imago of *A. australis* by comparing two geographically isolated populations, one from Reedy Creek Drain, south-east South Australia, and one from Rocky River, Southern Flinders Ranges, South Australia. Of the 25 morphometric characters compared nine were significantly different at the 5% level. Body length and femur lengths were also compared, and although the fore and hind femora lengths differed significantly, the middle femur length and body length did not. Significant characters are given in Table II.5 and a high degree of overlap of most characters is apparent. The non-significant characters are tabulated in Appendix 3.

The major vein system of the fore and hind wings did not vary, but the cross vein system of both wings was analysed for variation in cross vein number. The results could not be statistically analysed, but they are tabulated (Table II.3) to illustrate the variation. Left and right wings were also found to be different.

TABLE II.5 Geographical variation in some morphometric characters of *A. australis* male imagos from Reedy Creek Drain, South East South Australia, and Rocky River, Southern Flinders Ranges, South Australia.

Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$

	Rocky River Population			Reedy Creek Drain Population					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
FWL/BL	1.02	0.03	0.98-1.05	0.95	0.03	0.89-1.02	16	3.98	***
HWL/BL	0.30	0.01	0.28-0.31	0.28	0.01	0.26-0.30	15	3.25	***
FFL(mm)[1]	2.61	0.12	2.43-2.72	2.18	0.10	2.02-2.30	14	7.60	***
FT$_1$L/FFL	0.17	0.02	0.14-0.19	0.07	0.01	0.06-0.08	14	15.17	***
FT$_3$L/FFL	0.41	0.02	0.38-0.43	0.46	0.03	0.42-0.51	14	3.55	**
FT$_4$L/FFL	0.33	0.03	0.29-0.36	0.35	0.01	0.33-0.38	14	2.23	*
FT$_5$L/FFL	0.20	0.01	0.19-0.20	0.22	0.01	0.21-0.23	14	3.46	**
MT$_i$+T$_1$L/MFL	0.98	0.03	0.93-1.10	1.03	0.02	1.00-1.07	13	3.81	**
MT$_3$L/MFL	0.10	0.01	0.09-0.11	0.09	0.01	0.08-0.10	13	2.58	*
MT$_4$L/MFL	0.09	0.01	0.09-0.11	0.08	0.01	0.08-0.10	13	2.41	*
HFL.(mm)[1]	2.42	0.22	2.02-2.62	2.02	0.20	1.80-2.32	13	3.74	**

[1],Non proportional characteristics

Material Examined. South Australia : South East; Brown Lake, Bakers Range Drain, Eastern Division Diversion Drain, Mt. Hope Drain, Reedy Creek Drain, Sutherlands Drain and Valley Lake. Mt. Lofty Ranges; Marne R., Para R., Torrens R., Southern Flinders Ranges; Back Creek, Julia Creek, Rocky River. Victoria : Clunes, Tarango Dam, Neerin, Lake west of Harrow, L. Hattah, L. Wendouree, Ballarat, Konongwootong Reservoir, Rocklands Reservoir, Surrey R. Tasmania : Break O'Day R., Lagoon of Islands, L. Leake.

II.4.1.2 *Atalophlebia australasica* (Pictet) 1843

Baetis australasica	Pictet, 1843 : 189-190
	Walker, 1853 : 559
Leptophlebia australasica	Eaton, 1871 : 78-79
Atalophlebia australasica	Eaton, 1884 : 86-87
	Ulmer, 1916 : 2-3
	Harker, 1950a : 28
	1954 : 248-249

Male Imago

	$\bar{x}$	SD	n	Range
Body Length	10.10	0.86	26	8.60 - 11.46
Notal Length	3.13	0.24	8	2.84 - 3.60
Pronotal Width	1.09	0.10	8	2.84 - 3.60
Mesonotal Width	1.54	0.13	8	1.44 - 1.80
Fore Wing Length	10.33	1.10	18	9.23 - 12.83
Hind Wing Length	3.02	0.41	18	2.40 - 3.96
Cerci Length	28.20	2.72	8	24.00 - 31.00

Head : dark brown to black. Antennae black, 1mm long. Dorsal compound eyes dark red/grey, lateral eyes dark grey.

Thorax : Shiny black. Pronotum narrower than head. Mesonotum humped, without markings. Legs; fore legs long, black with two darker bands on femur, one mid, one distally, T_1 partially fused to tibia. Middle and hind legs shorter than fore leg, light yellow/brown with two black bands on femora, one mid, one distal, tibiae with one proximal band, T_1 fused to tibia with join apparent, tarsal segments 1-4 with short apical spine. Fore leg femur length 1.20 x middle leg femur length, and 1.06 x hind leg femur length. Ratios of leg segments;

fore leg 1.00 : 1.39 : 0.13 : 0.53 : 0.48 : 0.39 : 0.20 (2.26mm)

middle leg 1.00 : 0.93 : 0.08 : 0.11 : 0.09 : 0.08 : 0.16 (1.88mm)

hind leg 1.00 : 1.01 : 0.08 : 0.09 : 0.08 : 0.07 : 0.15 (2.13mm).

Sternum; dark brown. Prosternum triangular, posterior width equal to anterior width of mesosternum, longitudinal carinae slightly separated mesally. Mesosternum; basisternum length 1.12 x width, 0.66 x furcasternum length, lateral margins anteriorly expanded, posterior margin truncated, furcasternum length 0.71 x width, lateral margins of median longitudinal invagination parallel, posterior margin concave with a short triangular indentation.

Wings : hyaline, fore wing (Fig. II.3a) 2.77 x longer than wide, pterostigmal region brown, costal and subcostal cross veins broadly shaded with black, bulla in Sc surrounded by black marking, covering one-two cellules, cross veins of pterostigma slanted, forked, cross vein system dense, except in cubital and anal regions. Three bullae present, one in each of Sc, R_2 and $R_{4\ \&\ 5}$. Hind wing (Fig. II.3b) 1.60 x longer than wide, costal margin convex to half wing length, then curves down, joins Sc 9/10 of wing length, costal space with 1-3 proximal and 6-10 distal cross veins, R_1 straight, Rs joins MA in distal half, MA straight, MP forked in centre of wing, cross vein system fairly complete, varies between individuals, and even left and right wings (Table II.6).

Abdomen : light brown with darker markings dorsally (Fig. II.3h) ventrally grey with light patches on segments 3-9, segments 6-8 with paired patches projecting into the light regions, segments 1-2 grey (Fig. II.3i). Cerci stout, black/brown with the last 3-5mm buff, appendix dorsalis absent.

Genitalia : (Figs. II.3c, d) forceps three segmented, first segment long, broad, narrows half way along length, second segment short, rectangular, with smooth external margin, distal segment longer, ovoid. Penes broad at base, with concave lateral margins and a bulbous distal region, fused, centrally, giving a triangular apex (Figs.II.7c, d).

Fig. II.3. *Atalophlebia australasica*. a - d, male imago: a, fore wing; b, hind wing; c, genitalia, ventral view; d, genitalia, lateral view. e - f, female imago: e, abdominal segments 7 - 10, ventral view; f, abdominal segments 7 - 10, lateral view. g - i, male imago: g, fore claw; h, dorsal abdominal colour pattern; i, ventral abdominal colour pattern.

Scale lines : a - f, h - i 1mm.
g 0.1mm.

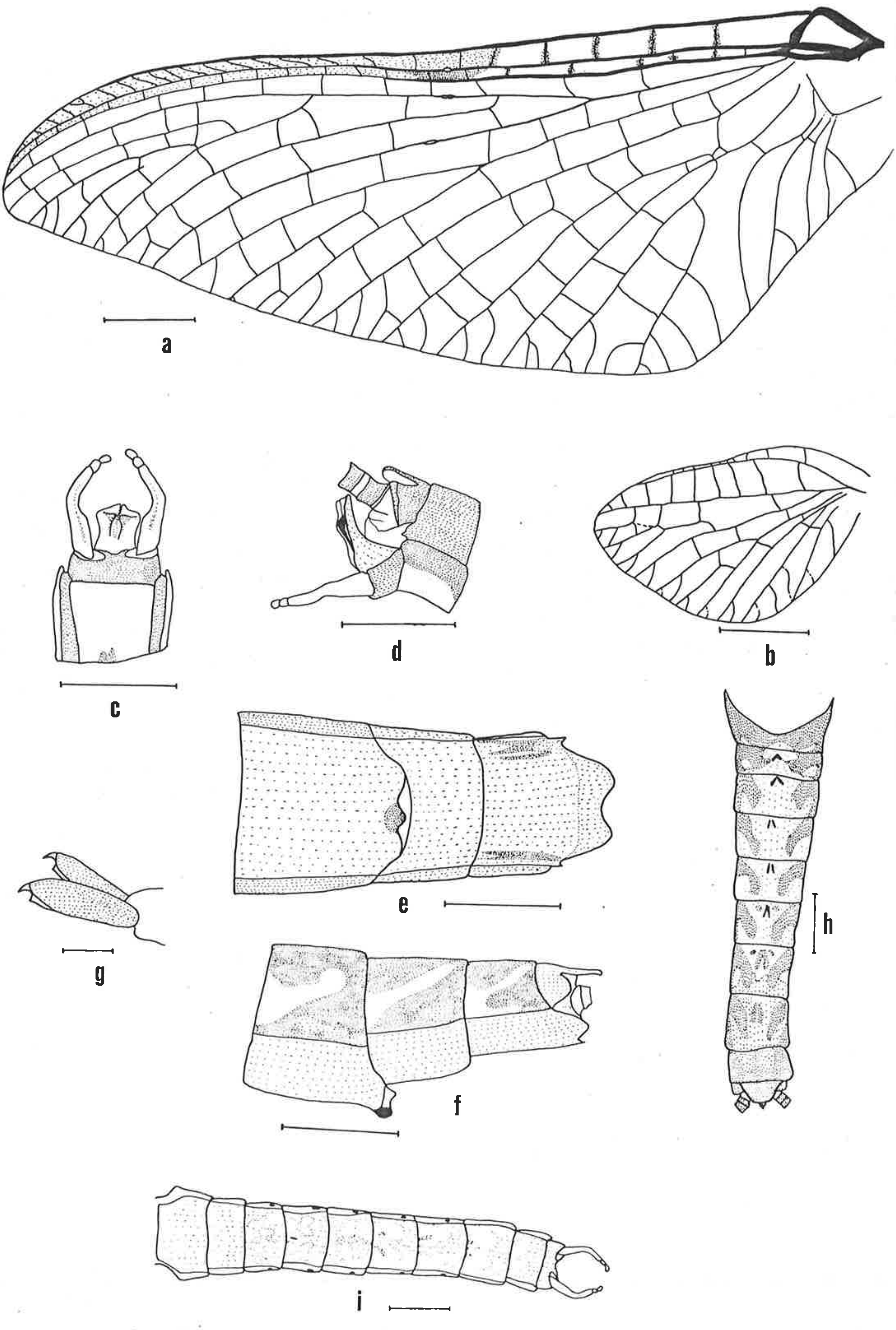
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TABLE II.6.

Variability of expression of the cross vein system in wings of *Atalophlebia australasica* from South Australia.

(n = 8).

Vein System	Left Wing Range	Right Wing Range
Fore wing :		
C/Sc basal half	6 - 9	7 - 9
C/Sc apical half	18 - 24	19 - 23
Sc/R_1 basal half	7 - 10	7 - 9
Sc/R_1 apical half	12 - 20	11 - 17
R_1/R_s	11 - 16	11 - 16
R_s system	31 - 40	31 - 39
R_{4+5}/MA	9 - 13	10 - 13
MA system	6 - 10	7 - 10
MA/MP	9 - 12	8 - 12
Hind wing :		
C/Sc basal half	0 - 1	0 - 1
C/Sc apical half	4 - 10	4 - 9
Sc/R_1	6 - 8	7 - 8

Mature Male Nymph. (Fig. II.14b).

	$\bar{x}$	SD	n	Range
Head Width	2.38	0.11	9	2.28 - 2.60
Notal Length	3.41	0.41	9	3.00 - 4.32
Pronotal Width	2.44	0.15	9	2.28 - 2.76
Mesonotal Width	2.70	0.22	9	2.48 - 3.12
Cerci Length	12.74	-	2	12.14 - 13.34
Appendix Dorsalis Length	12.82	0.35	3	12.42 - 13.40

Head : prognathous, dark brown/black, epicranial sutures light brown. Dorsal compound eyes red/black, lateral eyes black. Ocelli black posteriorly, white anteriorly. Antennae yellow/brown, longer than head is wide.

Thorax : dark brown with pale mid longitudinal line. Pronotum wider or narrower than head (geographically variable), lateral margins produced into a narrow curved transparent flange, antero-lateral margin with short spine setae, lateral margins with a few setae present or absent, posterior margin not fused to mesonotum. Mesonotal wing sheaths extending to middle of third abdominal segment, black just prior to emergence, brown earlier in last instar, mesonotum 1.11 x wider than head. Legs yellow brown with black bands on each segment, femora with two bands (one mid, one distal), tibiae with two bands, (one proximal, one distal), tarsi with a broad band covering proximal half (Fig. II.4a). Fore femur 1.05 x longer than middle femur, hind femur 1.15 x longer than fore femur. Tarsal claws short, curved, with 15-20 peg like denticles (Fig.II.4b). Ratios of leg segments;

fore leg	1.00 : 1.02 : 0.50 (2.24mm)

middle leg 1.00 : 0.98 : 0.37 (2.21mm)
hind leg 1.00 : 1.06 : 0.36 (2.42mm).

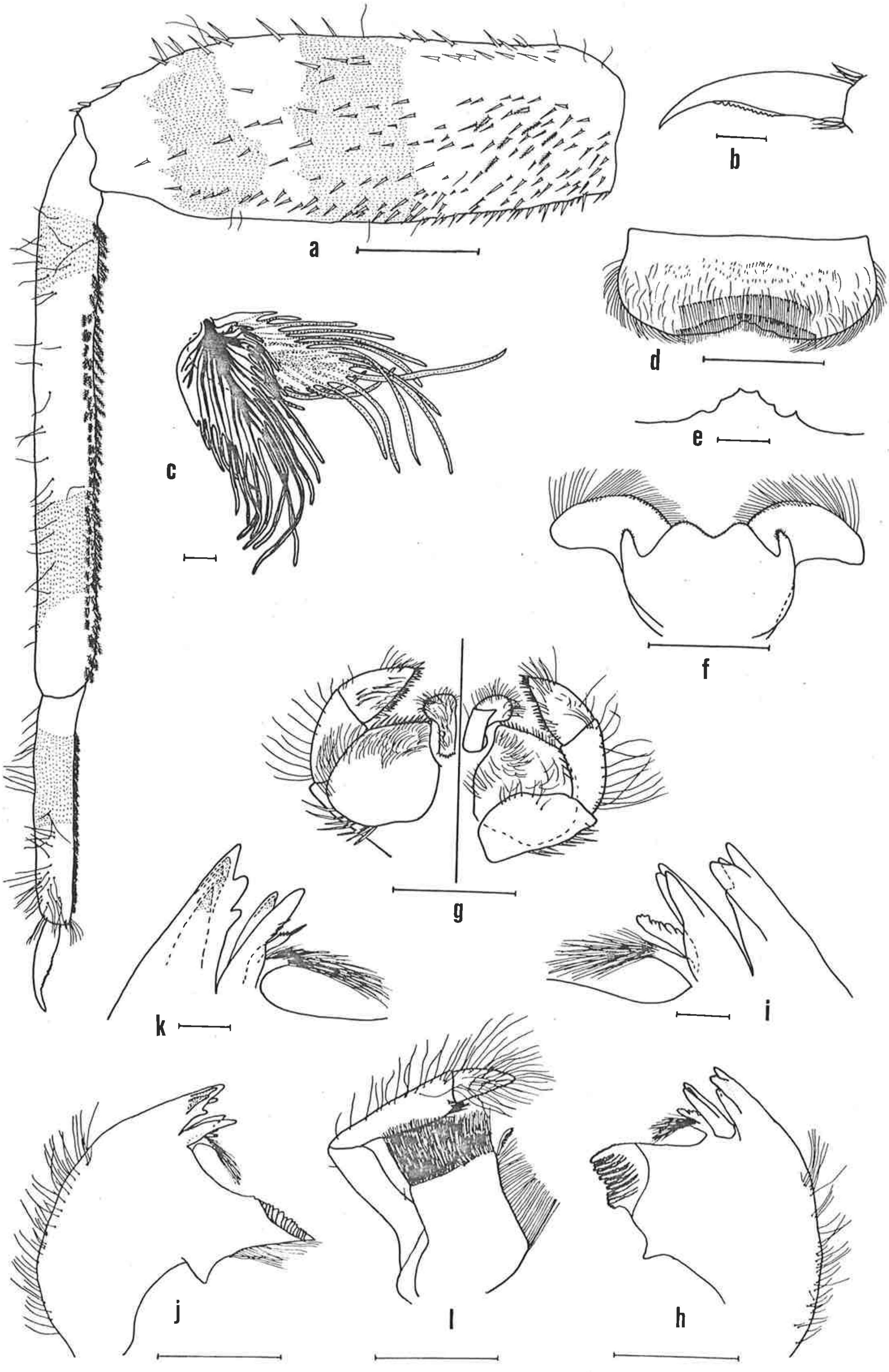
Femur length to width ratios; fore leg 3.18, middle leg 3.42, hind leg 3.61. Sternum; prosternum triangular, posterior width equal to anterior width of mesosternum, sternacostal suture absent, anterior sternal sutures convergent, fused apically. Mesosternum; basisternum length equal to furcasternum length, sternacostal suture present. Metasternum; basisternum 3.7 - 5 x wider than long, width equal to width of mesofurcasternum.

Abdomen : brown, patterned (Fig. II.14b), segments 9 and 10 narrowest, segments 2-9 carry lateral flanges produced posterolaterally into sharp backward directed projections, segment 9 with two spines, outer largest, inner rounded; segment 10 with rounded lateral margins, posterior margin of tergum with spines arranged singularly. Cerci well developed, appendix dorsalis longer than lateral filaments. Gills; multifurcate (Fig. II.4c), each gill consisting of a pair of lamellae with 8-20 tracheal filaments per lamella, gills on segments 3-5 largest, 1 and 7 smallest.

Mouthparts : labrum (Fig. II.4d) 3.41 x wider than long, lateral borders rounded, with long setae, mid anterior margin indented, rugose (Fig. II.4e) with two transverse rows of long setae posterior to indentation. Left mandible (Fig. II.4h); incisors large and separate, outer incisors with three large teeth, inner with three large teeth, prostheca robust, wide, outer margin crenulated with 6-8 blunt teeth, blunt apically (Fig. II.4i), molar region with crenulated teeth in 10-12 rows. Right mandible (Fig. II.4j); outer incisors with five teeth, inner incisors with two teeth and four small spines on inner lateral margin, prostheca, slender, with crenulations on outer margin of 2-4 tubercles, distally with a long spine (Fig.II.4k), molars with 10-15 transverse grinding ridges, fringed with long fine setae. Hypopharynx (Fig. II.4f); median lobe divided, with two slender lateral processes, apices of lobes lined with very short setae, paragnaths large, strongly convex, anterior margin fringed with long setae. Maxillae (Fig. II.4*l*); galeo-lacinia rectangular, dorsal brush of curved setae, row of 10-12 rake setae ventrally, rake setae interspersed within dorsal brush, rake spine at inner apical corner, inner margin lined with long fine setae, palpi three segmented, proximal segment 2.80 x longer than wide, lined with few setae, segment ratios, 1.00 : 1.19 : 0.69 : (0.41mm), second segment lined with long fine setae, inner border with pinnate setae, distal segment rounded at apex, covered with long fine setae. Labium (Fig. II.4g); palpi three segmented, proximal segment long and broad, 1.97 x longer than wide, narrows distally, outer margin with long setae, segment ratios 1.00 : 0.67 : 0.68 (0.42mm), second segment narrow proximally, broadest distally, lined with long fine setae, inner margin of distal segment with short stout spines, longer fine setae on both dorsal and ventral surfaces. Glossae small, dorsally rectangular, covered in short setae, paraglossae broad, outer margin convex, lined with long fine setae, dorsal and ventral surface with patches of fine setae.

Fig. II.4. *Atalophlebia australasica*, mature nymph: a, fore leg; b, fore claw; c, third abdominal gill; d, labrum, dorsal view; e, antero-median emargination of labrum, enlarged; f, hypopharynx; g, labium, dorsal (left) and ventral views; h, left mandible, ventral view; i, left incisors and prostheca, enlarged; j, right mandible, ventral view; k, right incisors and prostheca enlarged; l, right maxilla, ventral view.

Scale lines : a,c,d,f,g,h,j,l 0.5mm.
b,e,i,k 0.1mm.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Female Imago. larger than male, similar colour and dorsal markings, 9th abdominal sternite with shallow incision on posterior margin, 7th sternite produced posteriorly forming a bulbous projection (Figs.II.3e, f). Fore legs shorter than male, sternum and thorax broader than male, mesobasisternum length 0.81 x width, 0.63 x furcasternum length, furcasternum length 0.61 x width. Appendix dorsalis present.

Subimago : dull, black/brown, wings uniformly shaded grey, appendix dorsalis present.

Female Nymph : similar to male, dorsal compound eyes lacking, lateral eyes black.

Sexual Variation of Nymphs.

Sexual variation of morphometric characteristics as analysed from one population of *A. australasica* is summarized in Table II.7. As was found in *A. australis* nymphs, the sexual variation was predominantly in the thoracic and leg characteristics, with the female nymphs tending to be more robust and larger than the males. Characters examined which were statistically non-significant are presented in Appendix 4.

Diagnostic Characteristics.

1. Genitalia of male imago (Figs.II.3c, d; 7c, d).
2. Lack of appendix dorsalis in adult male.
3. Subimago with uniform grey wings.
4. Nymphs with multifurcate tracheal gill filaments (Fig. II.4c).

TABLE II.7. Morphological characters of *A. australasica* nymphs in which males differ from females.

Data refers to last instar nymphs from Jerusalem Creek, South East South Australia. Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$

Character	Males $\bar{x}$	Males S.D.	Males Range	Females $\bar{x}$	Females S.D.	Females Range	d.f.	t	
MNW/HW	1.02	0.03	0.98-1.06	1.09	0.04	1.06-1.15	10	3.85	**
PNW/HW	0.96	0.01	0.94-0.98	1.06	0.02	1.04-1.09	10	9.49	***
FFL/HW	0.86	0.02	0.84-0.88	0.93	0.02	0.90-0.96	14	6.98	***
MFL/HW	0.88	0.02	0.85-0.90	0.93	0.03	0.90-0.99	14	4.29	***
HFL/HW	1.03	0.02	1.00-1.06	1.12	0.05	1.06-1.20	13	4.20	**
FT_iL/FFL	1.03	0.02	1.01-1.06	1.05	0.01	1.04-1.07	14	3.44	**
FT_aL/FFL	0.51	0.02	0.48-0.53	0.45	0.01	0.44-0.46	14	8.05	***
MFL/FFL	1.03	0.01	1.01-1.05	1.00	0.03	0.95-1.03	13	2.35	*

5. 9th abdominal segment with two spines on the postero-lateral margin.

6. Form and shape of mandibles, incisors and prosthecae (Figs.II.4h - k).

History and Discussion.

Atalophlebia australasica, originally described by Pictet (1843), has been redescribed by Eaton (1871, 1884), by Ulmer (1916) and Harker (1954). The description given by Pictet was not extensive enough to enable recognition of this species as more Australian species were described. Eaton (1871, 1884) redescribed this species and illustrated the wings and genitalia. Ulmer (1916) designated material from northern Queensland as *A. australasica*, and described the male and female imagos, and the subimago. Ulmer noted differences in the venation of the hind wing of these specimens when compared with Eaton's (1884) illustration, but did not comment on the apparent differences in the genitalia as illustrated by Eaton. Harker (1950a) recorded that Ulmer (1919) had placed *A. australasica* as a synonym of *A. costalis* (Burmeister). In 1954, Harker noted, after examining material in the British Museum, that *A. australasica* as designated by Eaton was distinctly different from *A. costalis* as determined by Tillyard, and redescribed all stages of the species. Although the male imago description is of the holotype (as inferred by the statement "fore legs are missing in holotype and paratypes"), Harker included a record of a well developed appendix dorsalis. Pictet's (1843) description included only one caudal filament measurement, consistent with the accompanying illustration, and of descriptions of species lacking the appendix dorsalis. Eaton (1871, 1884) also included only one measurement. Ulmer (1916) recorded only the lateral cerci "Die Schwanzborsten (2 beim ♂) sind schwarzbraun ... " but recorded the presence of the appendix dorsalis in the male subimago. Harker (1954) also noted that material examined from Mt. Gambier (from Tillyard's 1934 collection) was consistent with her recognition of this species. Adult males of *A. australasica* from south-east South Australia and the Fleurieu Peninsula lack the appendix dorsalis, consistent with the type description. Harker's record mentions no variability of expression of the appendix dorsalis (as described for *A. australis* by Tillyard 1934). Therefore, since subsequent collections, as well as the type material all lack this filament, its presence as indicated by Harker must be suspect.

A comparison of Figs. II.3c, and II.7c, with the illustration of the *A. australasica* genitalia by Harker (1954) shows little resemblance. The South Australian material of this species, examined in this study, was initially considered different from previously described species. However, a comparison of an air dried specimen and a critical point dried specimen revealed two different penes characteristics. The air dried specimen closely resembles the illustration presented by Harker, from a dry, pinned preparation. The lateral lobes of air dried specimens curl in towards the mid line, producing a long narrow structure. The critical point dried specimens represent more closely the living, or alcohol preserved, characteristics of the genitalia, with the lateral lobes of the penes maintaining their lateral position.

Variation of Character Expression.

No variation of character expression has been recorded for this species, therefore qualitative and quantitative characteristics were considered and analysed. The diagnostic characters of this species were found to be consistently expressed, and upheld all seven of the requirements listed by Blackwelder (1967).

The variation in the cross vein system of the fore and hind wings is given in Table II.6. Morphometric variation in nymphal characteristics was analysed by comparing populations from the Mt. Lofty Ranges and from south-east South Australia. No imaginal comparisons were carried out due to the inadequate number of specimens from the south-east. The significant characters which are geographically variable are listed in Table II.8. Full results of all character analysis are included in Appendix 5.

Material Examined. South Australia : South East; Cress Ck., Deep Ck., Eight Mile Ck., Hitchcock Drain, Jerusalem Ck. Mt. Lofty Ranges; Blackfellow Ck., Brownhill Ck., Bull Ck., Cudlee Ck., Currency Ck., Dam at Carey's Gully, Dam at Ashton, Deep Ck., First Ck., Fourth Ck., Little Para R., Morialta Ck., Onkaparinga R., Sturt R., Torrens R., Wakefield R. Fleurieu Peninsula; Carrickalinga Ck., Coolawang Ck., The Deep Ck., (Delamere), Finnis R., Gold Digging Swamp, Hindmarsh R., Inman R., Kangarilla Ck., Myponga Ck., No Where Else Ck., Tookayerta Ck., Yankalilla R. Kangaroo Island; Breakneck R., De Mole R., Middle R., Rocky R., South West R. Victoria : Crawford R., Eumarella R., Fitzroy R., Glenelg R., Shaw R., Wannon R.

TABLE II.8. Geographical variation in some morphometric characters of *A. australasica* male nymphs from Jerusalem Creek, South East South Australia, and Sturt River, Mt. Lofty Ranges, South Australia.

Data refers to last instar nymphs from both populations. Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Character	Sturt River			Jerusalem Creek					
	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
MNW/HW	1.13	0.04	1.06-1.20	1.02	0.03	0.98-1.06	13	5.62	***
PNW/HW	1.02	0.02	1.00-1.06	0.96	0.01	0.94-0.98	13	6.15	***
MFL/HW	0.92	0.03	0.89-0.98	0.88	0.02	0.85-0.90	19	3.76	**
MFL/MFW	3.42	0.12	3.20-3.61	3.56	0.14	3.32-3.72	19	2.44	*
HT_iL/HFL	1.06	0.02	1.03-1.09	1.08	0.02	1.05-1.11	16	2.48	*
HFL/FFL	1.15	0.03	1.11-1.18	1.19	0.02	1.17-1.23	15	3.49	**
Labial palpi :									
BL/BW	1.97	0.12	1.77-2.20	1.71	0.10	1.55-1.82	22	5.28	***
ML/BL	0.67	0.02	0.63-0.70	0.71	0.07	0.63-0.77	22	2.71	*
AL/BL	0.68	0.05	0.55-0.77	0.73	0.03	0.70-0.78	22	3.08	**
Maxillary palpi :									
MBL/MBW	2.80	0.18	2.55-3.08	2.96	0.14	2.71-3.14	21	2.15	*

II.4.1.3 *Atalophlebia auratus* sp. nov.

Holotype Male Imago.

Body Length	7.95mm
Notal Length	2.60mm
Pronotal Width	1.04mm
Mesonotal Width	1.27mm
Fore Wing Length	7.44mm
Hind Wing Length	2.23mm
Cerci Length	19.67mm
Appendix Dorsalis Length	15.57mm

General colour yellow/brown, fore wings yellow, hind wings grey.

Head : dark brown. Antennae short, basal segment 0.12mm long, 1.5 x longer than wide, 2nd segment 0.1mm long, 2.5 x longer than wide, flagellum 0.24mm long. Dorsal compound eyes pink/brown, lateral eyes dark grey. Ocelli dark brown laterally, white anteriorly.

Thorax : shiny black. Pronotum narrower than head. Legs; fore legs long, femur and tibia dark brown, tarsal segments dark brown, no banding on any segment, T_1 partially fused to tibia. Middle and hind legs shorter, light brown without banding, tarsal segments 1-4 with distal spine, T_1 fused to tibia, join visible. Fore leg femur length 1.03 x middle leg femur length, and 0.95 x hind leg femur length.

Ratios of leg segments;

fore leg 1.00 : 1.14 : 0.09 : 0.40 : 0.40 : 0.28 : 0.19 (1.84mm) middle leg 1.00 : 0.77 : - : 0.08 : 0.10 : 0.08 : 0.16 (1.78mm)

hind leg 1.00 : 0.98 : - : 0.08 : 0.10 : 0.07 : 0.17 (1.94mm).

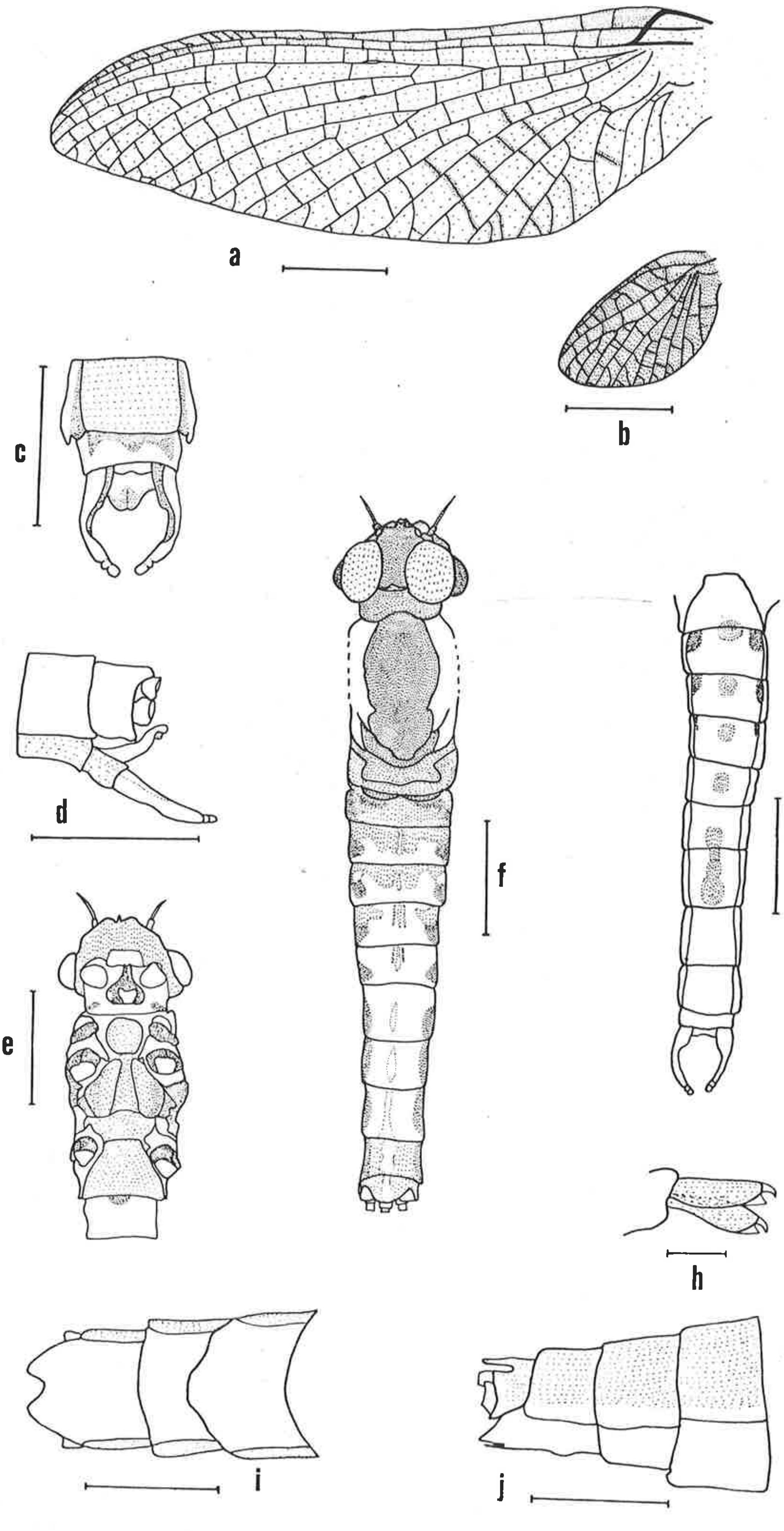
Tarsal claws similar, elongate, distally hooked (Fig. II.5h). Sternum dark black/brown. Prosternum triangular, longer than wide, posterior width equal to anterior width of mesosternum. Mesosternum; basisternum length 1.17 x width, 0.78 x furcasternum length, furcasternum length 0.89 x width, lateral margins of median longitudinal invagination divergent, posterior margin concave (Fig. II.5e).

Wings : fore wing (Fig. II.5a); tinged throughout with yellow/brown, veins yellow/brown, pterostigma darker than rest of wing, cubital region shaded grey, length 3.35 x width, pterostigmatic cross veins forked in left wing, simple, not forked in right wing, cross veins present in proximal half of costal region, cross vein system dense, except in cubital and anal regions. Hind wing (Fig. II.5b) grey/brown, darker than fore wing, shaded completely, length 2.06 x width, costal hump not large, costal vein joins Sc at nearly 4/5 of wing length, costal space with nine cross veins, R_1 straight, Rs connects to MA in centre of wing, MP forked in proximal half of wing, cross vein system dense, forked and anastomosed veins in subcostal space.

Abdomen : yellow/brown dorsally, lighter yellow ventrally, dorsal tergites with dark brown/black markings laterally, and light mid longitudinal stripe along all segments, segments 1, 9 and 10 darker, 10 almost black with light brown stripe (Fig. II.5f). Sternites yellow/grey, with light red/brown

Fig. II.5. *Atalophlebia auratus*. a - h, male imago: a, fore wing; b, hind wing; c, genitalia, ventral view; d, genitalia, lateral view; e, thoracic sterna; f, dorsal colour pattern; g, ventral abdominal colour pattern; h, fore claw. i - j, female imago: i, abdominal segments 7 - 10, ventral view; j, abdominal segments 7 - 10, lateral view.

Scale lines :		
	a - g, i, j	1mm.
	h	0.1mm.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circular markings on mid line, positioned anteriorly on segments 2, 3 and 4, centrally on 5, posteriorly on 6, joining a double marking on segment 7, segments 1, 8, 9 grey, and 1, 2, 3 marked antero-laterally with black (Fig. II.5g). Cerci long, appendix dorsalis well developed but not as long or robust as cerci.

Genitalia : (Figs. II.5c, d; 7e, f), forceps with long proximal segment, broadest proximally, narrows half way along length, 2nd segment short, globular, distal segment longer, ovoid, rounded apically. Penes broad at base, tapering towards apex with apices held close together, curving upwards in profile.

Mature Female Nymph. (Fig. II.14c)

Body Length	9.20mm
Head Width	2.03mm
Notal Length	2.22mm
Pronotal Width	1.90mm
Mesonotal Width	2.19mm
Cerci Length	15.20mm
Appendix Dorsalis Length	14.66mm

General colour brown.

Head : brown, epicranial sutures light brown. Lateral eyes black, ocelli black. Tentorial body almost square, length 0.95 × width. Antennae 4.8mm long.

Thorax : pronotum width 0.95 × head width, 2 stout spine setae on anterior margin, no setae on lateral margin, brown without distinct markings. Mesonotum brown without distinct markings, broad, width 1.08 × head width, equal to notal length, wing sheaths extending to 4th abdominal segment. Legs light brown without banding (Fig. II.6a). Inner margin lined with pinnate and spinous setae, fore leg with pinnate setae on femur, tarsal claws with 31-35 peg-like denticles (Fig.II.6b), segment ratios;

fore leg 1.00 : 0.98 : 0.49 (1.81mm)
middle leg 1.00 : 0.96 : 0.48 (1.81mm)
hind leg 1.00 : 0.96 : 0.47 (1.97mm).

Femur length to width ratios; fore leg 3.77, middle leg 4.11, hind leg 4.48. Sternum; prosternum triangular, length 0.73 x width, wider than anterior margin of mesosternum. Mesosternum; basisternum rectangular, width 0.68 x length. Metasternum; basisternum short, width 5.71 x length.

Abdomen : brown dorsally with black patches on lateral flanges of segments 1-7, segments 1-5 otherwise brown without markings, segments 6, 7, 8, 9 with central light stripe, segment 10 light brown. Postero-lateral margins of segments 2-9 with small, sharp, backward pointing projection; lateral margins with very few fine setae. Cerci and appendix dorsalis well developed, cerci longer. Gills; seven pairs, multifurcate, with numerous fine tracheal filaments on each lamella, gill seven smallest.

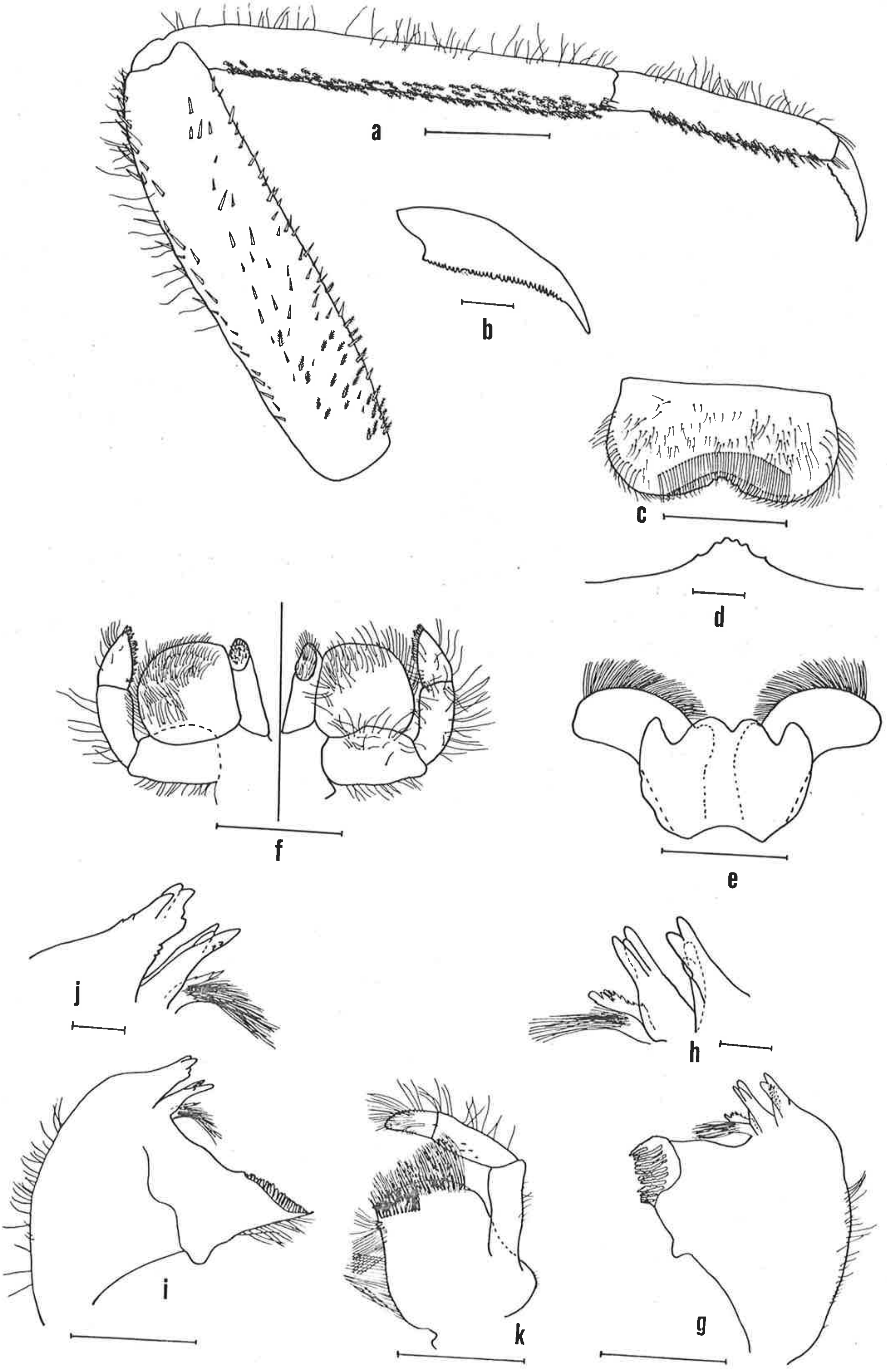
Mouthparts : labrum (Fig. II.6c) length 0.40 x width, lateral margins rounded, lined with long setae, anterior margin with median concavity lined with five rounded tubercles (Fig. II.6d), dorsally with two rows of long setae. Left mandible (Fig. II.6g); outer incisors with three apparent (four actual) teeth; inner incisors with three teeth, prostheca robust with rounded apex and 8-10 pointed teeth on external margin, long setal brush projecting from proximal half (Fig. II.11h), molar region with 10-12 transverse grinding ridges. Right mandible (Fig. II.6i);

outer incisors with three teeth and a fourth shoulder-like ridge on third tooth, two small tubercles on mesal margin, inner incisors with three teeth, inner most with two small tubercles laterally, prostheca long and narrow with one small external spine and two terminal spines (Fig. II.6j) molar region with numerous grinding ridges. Hypopharynx (Fig. II.6e) with divided median lobe and two slender lateral processes fringed with short setae, paragnaths large, convex, anterior border fringed with long setae. Maxillae (Fig. II.6k) galeo-lacinia rectangular, row of 10-12 rake setae on ventral surface placed just below apical brush (only one present in type specimen, scars of other setae present), mesal margin with long fine setae, palpi three segmented, segment ratios 1.00 : 1.10 : 0.67 (0.30mm), distal segment rounded, covered with long fine setae. Labium (Fig. II.6f); palpi three segmented, proximal segment broad, length 1.61 x width, narrows distally, inner and outer margins lined with long setae, external margin of middle segment lined with long setae, distal segment triangular, inner margin lined with short stout spines, outer margin with long fine setae, segment ratios 1.00 : 0.80 : 0.62 (0.38mm); glossae small, close together, dorsally with stout spines, ventrally with long fine setae, paraglossae long and broad, lined with long setae, dorsal surface with dense setae.

Female Imago. Reared in laboratory. Wing and body coloration resemble male, body robust, filled with eggs. Ninth abdominal segment with a deep ventral cleft (Fig. II.5i); sternite of seventh abdominal segment slightly produced posteriorly (Fig. II.5j).

Fig. II.6. *Atalophlebia auratus*, mature nymph: a, fore leg; b, fore claw; c, labrum, dorsal view; d, antero-median emargination of labrum, enlarged; e, hypopharynx; f, labium, dorsal (left) and ventral views; g, left mandible, ventral view; h, left incisors and prostheca, enlarged; i, right mandible, ventral view; j, right incisors and prostheca, enlarged; k, left maxilla, ventral view.

Scale lines :	a,c,e,f,g,i,k	0.5mm.
	b,d,h,j	0.1mm.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Subimago. Similar to male imago, wing colour dull yellow/grey, without λ marking.

Male Nymph. Smaller than female, head with red/brown compound eyes.

Diagnostic Characters.

1. Genitalia of male imago; shape of forceps segments two and three and shape of penes (Fig. II.5c, d; 7e, f).
2. Wing coloration in both fore and hind wings.
3. Lack of banding on legs of adults.
4. Multifurcate gills of nymph.
5. Only one postero-lateral spine on abdominal segment 9.
6. Shape of mandibles, incisors and prosthecae (Figs. II.6g - j).
7. Lack of banding on legs of nymphs (Fig. II.6a).
8. Dorsal colour pattern of nymph and adults (Fig. II.14c; and Fig. II.5f).

Type Locality.

Bakers Range Main Drain, west of Penola, south-east South Australia. Grid Reference on 1:250,000 map series, Penola Sheet, 357393. Collected 22nd November, 1977 by D. N. and P. J. Suter.

Type Specimens.

A. auratus is only known from the type locality, and collecting data other than for the type series is given in Appendix 3.

Holotype male and paratypes are placed in the National Museum of Victoria. The wings and legs of the holotype male are mounted on slides, and the mouthparts, legs and gills of the female nymph are also mounted on slides. The genitalia and body of the holotype are maintained in ethanol.

Type Habitat.

Near the source of Bakers Range Main Drain, which is a man made drain, draining the swamps of Bakers Range in the south-east of South Australia. The water at the type locality was evaporating rapidly during November, 1977 when the type collection was made. *A. australis* was also present at this locality.

Etymology of Specific Epithet

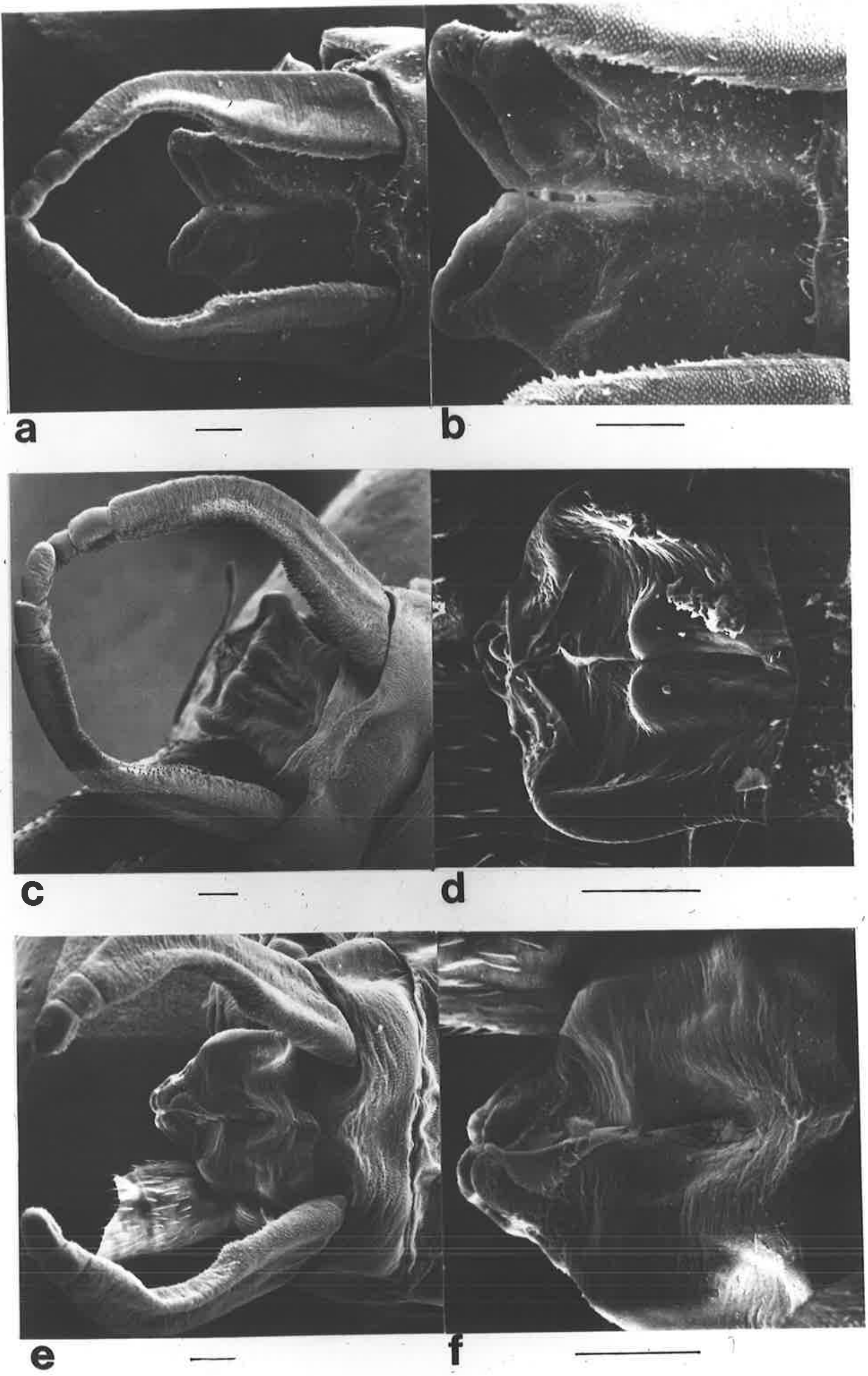
The specific epithet *auratus* (L); ornamented with gold, refers to the golden coloration of the forewings which make this species distinct from all other described *Atalophlebia* species.

Affinities

In adult characters the wing coloration, genitalia and lack of banding of the legs distinguish this species from other described species in the genus *Atalophlebia*. The nymph, however, resembles the nymph of *A. australasica* in possessing multifurcate

Fig. II.7. SEM micrographs of genitalia of *Atalophlebia* male imagos. a - b, *Atalophlebia australis*: a, genitalia, ventral view; b, penes, ventral view, enlarged. c - d, *Atalophlebia australasica*: c, genitalia, ventral view; d, penes, ventral view, enlarged. e - f, *Atalophlebia auratus*: e, genitalia, ventral view; f, penes, ventral view, enlarged.

Scale lines : 100μm.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gills. Although smaller than *A. australasica* (a character to be used with great care) the lack of banding of the legs, the presence of only one postero-lateral spine on the 9th abdominal segment, the mandible incisors and prosthecae all distinguish *A. auratus* from *A. australasica*.

Discussion of Taxonomic Characters

An assessment of useful taxonomic characters was made using the three species of *Atalophlebia* recorded in South Australia. Because very few specimens of *A. auratus* were available only qualitative comparisons were made using all three species. Table II.9 lists all the qualitative characteristics which were found to be consistently expressed in the specimens available for the present study, and each species of *Atalophlebia* is compared. The genitalia of the species are not included in this table, but of all the characteristics, this was the character on which most weighting was placed in the study of the male imagos. The characters in Table II.9 support this weighting, verifying the species separation using the genitalia only. The major venation of the fore and hind wings was considered useful only at the generic level, and the cross-venation too variable to be of any taxonomic value.

In the nymphs the most reliable characteristics for specific identification were the mouthparts, especially the incisors and prosthecae of the mandibles. In all species examined the left mandibular prostheca was robust, but the structure was distinctive. The right mandibular prostheca was long and slender, but again each was characteristic of the species.

TABLE II.9. Comparison of qualitative characteristics of *Atalophlebia australis*, *A. australasica* and *A. auratus* from South Australia.

Character	*A. australis*	*A. australasica*	*A. auratus*
Male Imago.			
Body colour	Yellow-brown	Black-brown	Yellow-brown
Fore wing colouration	Pterostigma only (yellow)	Pterostigma only (brown)	Totally yellow
Hind wing colouration	Clear	Clear	Grey
Penes	Separate apically	Fused apically with lateral lobes	Fused apically without lateral projections
Legs	Femur banded	Femur banded	No banding
Fusion of Tarsal Segment 1 of Fore leg	Partial	Partial	Partial
Fusion of Tarsal Segment 1 of Middle and Hind legs	Fused	Fused	Fused
Appendix-dorsalis	Present-Absent	Absent	Present
Nymph.			
Dorsal Eye colour (♂)	Sepia	Red-black	Pink/brown
Lateral Eye colour	Black	Black	Black
Legs : Banding	Femora 2 bands	2 bands	Absent
	Tibiae 2 bands	2 bands	Absent
	Tarsi 1 band	1 band	Absent
Postero-lateral spines on abdominal segment 9.	Single	2 spines	Single
Abdominal Tergite Spines	Large singular spines with smaller basal spines	Singular spines	Single spines with smaller basal spines
Gills	Trifurcate	Multifurcate	Multifurcate
Left Mandible Incisors - Outer	4	3	4
" Inner	3	3	3
Prostheca	Robust-serrated	Robust-serrated	Robust-serrated
Right Mandible Incisors Outer	3	5	3
" Inner	2	2	3
Prostheca	Long, slender with 4 spines	Slender-serrated	Long, narrow

These structures alone would probably be useful for distinguishing species, but it was common to find the incisors worn, and often the teeth were indistinguishable. However, the prosthecae remained distinctive, and these characters combined with the gill structure, labrum shape and dentition, abdominal spination, and leg banding, enabled species recognition.

Quantitative or morphometric character expression was analysed using *A. australis* and *A. australasica* male imagos and male and female nymphs. Characteristics which were shown to be geographically variable in the adults, and geographically and/or sexually inconsistent in nymphs were not considered useful characteristics in separation of the two species. Although all characters were assessed, including the geographically and sexually variable ones, only seven characters in the imago and four in the nymphs were consistently expressed within the available material and statistically different in both species. In the imago comparison a further two characters different significantly, but they exhibited geographical variation. The nymphal comparison included a further 11 significant characters, three of which were sexually variable, four geographically inconsistent, and four both sexually and geographically variable. Because of this great variation of expression, although there was statistical difference, the overlap of the two species' ranges was such that very little confidence could be placed on these morphometric characters. Only one character, maxillary palpi proximal segment L/W, showed no overlap in the comparison.

Table II.10 lists the statistical parameters of the two species of *Atalophlebia* which were statistically different. Although these characters are useful in the separation of *A. australis* and *A. australasica* their value in the separation of other species in this genus will need to be assessed. However, their use has not been of primary importance in the recognition of the species concerned, but are valuable characters in the support of the species separation initially developed using qualitative characters.

II.4.2 Genus *Atalonella* Needham and Murphy 1924.

Ulmer, 1919 : 20 (In *Atalophlebia*)
Needham and Murphy, 1924 : 35-37
Lestage, 1931 : 52
Traver, 1946 : 420
Harker, 1950a : 30-32
1954 : 242-243
1957 : 69-71
Riek, 1970a: 239
Peters and Edmunds, 1972 : 1411
Tsui and Peters, 1975 : 540-542

Male Imago Characteristics. Wings; fore wing tornus not well developed, cross veins in the proximal half of the costal area weak or absent, cross veins of pterostigma simple, not forked or anastomosed. Hind wing, costal border bends down to meet Sc at 3/4 of wing length, no intercalary in the fork of MA, no cross veins posterior to CuA. Tarsal claws paired, similar, long and

TABLE II.10. Morphometric characters which are useful in distinguishing the two species *Atalophlebia australis* and *A. australasica* in South Australia.

Characters which were geographically or sexually variable are indicated G. or S. respectively, or G.S. if both.

Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

	A. australis			*A. australasica*					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
Male Imagos :									
MNW/BL	0.18	0.01	0.16-0.20	0.16	0.01	0.14-0.17	25	3.66	**
PNW/BL	0.13	0.01	0.12-0.15	0.11	0.01	0.10-0.13	17	4.38	**
CL/BL	2.44	0.36	2.14-2.84	2.93	0.21	2.66-3.25	11	2.84	*
NL/MNW	1.90	0.16	1.62-2.23	2.03	0.05	1.97-2.14	25	2.19	*
MSL/BL(S)	0.16	0.01	0.14-0.17	0.15	0.01	0.13-0.17	22	2.26	*
MFSL/BL(S)	0.10	0.01	0.09-0.11	0.09	0.01	0.08-0.10	22	3.67	**
MT$_5$L/MFL	0.19	0.02	0.16-0.22	0.16	0.01	0.14-0.18	12	2.46	*
HT$_5$L/HFL	0.16	0.12	0.16-0.19	0.15	0.01	0.13-0.16	12	3.60	*
HT$_i$L/HFL	0.96	0.03	0.91-0.99	1.01	0.02	0.98-1.04	12	3.93	**

Continued ....

Table II.10 (Cont.)

	A. australis			*A. australasica*					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
Male Nymphs :									
MT$_i$L/MFL	0.97	0.02	0.94-1.00	0.99	0.02	0.96-1.02	54	4.25	***
MT$_a$L/MFL	0.43	0.02	0.35-0.45	0.37	0.01	0.35-0.40	54	12.58	***
HT$_a$L/HFL	0.42	0.02	0.38-0.44	0.36	0.02	0.32-0.39	48	13.65	***
MNW/HW(G.S)	1.14	0.07	1.06-1.29	1.09	0.06	0.98-1.15	33	2.26	*
FFL/HW(S)	0.87	0.04	0.82-0.96	0.89	0.04	0.84-0.96	54	2.51	*
MFL/HW(G.S)	0.88	0.05	0.83-1.00	0.91	0.03	0.85-0.99	54	2.82	**
HFL/HW(S)	0.97	0.08	0.92-1.05	1.05	0.05	1.00-1.20	49	4.22	***
FT$_i$L/FFL(S)	1.06	0.02	1.01-1.11	1.03	0.04	1.01-1.07	53	3.69	***
MFL/MFW(G.S)	3.33	0.14	3.12-3.58	3.48	0.14	3.20-3.72	54	4.02	***
HT$_i$L/HFL(G)	1.03	0.03	0.97-1.06	1.07	0.02	1.03-1.11	48	6.16	***
HFL/FFL(G.S)	1.14	0.02	1.10-1.18	1.18	0.04	1.11-1.23	45	4.82	***
labial palpi :									
ML/BL(G)	0.79	0.06	0.65-0.90	0.69	0.05	0.63-0.77	59	6.73	***
AL/BL(G)	0.58	0.09	0.40-0.73	0.69	0.05	0.55-0.78	56	5.96	***
maxillary palpi									
MBL/MBW(G)	2.87	0.28	1.63-2.43	2.17	0.25	2.50-3.14	55	9.62	***
Labrum L/W	0.35	0.02	0.33-0.38	0.30	0.02	0.25-0.33	27	6.49	***

slender, distally hooked.

Male genitalia; forceps three segmented, proximal segment broad at base, narrows half way along length, proximal half of penes fused, distal half may be divided or fused. Ninth abdominal sternite of female deeply cleft posteriorly. Appendix dorsalis longer than cerci.

Mature Male Nymph Characteristics. Head prognathous, tentorial body width slightly greater than length. Mandibles robust, with curved outer margins, incisors paired, separate, prosthecae with brush of setae inserted at base. Gills on abdominal segments 1-7 alike, with paired lamellae, linear-lanceolate with only a single tracheal filament per lamella. Postero-lateral spines on abdominal segments 6-9, spines progressively larger posteriorly. Apex of tarsal claws hooked, narrow, denticles on claws numerous, larger distally. Appendix dorsalis longer than cerci.

History and Discussion

The genus *Atalonella* has had a very turbulent history being criticised regularly since its designation in 1924 by Needham and Murphy. Two species *A. ophis* and *A. fusca* (Ulmer, 1919) were included in this new genus, the former species from Chile and the latter from Australia (Needham and Murphy stated that both species came from Chile, an error noted by Lestage (1931); Traver (1946); Peters and Edmunds (1972)). Harker (1950a) added further to Lestage's (1931) criticism of the erection of this genus, noting that the "tip of subcostal vein at nine tenth of wing length in *Atalophlebia*, three quarters in *Atalonella*" was the only constant character of those designated

by Needham and Murphy. In a subsequent paper Harker (1954) noted that no type species was designated by Needham and Murphy, "but the species described at the same time, *Atalonella ophis*, was probably considered as such" (Harker, 1954).
Needham and Murphy distinguished *A. ophis* from *Atalophlebia fulvipes* which later was transferred to *Atalophlebioides* by Ulmer (1938). Harker (1954) compared *Atalonella ophis* and *Atalophlebia australis*, the two genotypes, and concluded that these two species belonged to separate genera. Harker then re-defined *Atalonella* and transferred six Australian species described in *Atalophlebia* to *Atalonella*. Three of these, *A. brunnea*, *A. fuscula* and *A. delicatula*, were described by Tillyard (1936) who noted that "the Tasmanian species of *Atalophlebia* can be arranged in two quite distinct groups, one consisting of comparatively large species in which the nymphal gills are digitate, and the other consisting of much smaller species in which the gills are narrowly lanceolate." The smaller species were the ones transferred to *Atalonella*. *Atalophlebia inconspicua* mentioned in Tillyard's key was not described and was left in *Atalophlebia*. *Atalophlebia lucida* Ulmer 1919, *A. simillima* Ulmer 1919, and *A. parva* Harker 1950a were also transferred to *Atalonella* and a further species, *A. darkara* was described by Harker (1957) establishing eight Australian species of *Atalonella*.

Peters and Edmunds (1972) formally designated *A. ophis* as the type species of *Atalonella* and recognised the genus as distinct from other leptophlebiid genera. Tsui and Peters (1972) stated in their study of the morphology of the Gondwanian

Leptophlebiidae that, "the differences in the thoracic structures between the Australasian and South American *Atalonella* show the heterogeneity of this genus. These results support the contentions of M. L. Pescador (pers. comm.) and E. F. Riek (pers. comm.) that the genus *Atalonella* is polyphyletic and can be further subdivided taxonomically in both South America and Australia." The present study has not enabled any clarification of further taxonomic subdivision and, until further study of all Australian and South American species is performed, the new species recognised from South Australia, and *Atalophlebia inconspicua* Eaton are both placed in the genus *Atalonella*. *A. fuscula* (Tillyard) is redescribed and the nymph of *A. inconspicua* (Eaton) is described.

II.4.2.1 *Atalonella inconspicua* (Eaton) 1871 comb. nov.

Leptophlebia inconspicua	Eaton, 1871 : 79-80
Atalophlebia inconspicua	Eaton, 1884 : 87
	Ulmer, 1908 : 43-44
	Tillyard, 1936 : 31
	Harker, 1950a : 28
	1954 : 265

Male Imago.

	$\bar{x}$	SD	n	Range
Body Length	7.27	0.50	26	6.07 - 7.95
Notal Length	2.26	0.15	26	2.02 - 2.62
Pronotal Width	0.96	0.09	16	0.84 - 1.08
Mesonotal Width	1.19	0.08	26	1.04 - 1.32
Fore Wing Length	7.25	0.52	26	5.74 - 8.36
Hind Wing Length	1.43	0.14	26	1.20 - 1.80
Cerci Length	10.60	0.80	11	9.41 - 12.14
Appendix Dorsalis Length	12.67	1.01	10	11.11 - 14.02

General colour black, with light transparent regions between abdominal segments, giving a black and white banding appearance.

Head : black. Dorsal compound eyes light brown, raised, lateral eyes grey. Ocelli white. Antennae short, less than 1mm in length.

Thorax : dark brown/black, notopleural suture black. Legs; fore legs long, dark brown, without banding, T_1 partially fused to tibia. Middle and hind legs shorter, light brown, without bands. T_1 fused to tibia, suture apparent.

Ratios of leg segments;

fore leg 1.00 : 1.46 : 0.14 : 0.48 : 0.45 : 0.33 : 0.17 (2.13mm)

middle leg 1.00 : 1.07 : 0.06 : 0.08 : 0.08 : 0.07 : 0.16 (1.44mm)

hind leg 1.00 : 1.13 : 0.06 : 0.08 : 0.08 : 0.07 : 0.16 (1.49mm).

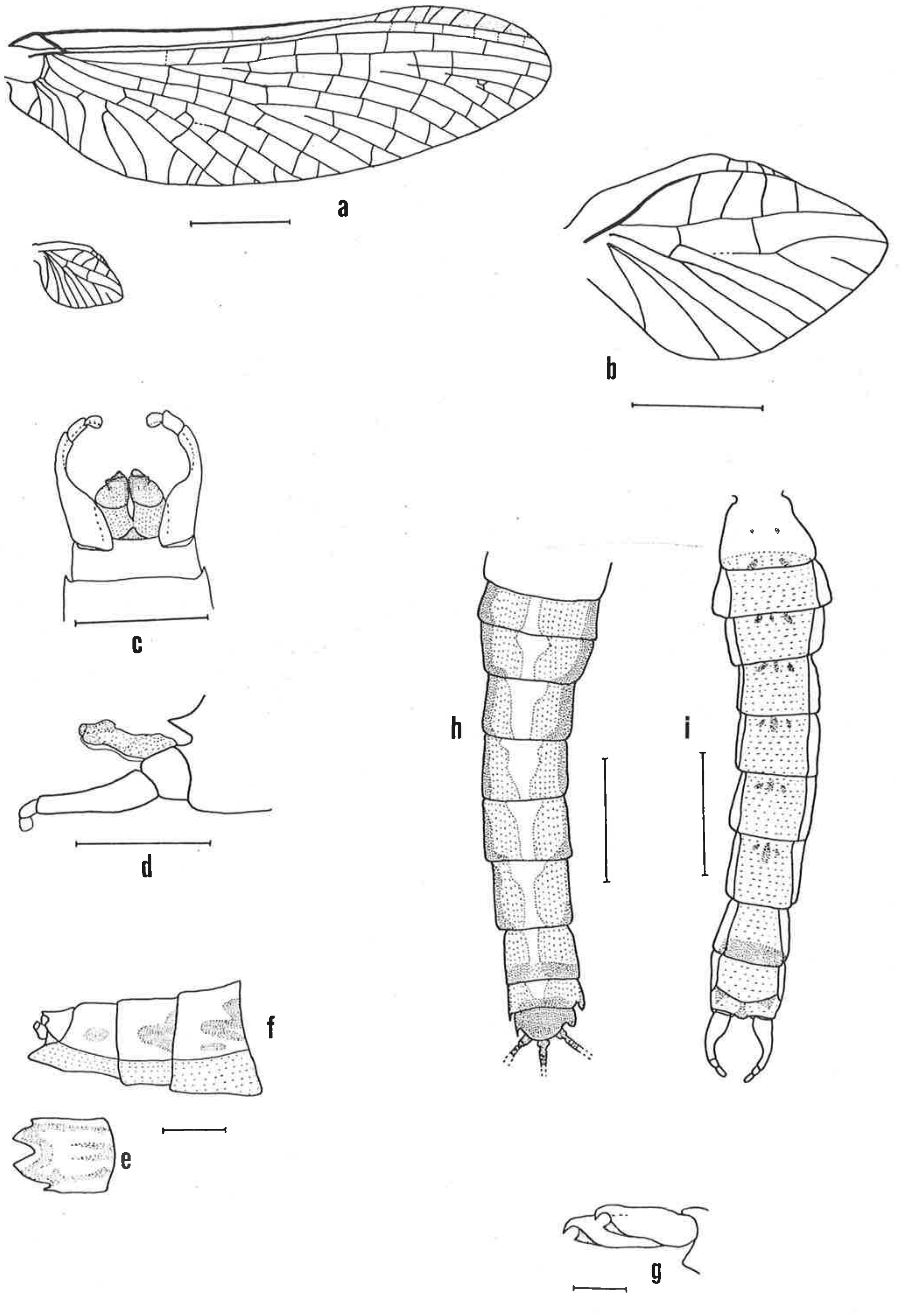
Sternum dark brown. Prosternum with longitudinal carinae separate. Mesosternum; basisternum length equal to or slightly greater than (1.08 x) basisternum width, 0.97 x furcasternum length, furcasternum length 0.56 x width, lateral margins of median longitudinal invagination almost parallel, posterior margin concave.

Wings : hyaline, with dark brown venation. Fore wing (Fig. II.8a) 3.29 x longer than wide, pterostigmal region slightly opaque, with simple cross veins in distal 1/3 only, absent in proximal 2/3 of costal space, proximal region of subcostal space without cross veins, distal region with very faint cross veins, cubital and anal regions with few cross veins. Two bullae present, one in Sc, one in $R_{4 \& 5}$. Hind wing (Fig. II.8b) 1.55 x longer than wide, Sc joins C at 3/4 of wing length, costal hump not large, 4-5 cross veins in distal region of costal space, absent in proximal half, subcostal space with 3-5 cross veins (rarely 6-7, Table II.12), Rs attached to MA and R_1 by a cross vein in proximal half of wing, MA straight, MP forked in centre of wing, cross veins absent in median, cubital and anal regions.

Abdomen : black with light central markings dorsally (Fig. II.8h). Each segment dark laterally with light regions both anteriorly and posteriorly giving a black and white banded appearance, segments 3-8 with a dorsal light brown stripe along median line, segments 9 and 10 dark brown, all segments light brown ventrally (Fig. II.8i). Cerci long, but shorter than appendix dorsalis.

Fig. II.8. *Atalonella inconspicua*. a - d, male imago: a, fore wing; b, hind wing; c, genitalia, ventral view; d, genitalia, lateral view. e - f, female imago: e, abdominal segment 10, ventral view; f, abdominal segments 7 - 10, lateral view. g - i, male imago: g, fore claws; h, dorsal abdominal colour pattern; i, ventral abdominal colour pattern.

Scale lines : a,h,i 1mm.
b - f 0.5mm.
g 0.05mm.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Genitalia : (Figs.II.8c, d); forceps three segmented, proximal segment long at base, narrows half way along length, 2nd segment short, rectangular, distal segment rounded, globular. Penes broad, fused along entire length, extending beyond construction of proximal segment of forceps, ventral lobes triangular with base separate anteriorly, sperm ducts open on mid line (Figs.II.15a, b).

Mature Male Nymph (Fig. II.14d)

	$\bar{x}$	SD	n	Range
Head Width	1.59	0.04	13	1.54 - 1.70
Notal Length	1.95	0.08	13	1.80 - 2.12
Pronotal Width	1.50	0.08	13	1.38 - 1.56
Mesonotal Width	1.58	0.07	13	1.50 - 1.72
Cerci Length	9.92	-	1	-
Appendix Dorsalis Length	10.77	-	1	-

Head : dark brown, light diamond shaped marking in centre of frons, epicranial suture light brown. Dorsal compound eyes dark reddish brown, lateral eyes black. Ocelli black. Antennae longer than head width. Tentorial body rectangular, 1.25 x longer than wide.

Thorax : pronotum width 0.90 x head width, dark brown, spine setae present on antero-lateral margin. Mesonotum dark brown with black wing sheaths (just prior to emergence) extending back to middle of fourth abdominal segment, light markings at base of wing sheaths. Mesonotal width 0.95 x head width. Legs brown, with no distinct banding, margins of femora and tibiae lined with spine setae (Fig. II.9a). Tarsal claws with 12-16 ventral peg-like teeth and a terminal curved tooth (Fig. II.9b). Ratios of leg segments;

fore leg	1.00 : 0.92 : 0.52 (1.39mm)
middle leg	1.00 : 0.92 : 0.44 (1.39mm)
hind leg	1.00 : 0.98 : 0.36 (1.49mm).

Femur length to width ratios, fore leg 3.17, middle leg 3.20, hind leg 3.35. Sternum; prosternum triangular, apex truncated, posterior width less than width of mesobasisternum. Mesosternum; basisternum length equal to furcasternum length, but narrower than furcasternum, sternacostal suture present. Metabasisternum narrower than mesofurcasternum.

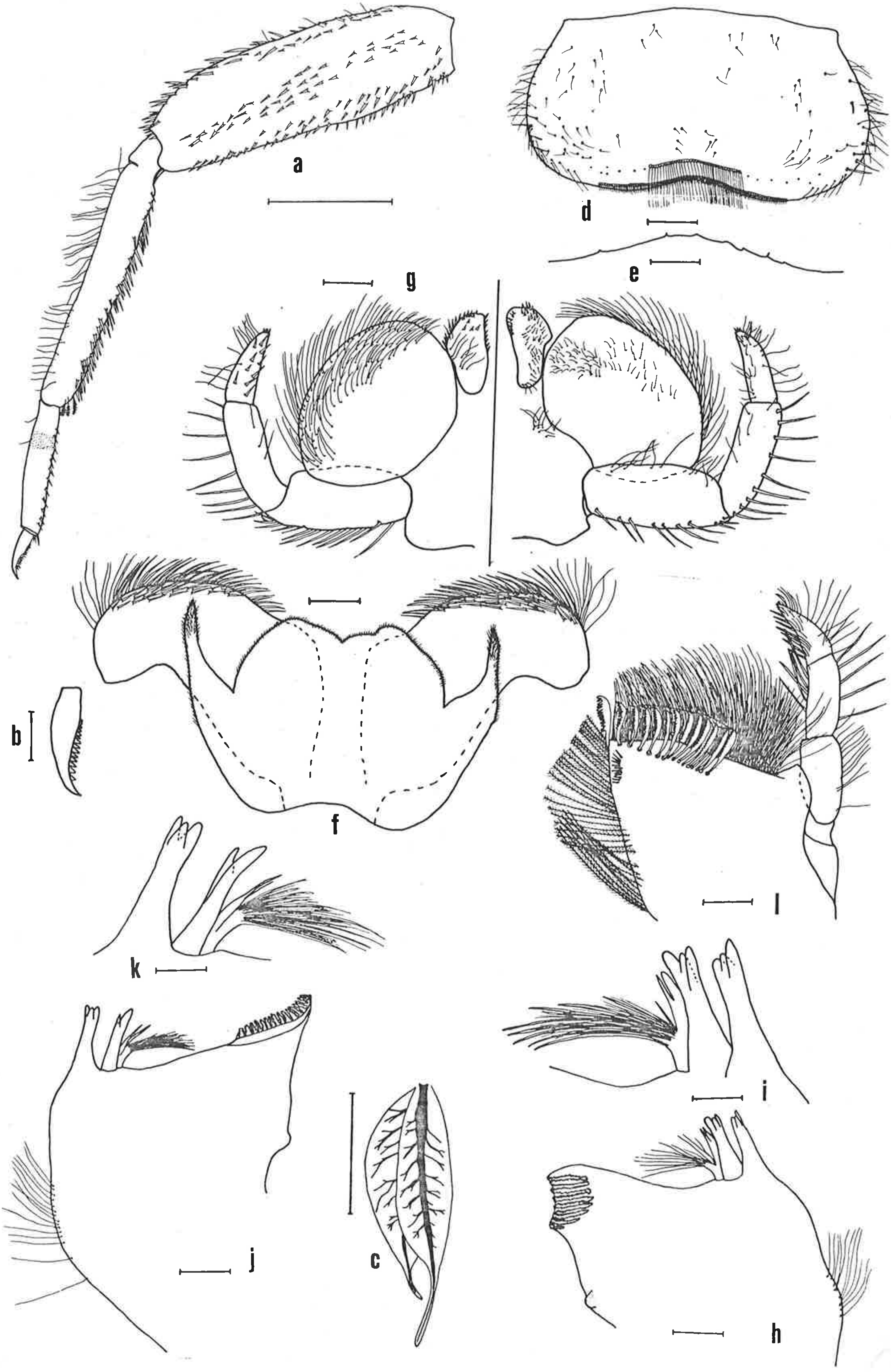
Abdomen : brown dorsally with a light stripe down mid-line (Fig. II.14d), segment ten brown, segments 6-9 with small backward pointing spine on postero-lateral margin, posterior margins of terga with large singular spines, with smaller spines between them. Cerci well developed, appendix dorsalis longer than cerci. Gills on segments 1-7 paired, lanceolate (Fig. II.9c), with a single terminal tracheal filament, lamellae with numerous tracheal branches, gills 1-4 largest, 5, 6, 7 progressively decreasing in size.

Mouthparts : labrum (Fig. II.9d); 2 x wider than long, lateral margins rounded, lined with setae, anterior margin with median cavity without obvious rounded denticles (Fig. II.9e), one row of short setae along anterior border, one short row of long setae directly behind median concavity. Left mandible (Fig. II.9h); outer incisors with three teeth, inner with three teeth, prostheca long and slender, apically with two rounded teeth (Fig. II.9i), molar region with 10-12 transverse ridges. Right mandible (Fig. II.9j); outer incisors with three teeth, inner with 2-4 teeth, prostheca simple, narrow with one apical spine (Fig. II.9k), molar region with transverse teeth. Hypopharynx (Fig. II.9f); median lobe deeply divided, paragnaths large, lined with long setae. Maxillae (Fig. II.9*l*); galeo-lacinia rectangular, broader than long with ventral row of 12 rake setae, and a rake spine on inner anterior margin, inner margin lined with long pinnate setae; palpi three segmented, proximal segment 2.06 x longer than wide, lined with long fine setae, segment ratios; 1.00 : 0.92 : 0.80 (0.22mm), distal segment rounded apically, lined with long setae. Labium (Fig. II.9g) with three segmented palpi, proximal segment 1.98 x longer than broad, second segment narrower, both lined with spine setae, distal segment rounded apically, with spine setae dorsally, apex with 3-4 short spines, segment ratios; 1.00 : 0.79 : 0.64 (0.35mm), glossae small, foot-like, lined with short spines, paraglossae broad, covered with long fine setae dorsally, short fine setae ventrally.

Female Imago : more robust than male, uniform brown, body 7.5 - 7.8mm long. Eyes lateral, light purple, dorsal compound eyes absent. Fore wings with cross veins along entire costal and subcostal spaces. Hind wings with some cross veins in radial, median and cubital sectors. Fore leg shorter than male, sternum and thorax more robust. Anal plate with a deep V shaped incision (Fig. II.8e), no apparent egg guide or ovipositor (Fig. II.8f). Egg oval, 0.12mm long, 0.09mm wide with a polar cap of two rings of tubular projections on each apex (Fig. II.16a).

Fig. II.9. *Atalonella inconspicua*, mature nymph: a, fore leg; b, fore claw; c, third abdominal gill; d, labrum, dorsal view; e, antero-median emargination of labrum, enlarged; f, hypopharynx; g, labium, dorsal (left) and ventral views; h, left mandible, ventral view; i, left incisors and prostheca, enlarged; j, right mandible, ventral view; k, right incisors and prostheca, enlarged; l, left maxilla, ventral view.

Scale lines :		
	a,c	0.5mm.
	b,d,f,g,h,j,l	0.1mm.
	e,i,k	0.05mm.


a
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i
j
c
h

Subimago : black with uniformly grey wings.

Female Nymph : similar to male, lacking dorsal compound eyes, lateral eyes black.

Sexual Variation of Nymphs.

Table II.11 lists the morphometric characters which differed significantly between male and female nymphs of *A. inconspicua* from Deep Ck., near Ashton, Mt. Lofty Ranges. Of the 27 characters compared, eight differed at the 5% level of significance. Of these, six were thoracic or leg characters and two were mouthpart characters. The statistical parameters of non-significant characters are tabulated in Appendix 6.

Diagnostic Characteristics.

1. Genitalia; penes shape, broad, fused, with triangular ventral lobes (Fig. II.8c, d; 15a, b).
2. Lack of cross veins in proximal regions of C and Sc spaces of fore wings (Fig. II.8a).
3. Egg morphology, polar caps with two rows of tubular processes. (Fig. II.16a).
4. Nymphal gills lanceolate (Fig. II.9c).
5. Mandibles, incisors and prosthecae shape (Figs.II.9h-k).
6. Proximal segment of labial palp long and narrow (Fig. II.9g).
7. Dorsal white stripe on abdomen (Fig. II.14d).

TABLE II.11. Some morphometric characters of *Atalonella inconspicua* nymphs in which males differ from females. Data refers to a population of *A. inconspicua* from Deep Creek, Mt. Lofty Ranges, South Australia, and to last instar nymphs only. Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Character	Males $\bar{x}$	Males S.D.	Males Range	Females $\bar{x}$	Females S.D.	Females Range	d.f.	t	
MNW/HW	0.95	0.04	0.88-1.00	1.06	0.05	0.98-1.12	11	4.19	**
PNW/HW	0.90	0.03	0.86-0.94	1.03	0.04	0.99-1.09	11	7.29	***
FFL/HW	0.87	0.03	0.82-0.91	0.92	0.03	0.88-0.95	17	3.52	**
MFL/HW	0.86	0.06	0.80-0.94	0.92	0.03	0.88-0.96	15	2.56	*
HFL/HW	0.93	0.04	0.88-1.00	1.00	0.05	0.92-1.06	20	3.75	**
FT_aL/FFL	0.52	0.07	0.38-0.58	0.42	0.07	0.31-0.48	16	3.04	**
Labial paraglossae :									
PL/PW	1.00	0.05	0.94-1.06	0.94	0.07	0.82-1.00	20	2.60	*
Maxillary palpi :									
MBL/MBW	2.06	0.15	2.00-2.50	1.91	0.12	1.82-2.20	22	2.74	*

History and Discussion

Until this study this species had the distinction of being the first and only species described from South Australia. Eaton (1871) described and placed it in *Leptophlebia,* noting the black and white patterning of the abdomen. His illustration of the genitalia differs from the scanning electromicrograph (Figs.II.15a, b) as he showed separate penes lobes. This separation of the two lobes of the penes is observed with air dried specimens, and may occur with slide mounted material. Living, critical point dried, and alcohol preserved specimens possess genitalia with the two lobes held close together as illustrated in the micrograph. The type locality of this species is Adelaide, but the river or stream from which the holotype was collected is unknown. In 1884 Eaton placed *Atalonella inconspicua* in the new genus *Atalophlebia* where it has remained until the present study. Ulmer (1908) added to Eaton's description from material from the south-west of Western Australia. He included illustrations of male genitalia, both wet preserved in alcohol and dried, showing the separation of the paired penes lobes in the dried preparation. From the illustrations of the wings (the presence of cross veins in the proximal half of the C and Sc regions of the fore wing) and genitalia it is difficult to know if the species described by Ulmer is *A. inconspicua* or a different species. One of the two localities mentioned by Ulmer (Lion Mill and Brunswick) is still extant, but Lion Mill no longer exists, and no record of it exists in the south-west of Western Australia. Lyalls Mill, in the same region as Brunswick, may be the locality mentioned by

Ulmer, but as a mayfly habitat it now is extinct. Samples from Brunswick have been made available for this study, but no *Atalonella* specimens were present. Until specimens from this area are available some doubt must be placed on Ulmer's identification.

As mentioned in the History and Discussion section of the genus *Atalonella*, Tillyard (1936) recognised two groups within the genus *Atalophlebia*, and he included *A. inconspicua* in the group with the smaller species [i.e. "smaller species, expanding from one-half to three-quarters of an inch (fore wing from 5 to 8mm long)"]. Since this species is not recorded in Tasmania, no description was given, and in fact it is only referred to in the adult key. All the other species from the smaller sized group were later placed in the genus *Atalonella* by Harker (1954), but *A. inconspicua* was left in *Atalophlebia*.

The nymphs and adults of this species, as described above, have characteristics which distinguish them from the genus *Atalophlebia*, but are consistent with the generic characteristics of *Atalonella*. Consequently *A. inconspicua* is now formally placed in the genus *Atalonella*.

Variation of Character Expression

No record has been made of variation in character expression in this genus. Geographical variation was analysed for male imagos and nymphs (both male and female) by comparing morphometric character expression in representatives from two isolated populations, one from Spring Creek, Southern Flinders Ranges, and one from Deep Creek, Mt.

Lofty Ranges. Wing vein variation in the male imagos from these two populations was also compared, but not statistically.

In the forewings of male imagos from both populations the number of cross veins in the proximal half of the cubital and subcostal spaces was consistently zero, but in all other sectors the variation was wide (Table II.12), and of little taxonomic value. The morphometric characteristics analysed from both populations also expressed variation, but of the twenty characters analysed only three were statistically different and the statistical parameters are given in Table II.13.

The geographical variation expressed in the nymphs of *A. inconspicua* was greater than that found in the imagos, where ten of the twenty-seven characters compared were statistically different. With the exception of the paraglossae length/width ratio all others which were sexually variable were not geographically different when both male and female ratios were combined. The statistical parameters of the significant characters of the nymphs are listed with the three significant imago characters in Table II.13. The statistical parameters of the non-significant characters are listed in Appendix 7.

Material Examined. South Australia : Mt. Lofty Ranges; Aldgate Ck., Blackfellow Ck., Brownhill Ck., Bull Ck., Currency Ck., Deep Ck., Fifth Ck., Finnis R., Fourth Ck., Little Para R., Marne R., Morialta Ck., Onkaparinga R., Scott Ck., Sturt R., Torrens R. Southern Flinders Ranges; Back Ck., Nectar Brook Dam, Rocky R., Schumacher Ck., Skillogalee Ck., Spring Ck., Wakefield R. Fleurieu Peninsula; Anacotilla Ck., Carrickalinga Ck., Coolawang Ck., The Deep Creek (Delamere), Gold Digging Swamp,

TABLE II.12.

Variability of expression of the cross vein system in wings of *Atalonella inconspicua* from South Australia.

(n = 14)

Vein Sector	Left Wing Range	Right Wing Range
Fore wing :		
C/Sc basal half	0	0
C/Sc apical half	7 - 11	7 - 10
Sc/R_1 basal half	0	0
Sc/R_1 apical half	2 - 7	2 - 8
R_1/R_s	6 - 11	7 - 10
R_s system	21 - 30	21 - 31
R_{4+5}/MA	6 - 11	5 - 10
MA system	2 - 8	3 - 7
MA/MP	6 - 8	5 - 8
Hind wing :		
C/Sc	3 - 5	3 - 5
Sc/R_1	3 - 7	3 - 6
Anal	0	0

TABLE II.13. Geographical variation of morphological characters of *A. inconspicua* from Spring Creek, Southern Flinders Ranges and Deep Creek, Mt. Lofty Ranges, South Australia.

Abbreviations as for Tables II.1 and II.4. * $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

	Spring Creek			Deep Creek					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
Male Imagos :									
FWL/BL	0.92	0.09	0.75-1.05	1.12	0.14	0.93-1.36	14	3.55	**
HWL/BL	0.19	0.02	0.17-0.22	0.22	0.03	0.17-0.26	14	2.33	*
NL/BL	0.31	0.01	0.30-0.33	0.33	0.03	0.28-0.36	14	2.29	*
Nymphs :									
FFL/FFW	2.94	0.20	2.88-3.88	3.19	0.22	2.50-3.33	35	3.51	**
MFL/MFW	2.91	0.19	2.83-3.57	3.16	0.18	2.43-3.20	35	4.26	***
HFL/HFW	3.11	0.24	2.80-3.81	3.36	0.21	2.61-3.52	35	3.31	***
HT_iL/HFL	1.01	0.03	0.91-1.03	0.97	0.03	0.96-1.06	33	3.93	***
HT_aL/HFL	0.35	0.02	0.31-0.40	0.36	0.03	0.32-0.39	32	2.09	*
Labial palpi :									
ML/BL	0.85	0.07	0.61-0.93	0.79	0.05	0.72-1.00	43	3.25	**
Paraglossae L/W	0.91	0.03	0.85-0.94	0.97	0.06	0.82-1.06	34	3.34	**
Maxillary palpi :									
MAL/MBL	0.73	0.06	0.64-1.00	0.79	0.09	0.64-0.89	40	2.82	**

Hindmarsh R., Kangarilla Ck., Myponga Ck., Yankalilla R.

Kangaroo Island; Breakneck R., Cygnet R., De Mole R., Grassy/Sheep Ck., Middle R., North East R., Rocky R., South West Bay R., South West R., Stunsail Boom R.

II.4.2.2 *Atalonella fuscula* (Tillyard) 1936

Atalophlebia fuscula	Tillyard, 1936 : 44-47
Atalophlebia fuscula	Harker, 1950a : 28
Atalonella fuscula	Harker, 1954 : 242-243, 264
	Scholes, 1961 : 31-33

Male Imago.

	$\bar{x}$	SD	n	Range
Body Length	6.58	0.32	23	5.82 - 7.01
Notal Length	2.02	0.11	21	1.84 - 2.20
Pronotal Width	0.87	0.06	10	0.74 - 0.92
Mesonotal Width	1.02	0.09	20	0.82 - 1.12
Fore Wing Length	6.41	0.28	22	5.90 - 6.97
Hind Wing Length	1.29	0.09	23	1.12 - 1.40
Cerci Length	10.32	0.62	12	9.23 - 11.11
Appendix Dorsalis Length	11.67	0.76	8	10.77 - 13.00

General colour black with lighter markings.

Head : black. Dorsal compound eyes raised, rounded, brown/grey, lateral eyes grey. Ocelli white. Antennae short, less than 1mm long.

Thorax : black. Pronotum dark brown, with a narrow median longitudinal white line. Mesonotum black, scutoscutellum edged with brown, with three longitudinal grooves, two small white patches antero-laterally. Legs; fore legs long, black without banding, T_1 partially fused to tibia. Middle and hind legs similar, shorter than fore legs, brown without banding, T_1 fused to tibiae, join difficult to distinguish, therefore segment ratio of tibia length to femur length is tibia + T_1 length to femur length.

Ratios of leg segments;

fore leg 1.00 : 1.29 : 0.14 : 0.49 : 0.44 : 0.28 : 0.16 (1.64mm)

middle leg 1.00 : 1.15 : - : 0.11 : 0.09 : 0.09 : 0.15 (1.38mm)

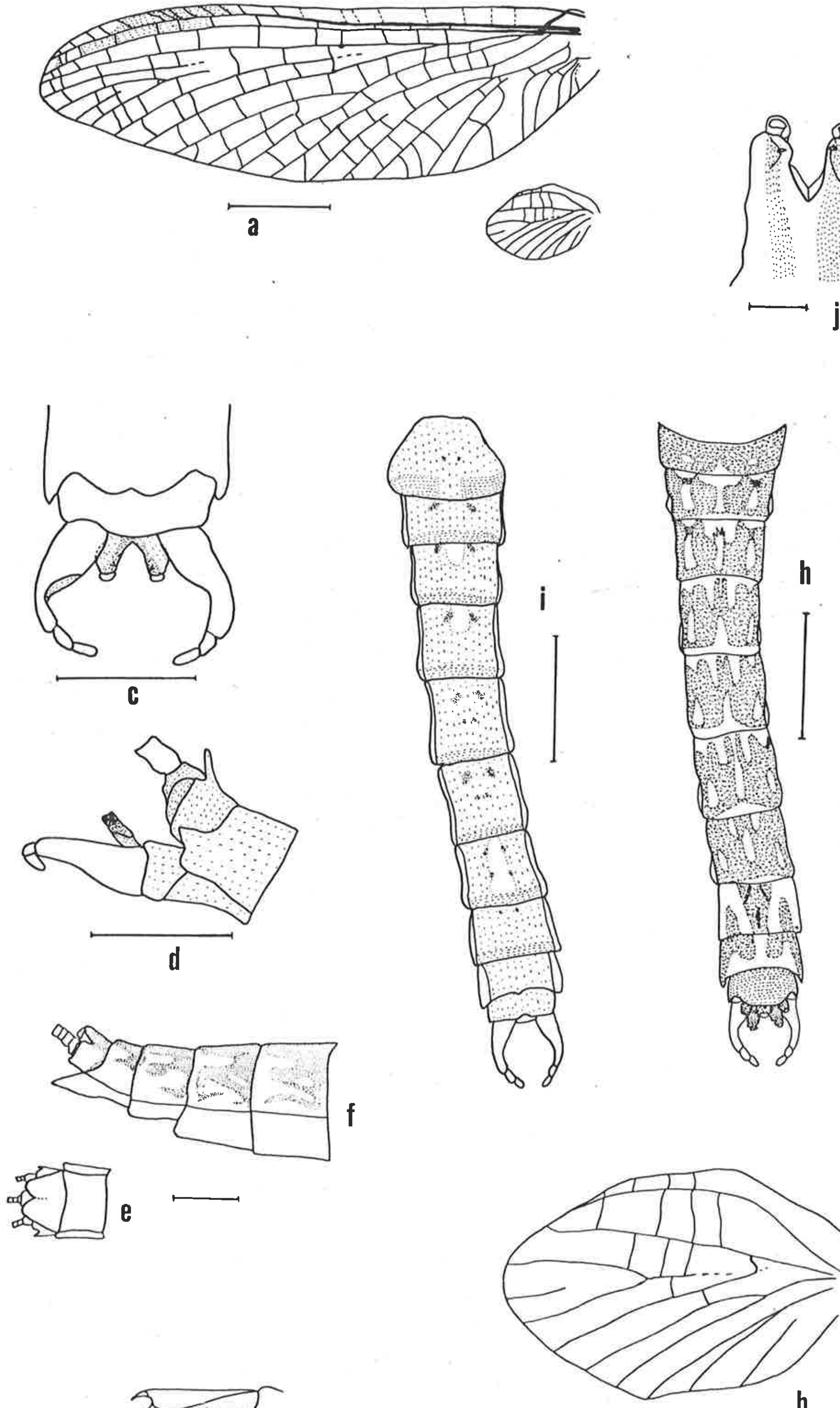
hind leg 1.00 : 1.20 : - : 0.09 : 0.08 : 0.09 : 0.15 (1.58mm).

Fore leg femur length 1.19 x middle leg femur length, and 1.04 x hind leg femur length. Sternum dark brown. Prosternum triangular, truncated anteriorly, longitudinal carinae separate. Mesosternum; basisternum length 1.09 x width, 0.97 x furcasternum length, furcasternum length 0.55 x width, lateral margins of longitudinal invagination parallel, posterior margin slightly concave.

Wings : hyaline with dark brown venation. Fore wing (Fig. II.10a) 3.13 x longer than wide, pterostigmal region slightly tinged with brown, cross veins slanted, simple, costal space proximal to bulla with 3-7 very faint cross veins, subcostal space with 2-4 cross veins in proximal half, 7-10 in distal half. Variation in the cross vein system is tabulated in Table II.14. Four bullae present, one in each of Sc, R_2, $R_{4 \& 5}$ and MP.

Fig. II.10. *Atalonella fuscula*. a - d, male imago: a, fore wing; b, hind wing; c, genitalia, ventral view; d, genitalia, lateral view. e - f, female imago: e, ventral view of abdominal segment 10; f, abdominal segments 6 - 10, lateral view. g - j, male imago: g, fore claws; h, dorsal abdominal colour pattern; i, ventral abdominal colour pattern; j, penes enlarged, ventral view.

Scale lines : a,h,i 1mm.
b,c,d,e,f 0.5mm.
j 0.1mm.
g 0.05mm.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j
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TABLE II.14.

Variation of cross vein expression in the wings of *Atalonella fuscula* from South Australia.

(n = 7).

Vein Sector	Left Wing Range	Right Wing Range
Fore wing :		
C/Sc basal half	4 - 7	3 - 6
C/Sc apical half	9 - 14	10 - 15
Sc/R_1 basal half	2 - 4	2 - 3
Sc/R_1 apical half	7 - 11	7 - 10
R_1/R_s	8 - 10	8 - 11
R_s system	22 - 30	23 - 29
R_{4+5}/MA	7 - 10	8 - 10
MA system	5 - 7	4 - 7
MA/MP	7 - 8	8 - 9
Hind wing :		
C/Sc	3 - 4	3 - 4
Sc/R_1	4 - 5	5 - 6
Anal	0	0

Hind wing (Fig. II.10b) 1.52 x longer than wide, Sc joins C at 3/4 of wing length, costal hump small, 3-4 cross veins in distal region of costal space, absent in proximal half, subcostal space with 4-6 cross veins, three obvious, rest faint. Rs joins MA in proximal half of wing, MA straight, MP branches in proximal third of wing, cross veins absent in median, cubital and anal regions.

Abdomen : black, with brown and light brown markings (Fig. II.10h), segments 8, 9 light brown, segment 10 black; ventral pattern of black spots on segments 1-7 (Fig. II.10i). Cerci long, appendix dorsalis longer.

Genitalia : (Figs. II.10c, d); forceps three segmented, proximal segment broad at base, narrows half way along length, second segment square, distal segment oval, globular. Penes lobes widely separated, cylindrical, constricted near apex, apex rounded, lobes apparently sheathed, inner margin with a small spine hidden within sheath, visible in mounted preparations examined using transmitted light (Fig. II.10j), but not in the Scanning Electron Micrographs (Figs. II.15c, d).

Mature Male Nymph (Fig. II.14e).

	$\bar{x}$	SD	n	Range
Head Width	1.44	0.06	6	1.36 - 1.50
Notal Length	1.71	0.07	4	1.64 - 1.80
Pronotal Width	1.28	0.04	4	1.22 - 1.32
Mesonotal Width	1.33	0.06	4	1.26 - 1.40

Cerci and appendix dorsalis damaged in available specimens.

Head : dark brown, with white epicranial sutures and a diamond shaped marking in centre of frons. Dorsal compound eyes reddish brown, lateral eyes black. Ocelli black. Antennae longer than head width. Tentorial body square.

Thorax : pronotum width 0.91 x head width, brown with central and anterior light patches, spine setae on antero-lateral margins. Mesonotum width 0.94 x head width, brown with black wing sheaths extending posteriorly to fourth abdominal segment. Legs brown, not banded (Fig. II.11a), margins of segments lined with long setae. Tarsal claws with 12-16 peg-like teeth (Fig. II.11.b). Ratios of leg segments;

fore leg	1.00 : 0.87 : 0.55	(1.18mm)
middle leg	1.00 : 0.84 : 0.39	(1.19mm)
hind leg	1.00 : 0.91 : 0.38	(1.40mm).

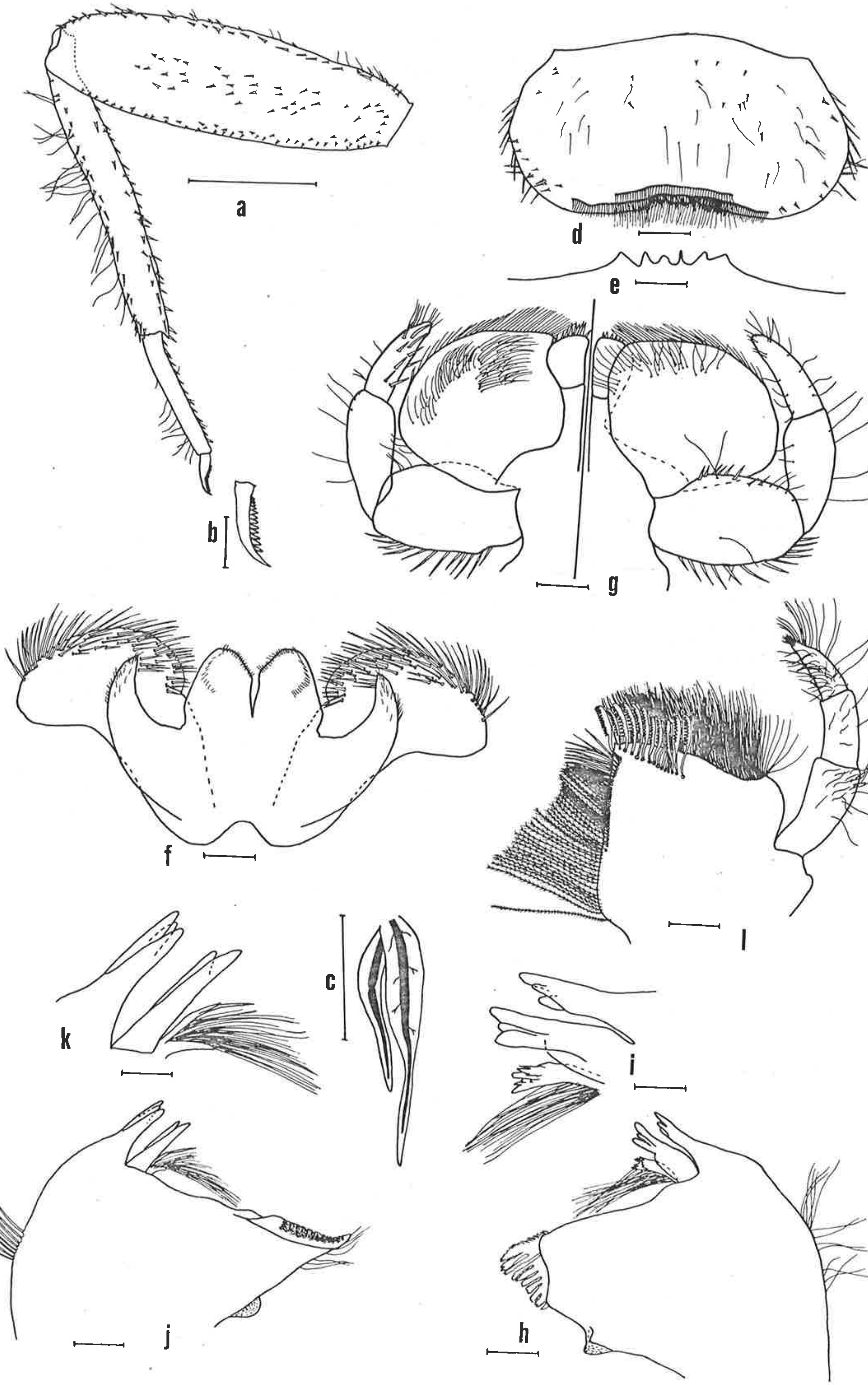
Femur length to width ratios; fore leg 2.74, middle leg 2.82, hind leg 3.11. Sternum; prosternum triangular, apex truncated, posterior width less than width of mesobasisternum. Mesosternum; basisternum narrower than furcasternum, but equal in length. Metasternum; basisternum narrower than mesofurcasternum, very short.

Abdomen : black with mid longitudinal row of light markings, light brown laterally, colour pattern irregular, segment 10 predominantly white with brown posterior margin (Fig. II.14e). Segments 6-9 with small backward pointing spines on posterior lateral margins. Spines on posterior margins of terga occur either separately or in pairs. Gills (Fig. II.11c); linear with single terminal tracheal filament, lamellae lacking tracheal branches, or, if present, very short, gill size increases from 1-3, decreases from 5-7, gills, 3, 4, 5 equal. Cerci well developed, appendix dorsalis longer.

Mouthparts : labrum (Fig. II.11d); 2 x wider than long; lateral margins rounded, lined with spine setae, anterior margin with median cavity with 4-6 rounded denticles (Fig. II.11e), one row of short setae along anterior margin and one row of long setae directly behind median cavity. Left mandible (Fig. II.11h); incisors large and separate, outer incisors with three apical teeth, inner insicors with three teeth, prostheca broad and robust, outer and apical margin serrated with numerous spines (Fig. II.11i), molar region with ten rows of transverse ridges. Right mandible (Fig. II.11j); outer incisors with three apical teeth, inner incisors with two teeth, prostheca simple, long and narrow with one long apical spine (Fig. II.11k), molar region of grinding ridges. Hypopharynx (Fig. II.11f); median lobe deeply divided with large lateral processes, lined with short fine setae, paragnaths large, lined with spine setae. Maxillae (Fig. II.11*l*); galeo-lacinia broad, rectangular, with a brush of setae apically, ventral row of 14 rake setae, and a rake spine on inner anterior margin, rake setae also throughout apical brush, inner margin lined with long pinnate setae; palpi three segmented, proximal segment 2.11 x longer than wide, lined distally with long fine setae. Segment ratio 1.00 : 0.71 : 0.78 (0.21mm); distal segment with long fine setal cover, apex with short fine setae. Labium (Fig. II.11g); with three segmented palpi, proximal segment 1.57 x longer than broad, lined with spine setae, second segment narrower, lined with fine setae, distal segment narrowest, with spine setae on

Fig. II.11. *Atalonella fuscula*, mature nymph: a, fore leg; b, fore claw; c, third abdominal gill; d, labrum, dorsal view; e, antero-median emargination of labrum, enlarged; f, hypopharynx; g, labium, dorsal (left) and ventral views; h, left mandible, ventral view; i, left incisors and prostheca, enlarged; j, right mandible, ventral view; k, right incisors and prostheca, enlarged; l, left maxilla, ventral view.

Scale lines :	a,c	0.5mm.
	b,d,f,g,h,j,l	0.1mm.
	e,i,k	0.05mm.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dorsal edge, segment ratios : 1.00 : 0.71 : 0.69 (0.29mm); glossae small, lined apically with short spine setae, paraglossae broad lined with fine setae, dorsal half with long fine setal cover.

Female Imago : more robust than male, fore legs shorter, wings similar, hind wings with more cross veins in radial, median and cubital sectors, sternum and thorax broader. Anal plate with a deep V shaped incision (Fig. II.10e), no egg guide or ovipositor (Fig. II.10f). Eggs oval 0.12mm x 0.09mm, polar caps with three rings of tubular processes (Fig. II.16b).

Subimago : dull black, wings opaque, dark grey.

Female Nymph : similar to male, lacks dorsal compound eyes, lateral eyes black.

Sexual Variation of Nymphs.

The morphometric characters of the female nymphs which differed significantly from the males are listed in Table II.15. *A. fuscula* nymphs differed sexually mainly in leg characteristics with all femora to head widths, fore tarsus length/femur length and middle tarsus length/femur length characters, but the thoracic or mouthpart characteristics were not significantly different. The statistical parameters of non-significant characters are tabulated in Appendix 8.

Diagnostic Characteristics.

1. Male genitalia, lateral lobes of penes widely separate, small spine on mesal margin of lobes (Fig II.10c, d; 15c, d).

TABLE II.15. Morphological characters of *A. fuscula* nymphs in which males differ from females.

Data refers to last instar nymphs from Tookayerta Creek, Fleurieu Peninsula, South Australia. Abbreviations as for Tables II.1 and II.4. * $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

	Males			Females					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
MNW/NW	0.93	0.02	0.93-1.19	1.01	0.09	0.90-0.97	12	2.37	*
FFL/HW	0.81	0.02	0.79-0.85	0.87	0.04	0.82-0.91	16	4.96	***
MFL/HW	0.83	0.02	0.79-0.84	0.90	0.04	0.86-0.95	18	6.24	***
HFL/HW	0.96	0.02	0.93-0.99	1.07	0.05	1.01-1.13	14	6.28	***
FT_iL/FFL	0.87	0.04	0.80-0.91	0.90	0.02	0.89-0.93	16	2.28	*
FT_aL/FFL	0.55	0.01	0.52-0.57	0.48	0.01	0.47-0.49	16	11.97	***
MT_iL/MFL	0.84	0.02	0.81-0.87	0.86	0.02	0.84-0.90	18	2.56	*
Maxillary palpi :									
MAL/MBL	0.79	0.08	0.73-0.90	0.67	0.07	0.54-0.75	15	3.27	**

2. Cross veins in proximal region of costal and subcostal spaces (Fig. II.10a).

3. Egg polar cap with three coronae of tubular processes (Fig. II.16b).

4. Nymphs have linear gills with few tracheal branches on lamella (Fig. II.11c).

5. Mandibles, shape of incisors and prosthecae (Figs. II.11h-k).

6. Proximal segment of labial palpi broad (Fig. II.11g).

7. Abdominal colour pattern irregular (Fig. II.14e).

History and Discussion

Tillyard (1936) described the adults (male and female), subimago and nymph of *A. fuscula* placing it in his distinct group of species of the genus *Atalophlebia*. Harker (1954) recognised that all the species Tillyard placed in this second group of small sized species belonged in the genus *Atalonella*, and *A. fuscula* was included in this new combination.

The male genitalia is very distinctive in *A. fuscula*, with a small spine on the mesal margins of the penes lobes, but the associated nymph in South Australia differs from the description and illustration given by Tillyard (1936). The gill illustrated by Tillyard shows a more lanceolate lamella with numerous tracheal branches, both shape and tracheation are inconsistent with the associated nymphs from South Australia. Nymphs of Tillyard's description were not found at Tookayerta Creek (the only locality where *A. fuscula* is present on the

Fleurieu Peninsula), but one of a similar description to his was recorded from Deep Creek, east of Port Macdonnel in the south-east of South Australia. At the time of this record *A. fuscula* male and female imagos were flying. Similar nymphs from the Grampians, Victoria, were bred through and *A. pilosa* sp. nov. was the associated adult. Field observations suggest that *A. fuscula* emerges before *A. pilosa*, therefore leaving *A. pilosa* nymphs in the stream. This results in the latter species being the dominant nymph in stream collections, rather than the nymphs of the flying *A. fuscula*. *A. pilosa* then emerges later. This observation was repeated in the south-east of South Australia, the Grampians, Victoria, and in Tasmania. The nymphs of *A. fuscula* from Tasmania (collected in February 1978 and associated with adults) were similar to those in South Australia. From these observations it appears that Tillyard indirectly associated the nymph in the stream with the flying adults and emerged subimagos, rather than by breeding through the nymphs and directly associating these with the resulting adults.

Variation of Character Expression

Only qualitative characteristics were assessed for variability and value in the species designation of *A. fuscula*. Of these, the diagnostic characteristics listed above were found to be consistently expressed throughout the known distribution of this species. The abdominal colour pattern of the nymphs is variable within any one population, but the lack of a distinct pattern is consistent.

Material Examined. South Australia : South East; Cress Ck., Deep Ck., Eight Mile Ck. Fleurieu Peninsula; Tookayerta Ck. Victoria : Aire R., Albert R., Beehive Ck., Crawford R., Cumberland Falls (Marysville), Darlots Ck., Genoa Ck., Howqua R., Jimmy's Ck., Little R., McKenzie R., Mt. Zero Channel, Stony Ck. (Halls Gap), Tanjil R., Tarwin R., Toorongo Falls (Noojee). New South Wales : Leatherbarrel Ck., Styx R., Wallagaraugh R. Tasmania : Break O'Day R., Dee R., George R., Great Forester R., Isis R., Macquarie R., Rostrevor Ck.

II.4.2.3 *Atalonella pilosa* sp. nov.

Holotype Male

Body Length	7.50mm
Notal Length	1.90mm
Pronotal Width	0.93mm
Mesonotal Width	1.17mm
Fore Wing Length	7.67mm
Hind Wing Length	1.23mm
Cerci Length	9.50mm
Appendix Dorsalis Length	12.00mm

Head : black brown, with a light brown marking mid dorsally. Dorsal compound eyes large, pink/brown, lateral eyes grey. Ocelli white.

Thorax : pronotum black, narrower than head. Mesonotum black without distinct markings. Legs; fore leg long, without banding, femur dark brown, tibia and tarsi light brown, T_1 partially fused to tibia; middle and hind legs with dark brown femora each with one black band at 3/4 of length, tibiae and tarsi light brown, T_1 fused to tibia.

Ratios of leg segments;

fore leg 1.00 : 1.52 : 0.08 : 0.48 : 0.51 : 0.38 : 0.15 (1.92mm)

middle leg 1.00 : 1.22 : - : 0.07 : 0.07 : 0.07 : 0.11 (1.62mm)

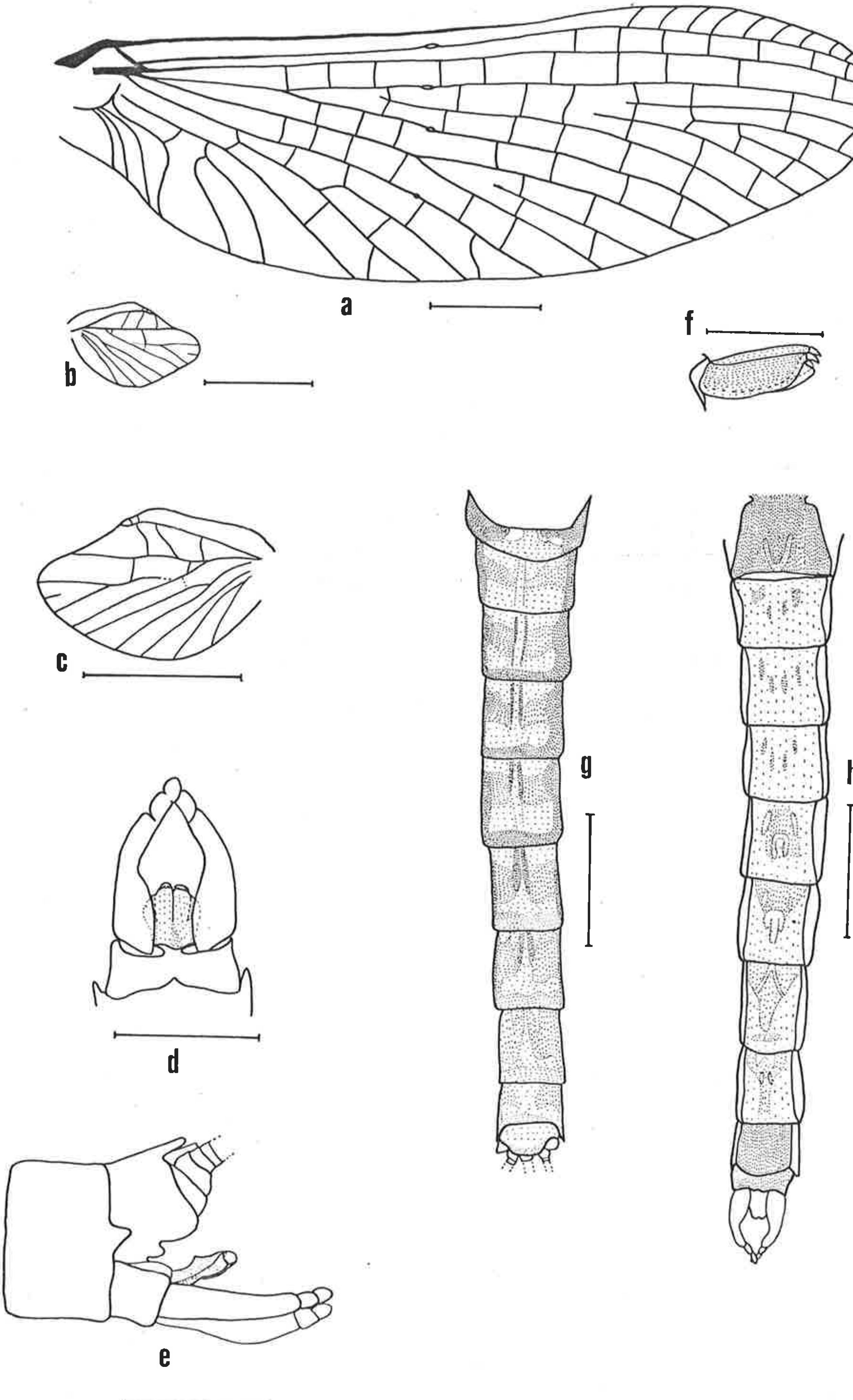
hind leg 1.00 : 1.35 : - : 0.09 : 0.08 : 0.07 : 0.13 (1.67mm).

Tarsal claws paired, similar, each long and slender, terminally hooked (Fig. II.12f). Sternum; prosternum, longitudinal carinae separate. Mesosternum; basisternum 1.3 x longer than wide, but equal to furcasternum length, furcasternum; lateral margins of median longitudinal invagination divergent, posterior margin concave.

Wings : hyaline, veins brown. Fore wing (Fig. II.12a), 3.3 x longer than wide, pterostigmal region with simple, slanted cross veins, proximal 2/3 of costal space without cross veins, subcostal space without proximal cross veins, distal region with seven. Four bullae present, one in each of Sc, R_2, $R_{4\&5}$ and MP. Hind wing (Figs. II.12b, c) 1.52 x longer than wide, Sc joins C at 3/4 of wing length, costal hump large, without cross veins proximally, with two distal cross veins, subcostal space with three cross veins, Rs joins MA and R_1 in proximal half of

Fig. II.12. *Atalonella pilosa*. a - h, male imago: a, fore wing; b, hind wing; c, left hind wing, enlarged; d, genitalia, ventral view; e, genitalia, lateral view; f, fore claws; g, dorsal abdominal colour pattern; h, ventral abdominal colour pattern.

Scale lines : a,b,g,h 1mm.
c - e 0.5mm.
f 0.1mm.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wing, MA straight, MP forked in proximal half of wing, cross veins absent in median, cubital and anal sectors.

Abdomen : dark brown with mid dorsal light brown regions on segments 2-7, on segments 3-6 light brown region edged laterally with paired longitudinal black stripes, segments 8-10 dark brown (Fig. II.12g); ventrally light brown with irregular patterning (Fig. II.12h). Cerci long, appendix dorsalis longer than cerci, base of each segment of caudal filaments tinged with brown, giving a banded appearance.

Genitalia : (Figs. II.12d, e) forceps three segmented, proximal segment long, broad at base, constricted half way along length, second segment short ovoid, distal segment globular. Penes paired, fused, extending to constriction of proximal segment of forceps, apex with two lobes, ventral surface lacking lobes (Fig. II.12d; 15e, f).

Mature Male Nymph (Fig. II.14f).

Head Width	1.20mm
Notal Length	2.30mm
Pronotal Width	1.09mm
Mesonotal Width	1.31mm

Head : light brown, with a dark brown band across the ocelli, and a light marking in the centre of the frons. Dorsal compound eyes red/brown, lateral eye black, ocelli large, black with grey centres. Antennae damaged, but longer than head width. Tentorial body square.

Thorax : pronotum width 0.91 x head width, brown with lateral black crescents, lateral flanges translucent, few spine setae present on antero-lateral margin. Mesonotum brown with black wing sheaths extending posteriorly to fourth abdominal segment; mesonotal width 1.09 x head width. Legs light brown, without banding, margins of segments lined with long fine setae (Fig. II.13a); tibiae lined ventrally with pinnate setae, femora lined laterally with spine setae, and blunt peg-like setae, and basally with pinnate setae. Tarsal claws with 12 peg like teeth, long curved terminal tooth (Fig. II.13b). Ratios of leg segments;

fore leg 1.00 : 0.96 : 0.40 (1.70mm)
middle leg 1.00 : 0.95 : 0.31 (1.77mm)
hind leg 1.00 : 1.01 : 0.29 (1.93mm).

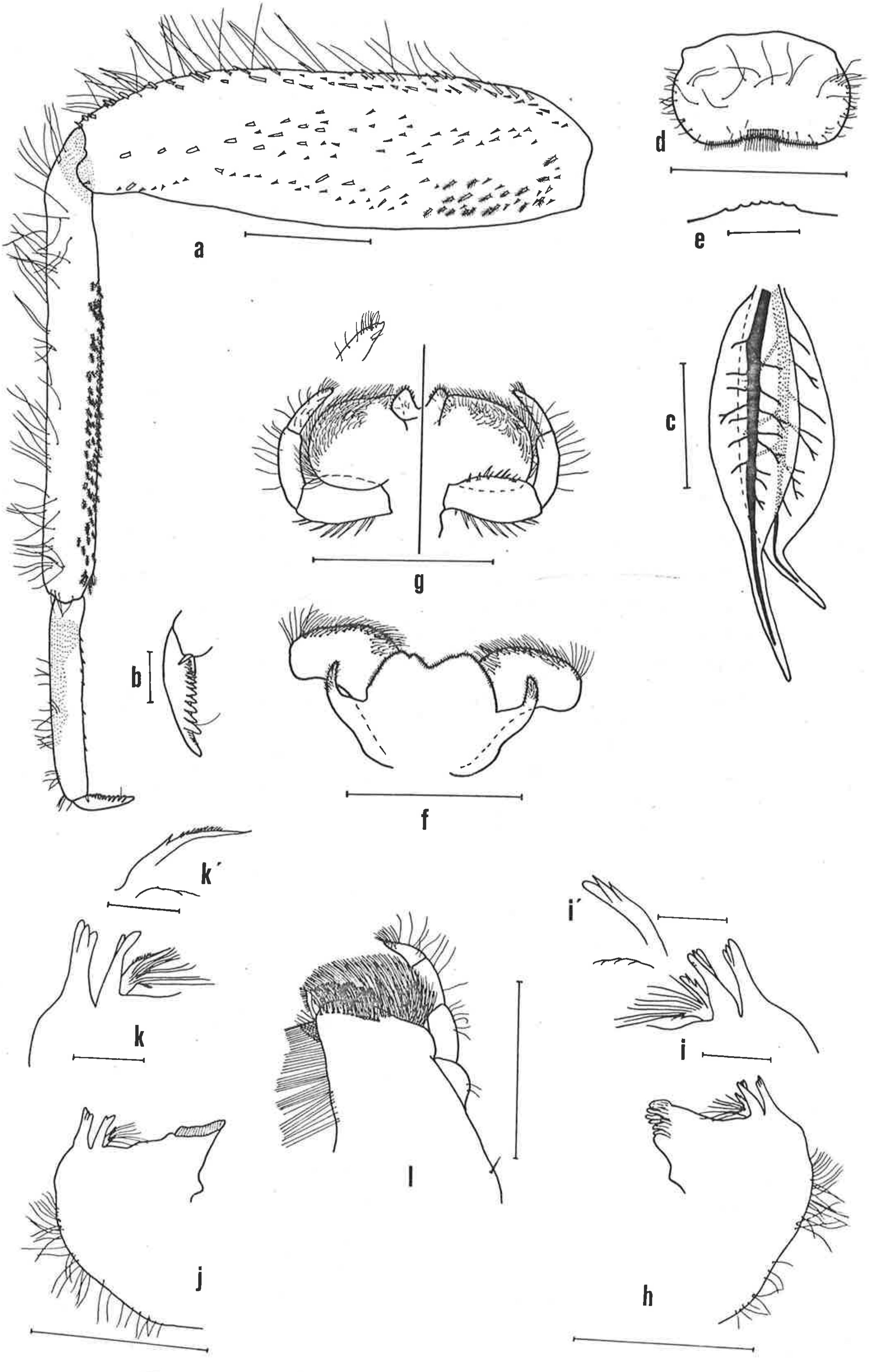
Femur length to width ratios; fore leg 3.13, middle leg 3.39, hind leg 3.70. Sternum; prosternum triangular, apex truncated, posterior width narrower than mesobasisternum. Mesosternum; basisternum width equal to furcasternum width, length of basisternum equal to furcasternum length, metasternum broader than mesofurcasternum, and very short.

Abdomen : dark brown with light central markings edged with darker brown markings on segments 3-5, dark brown/black markings laterally on segments 6-9, segment ten brown with a central light marking (Fig. II.14f). Segments 6-9 with small backward pointing spines on posterior lateral margins. Spines on posterior margin of terga large and singular with smaller basal single spines. Gills (Fig. II.13c) lanceolate with single terminal tracheal filament, lamellae with tracheal branches obvious, gill size increases from 1 - 3, decreases from 5 - 7, with gills 3, 4, 5 equal. Cerci and appendix dorsalis present, but damaged.

Mouthparts : labrum (Fig. II.13d) 1.5 × wider than long; lateral margins rounded, lined with spine setae, anterior margins with a median cavity with six rounded denticles (Fig. II.13e), one row of short setae along anterior margin and one row of longer setae directly behind median cavity. Left mandible (Fig. II.13h); incisors large and separate, outer incisors with three apical teeth, inner incisors with three apical teeth and two ridges on inner margin, prostheca broad basally, long and slender distally with three terminal teeth (Fig. II.13i), molar region with 10 - 12 rows of transverse ridges, lateral margins lined with long setae. Right mandible (Fig. II.13j); outer incisors with three apical teeth, inner incisors with two teeth; prostheca slender, elongate with a long terminal spine (Fig. II.13k), molar region with 9 - 10 parallel grinding ridges, outer margin lined with long setae. Hypopharynx (Fig. II.13f); median lobes slightly indented, lined apically with very short setae, paragnaths large, lined with long spine setae. Maxillae (Fig. II.13*l*); galeo-lacinia rectangular with an apical brush of setae, ventral row of rake setae, and a rake spine on inner anterior margin, rake setae also throughout apical brush; inner lateral margins lined with long pinnate setae; palpi three segmented, proximal segment 1.79 x longer than wide, lined with long fine setae. Segment ratio 1.00 : 0.68 : 0.68 (0.27mm);

Fig. II.13. *Atalonella pilosa*, mature nymph: a, fore leg; b, fore claw; c, third abdominal gill; d, labrum, dorsal view; e, antero-median emargination of labrum, enlarged; f, hypopharynx; g, labium, dorsal (left) and ventral views; h, left mandible, ventral view; i, left incisors and prostheca, enlarged; i', left prostheca, enlarged; j, right mandible, ventral view; k, left incisors and prostheca, enlarged; k', left prostheca, enlarged; l, left maxilla, ventral view.

Scale lines :	a,c,d,f,g,h,j,l	0.5mm.
	b,e,i,k	0.1mm.
	i',k'	0.05mm.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distal segment with long fine setal cover. Labium (Fig. II.13g); with three segmented palpi, proximal segment 2.26 x longer than broad, proximally with spine setae, margins with spine setae, second segment narrow, with few long fine setae, distal segment long and narrow, with short setal cover; apex with four short teeth, segment ratios; 1.00 : 0.77 : 0.49 (0.44mm); glossae small, lined apically with short spine setae, paraglossae broad lined with fine setae, dorsal and ventral surface with dense setal cover.

Female Imago : unknown, and therefore no comparison of egg morphology was performed.

Female Nymph : similar to male, lacks dorsal compound eyes, lateral eyes black. Body larger, and more robust than male.

Sexual Variation of Nymphs.

Very few specimens of this species were collected from South Australia, and from the Grampians, and therefore no comparison of variation of nymphs has been performed.

Diagnostic Characteristics.

1. Genitalia of male imago (Figs. II.12d, e; 15e, f).

2. Gills of nymphs lanceolate, similar to *A. inconspicua* (Fig. II.13c).

3. Labrum long (width 1.5 x greater than length) (Fig. II.13d).

4. Prostheca shape of left and right mandibles (Figs. II.13i, k).

5. Legs lined with numerous long fine setae (Fig. II.13a).

Type Locality.

Type material was collected from Second Wannon River on the road from Halls Gap to Dunkeld, Grampian Mountains, Victoria. Grid Reference on 1:250,000 map series Ballarat Sheet 547396. Collected 25th November 1977 by D. N. and P. J. Suter.

Type Specimens.

Holotype male, and nymphal exuvium are placed in the National Museum of Victoria. The wings and legs of the holotype are mounted on slides, and the body and genitalia are maintained in ethanol. The nymphal exuvium is mounted on slides. Three paratype males, two mature males and three mature female nymphs are included in the type series. Slides of a nymph, and adult male imago from Hitchcock Drain, south-east South Australia, are also included.

Type Habitat.

The Second Wannon River in the Grampians Mountains, is a moderately fast flowing stream over cobble sized rocks. A "kick sample" technique was used to collect nymphs, and therefore there is no certainty of the habitat being occupied by this species. Nymphs were collected with *A fuscula*, and therefore it is assumed that the habitat is similar to that of *A. fuscula*.

Etymology of Specific Epithet.

The specific epithet *pilosa* (L) for hairy, refers to the long, fine setae which line the margins of the legs distinguishing this species from *A. inconspicua* and *A. fuscula*.

Affinities.

In the adult characters *A. pilosa* resembles closely *A. inconspicua,* with the penes fused, and lacking spination. *A. fuscula* is distinctly different with V-shaped penes, and internal spines. Although superficially similar, the penes of *A. inconspicua* and *A. pilosa* are distinct, with *A. inconspicua* with obvious ventral lobes, and separated basal halves of the penes (Figs. II.15a, b). *A. pilosa* lacks the ventral loves, and the penes are fused along their entire length.

In nymphal characters, *A. pilosa* resembles *A. inconspicua,* possessing lanceolate gills, but lacks the obvious dorsal white stripe on the abdomen, characteristic of *A. inconspicua.* The mouthpart structre, especially the labrum (Fig. II.13d) and prosthecal structure (Figs. II.13i, k), and the fine setae on the legs, clearly distinguish *A. pilosa* from both *A. inconspicua* and *A. fuscula*.

History and Discussion.

As mentioned in the History and Discussion section of *A. fuscula* the description of *A. fuscula* nymphs given by Tillyard (1936) is similar to that of *A. pilosa*. The associated nymph of *A. fuscula* was found to differ from the description given by Tillyard. Collections in Tasmania, Victoria and South Australia showed that *A. fuscula* and *A. pilosa* co-existed, and that adult imagos, swarming above the streams, were not associated with the nymphs collected from the streams. *A. fuscula* and *A. pilosa* appear ecologically separated by the timing of maturation and the imago mating flights. It is, therefore, possible that Tillyard indirectly associated the nymphs and adults collected from the River Shannon, Tasmania. Consequently it appears that the nymph of *A. pilosa* was indirectly ascribed to *A. fuscula*. The present descriptions are based on associated material, and distinguishes the nymphs of these two co-occurring species.

Discussion of Taxonomic Characters.

An assessment of useful taxonomic characters was made for the three *Atalonella* species found in South Australia. *Atalonella pilosa* was not available in sufficient numbers from any one locality to allow quantitative comparisons between two distinct populations, but qualitative characteristics were evaluated for consistency of expression in all three species. Table II.16 lists all the useful qualitative characteristics which were consistently expressed in the specimens examined in the present study, and the characteristics of each species

Fig. II.14. Dorsal colour patterns of *Atalophlebia* and *Atalonella* mature nymphs. a, *Atalophlebia australis*; b, *Atalophlebia australasica*; c, *Atalophlebia auratus*; d, *Atalonella inconspicua*; e, *Atalonella fuscula*; f, *Atalonella pilosa*.

Scale lines : 1mm.

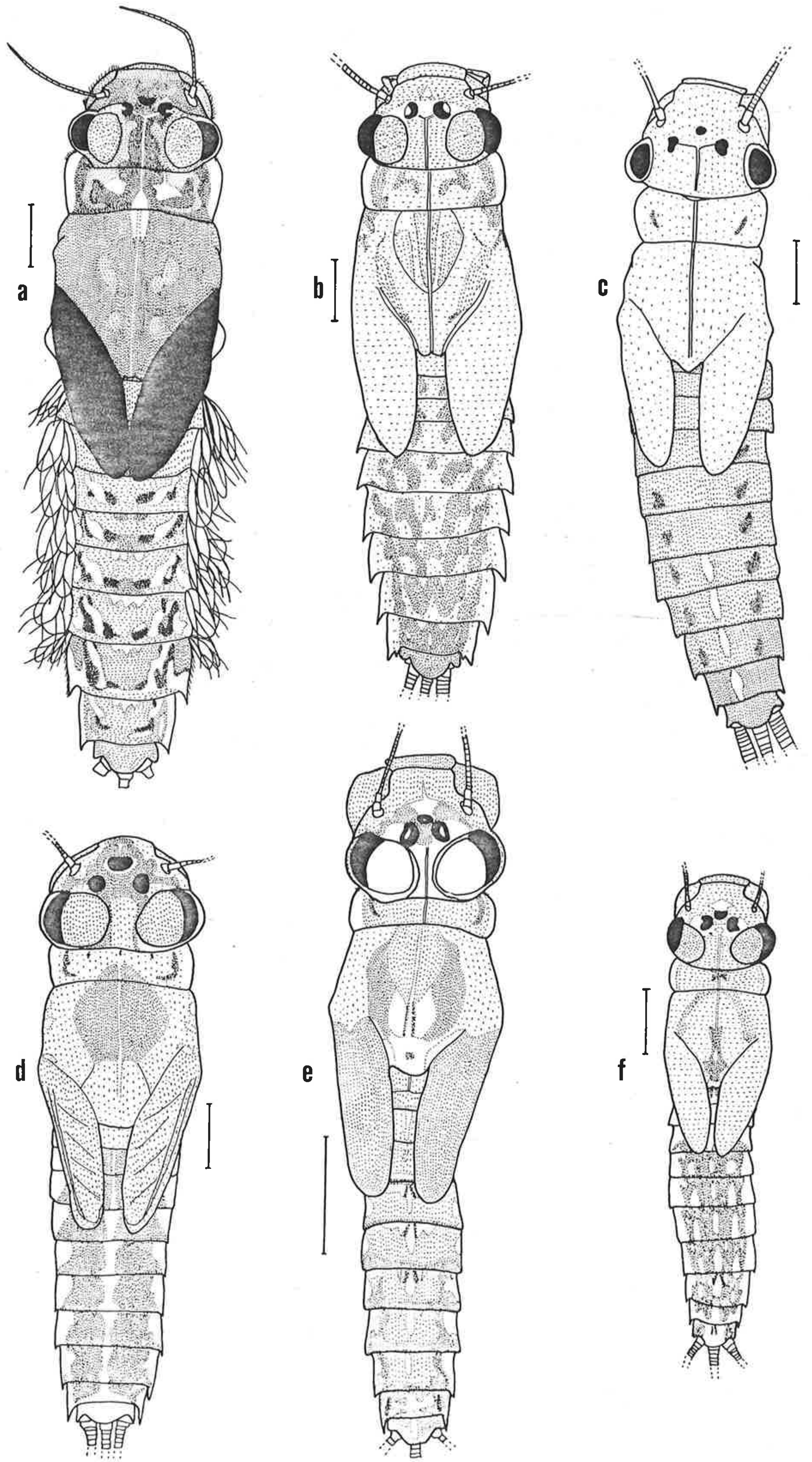
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Fig. II.15. SEM micrographs of genitalia of *Atalonella* male imagos. a - b, *Atalonella inconspicua*: a, genitalia, ventral view; b, penes, ventral view, enlarged. c - d, *Atalonella fuscula*: c, genitalia, ventral view; d, penes, ventral view, enlarged. e - f, *Atalonella pilosa*: e, penes, ventral view, enlarged; f, genitalia, ventral view.

Scale lines : a,c,f 100μm.
b,d,e 10μm.

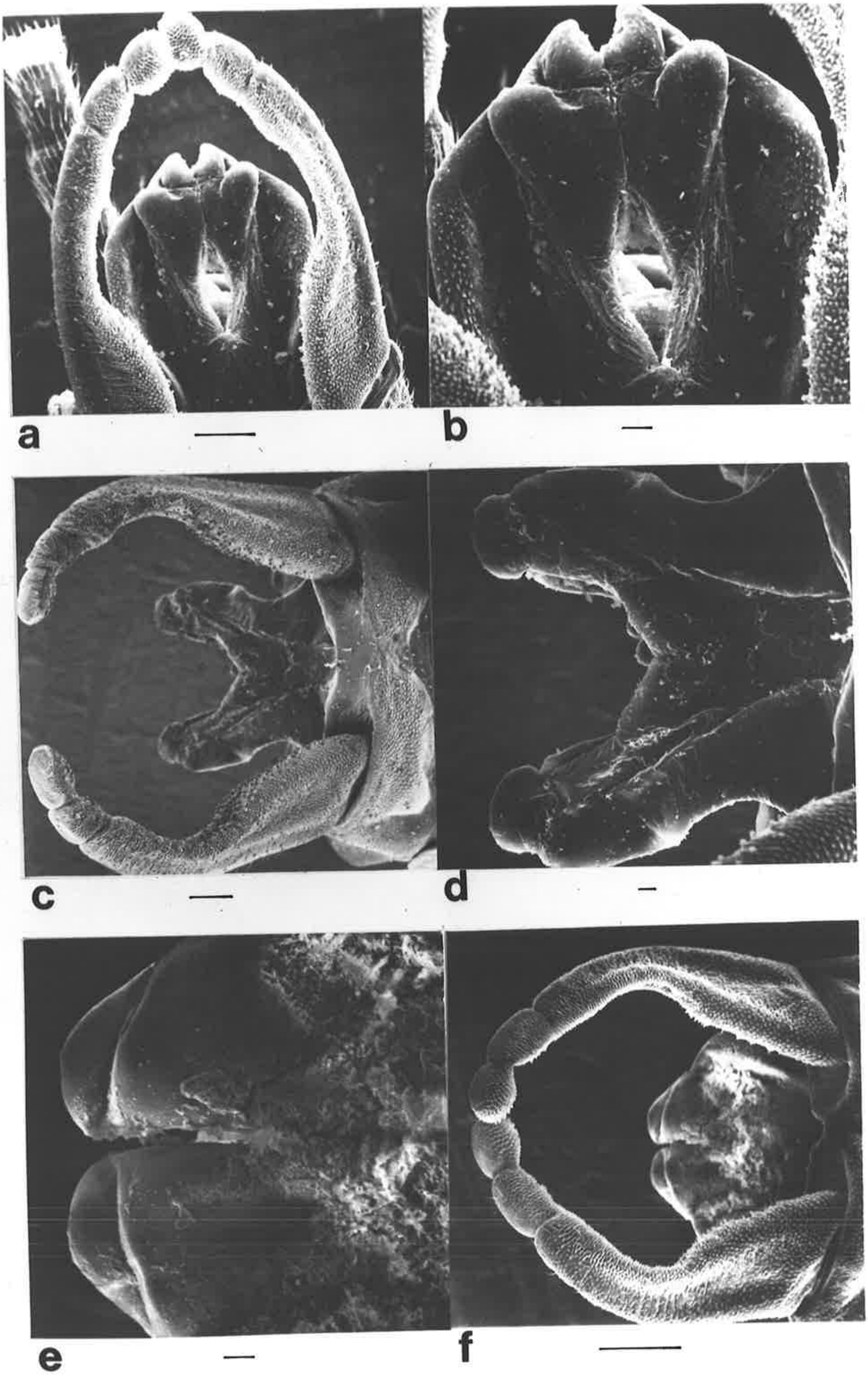
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TABLE II.16. Comparison of qualitative characteristics of *Atalonella inconspicua*, *A. fuscula* and *A. pilosa* from South Australia.

Character	*A. inconspicua*	*A. fuscula*	*A. pilosa*
Male Imago.			
Legs : banding	Absent	Absent	Present
Penes	Fused apically Ventral lobes present No internal spines	Separate apically Ventral lobes absent Internal spines present	Fused apically Ventral lobes absent No internal spines
Nymph.			
Legs : banding	Uniform brown	Absent	Present
Gills	Broad lanceolate	Linear	Broad lanceolate
Lamellae trachea	Plentiful, branched	Few, simple	Plentiful, branched
Left Mandible			
Incisors Outer	3	3	3
" Inner	3	3	3
Right Mandible			
Incisors Outer	3	3	3
" Inner	2	2	2
Prostheca Left	Slender, two terminal spines	Robust, apex serrated	Slender with lateral comb
" Right	Slender, two terminal spines	Slender, two terminal spines	Slender apex with three spines
Labial palpi	Slender	Broad	Slender
Labrum	Width ≑ 2 x Length	Width ≑ 2 x Length	Width < 2 x Length
Hypopharynx	Not divided	Deeply divided	Not divided

are compared. As was recorded in the genus *Atalophlebia*, the genitalia of *Atalonella* was very consistently expressed, and most weighting was placed on this character in the classification of the adults.

The major venation of the fore and hind wings were considered useful at the generic level, but the cross vein system of the fore wing was so variable within each species that the number of cross veins in any sector was considered of little taxonomic value. However, in South Australia the presence of cross veins in the basal half of the costal and sub-costal sectors of the fore wing was only recorded in *Atalonella fuscula*, distinguishing this species from *A. inconspicua* and *A. pilosa*. *A. brunnea*, *A. parva* and *A. darkara* all lack these cross veins (see Tillyard, 1936; Harker, 1950a and Harker, 1957 respectively), but *A. delicatula* resembles *A. fuscula* with abundant cross veins in the costal and sub-costal sectors (Tillyard, 1936). Therefore this character may help to distinguish a species group within the genus *Atalonella*.

The nymphal characteristics recorded in Table II.16 were also considered valuable taxonomic characters. As was recorded in the genus *Atalophlebia* the mouthparts showed consistent expression, and were therefore considered useful characters. The incisors of all *Atalonella* species recorded in South Australia were similar, but the mandibular prosthecae were distinctive. The labial palpi segment ratios, and length width ratios were useful in distinguishing *Atalonella fuscula* from *A. inconspicua* and *A. pilosa*. Labrum structure and dentition was also of value. All these characters combined with gill structure, and colour pattern supported the systematic diagnosis based primarily on the adult male genitalia.

Koss (1968) examined the eggs of many families of mayfly, and found that the structural morphology of the eggs in the families Heptageniidae, Leptophlebiidae, Caenidae, Ephemeridae and Polymitarcidae were useful for generic and specific determinations. His study showed clearly the value of the egg structure for the specific determination of female mayflies. To this end, the egg morphology of *A. inconspicua* and *A. fuscula* was determined using the Scanning Electron Microscope.

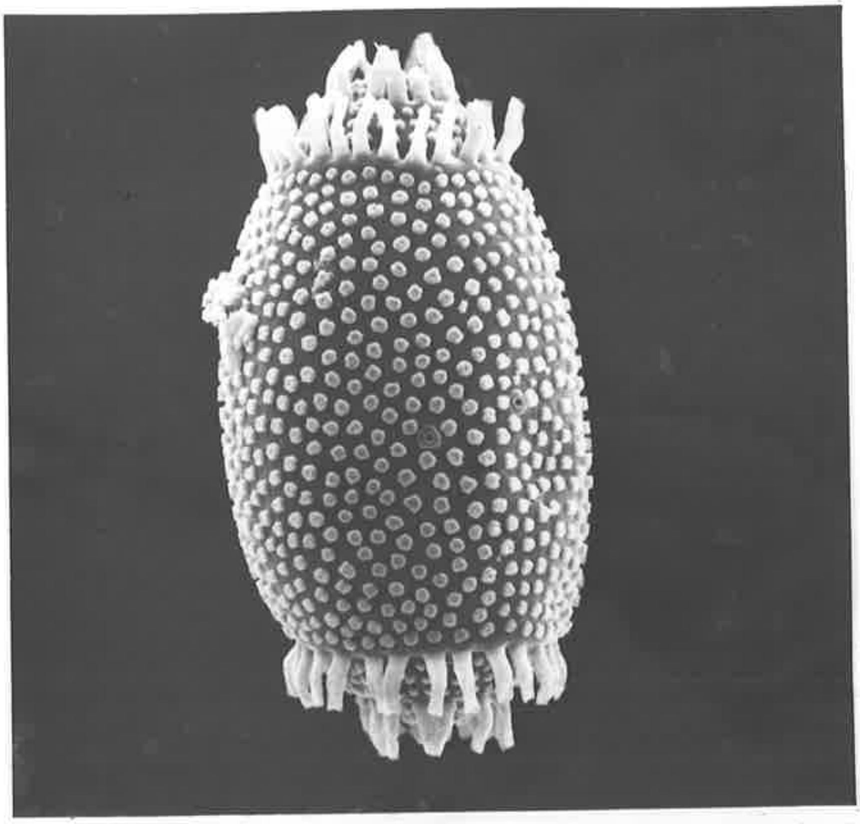
One of the difficulties with this study was obtaining fertilized, oviposited eggs. As recorded by Koss (1968) "most polar caps appear to be solid structures prior to their release into the water"; consequently eggs dissected from females were of limited use, especially if the polar cap structure was important (as found by Koss, and in this present study). Because of this, oviposited eggs were required, and these were obtained by collecting ovipositing females and placing them in containers of water, where they successfully laid. Two types of eggs were obtained with this technique; oval eggs with distinct polar caps and flat, compressed eggs without the polar caps. In the latter eggs no embryonic development (and therefore no hatching) occurred, and it is suggested that these eggs had not been fertilized. The lack of a polar cap in these eggs suggests that fertilization and oviposition is required before the full morphology of the egg is displayed. Eggs collected by dissecting fully mature female nymphs usually possessed the polar cap, but the apical tubular processes were fused to the egg, and did not allow the determination of the number of rows. Therefore association of female nymphs and adults was difficult.

Atalonella eggs are distinctive in possessing coronae of tubular structures at each end of the oval eggs (the polar cap). Koss noted that there are three types of attachment structures, the polar cap, accessory attachment structures, and an external adhesive layer. *Atalonella* eggs possess the polar caps and accessory attachment structures. The latter structures are similar in both *A. inconspicua* and *A. fuscula* (Figs. II.16a, b), but the polar caps differ, with *A. inconspicua* possessing two coronae on each cap, and *A. fuscula* three. Sperm guides are present in both species and two are obvious on the surface, visible with the Scanning Electron Microscope. Thus the only structural difference between the species is the number of coronae in the polar caps.

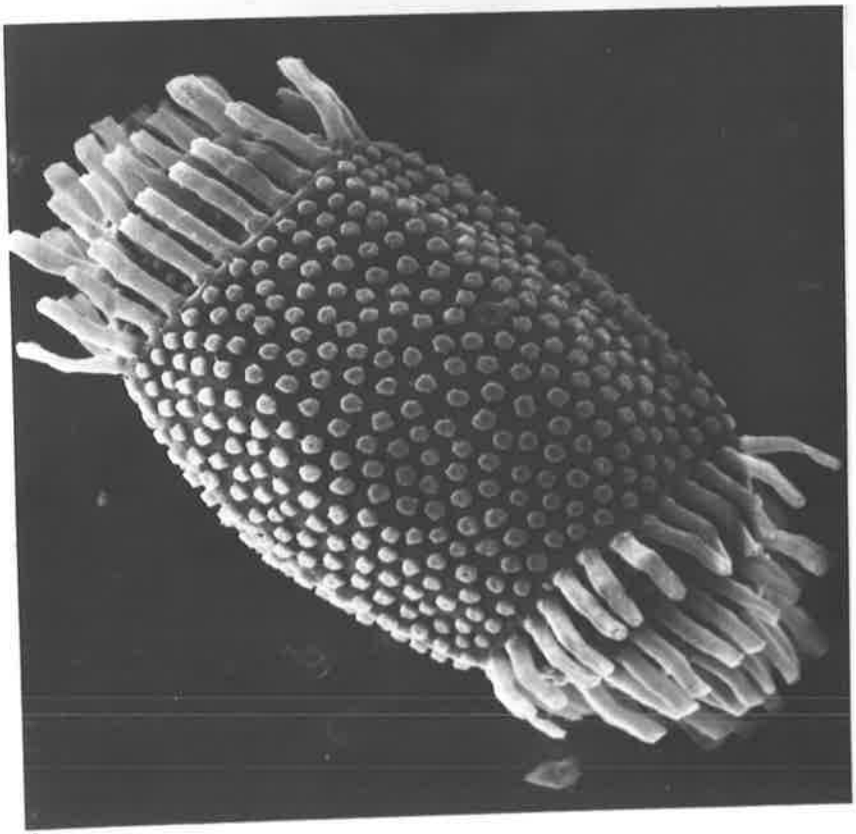
Harker (1950a) described the egg of *Atalophlebia parva*, and although her illustration gives little detail, the presence of the polar cap coronae is obvious. In 1954 Harker placed this species in *Atalonella*. Therefore, of the three eggs described for species in *Atalonella*, all possess the polar cap coronae. The thoracic structure and morphology of the Australian and South American representatives of *Atalonella* have been compared by Tsui and Peters (1975) who noted great

Fig. II.16. SEM micrographs of eggs of a, *Atalonella inconspicua*; and b, *Atalonella fuscula*, illustrating the general similarity of morphology, but distinct polar caps of each species.

Scale line : 10μm.



a



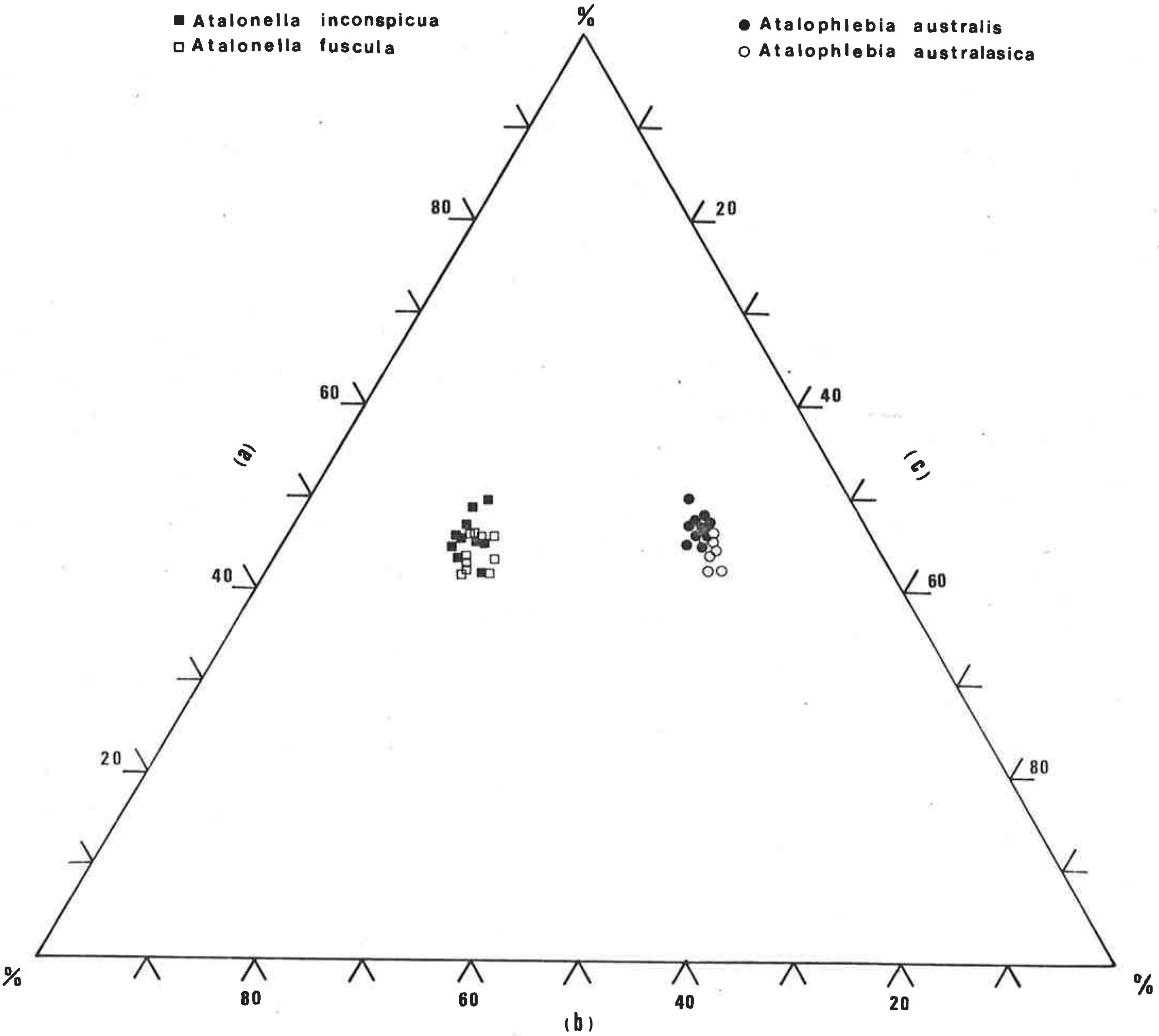
b

"heterogeneity of this genus". They also suggested that the genus, as it now stands, may be taxonomically subdivided in both South America and Australia. The presence of the polar cap in the three Australian species, *A. inconspicua*, *A. fuscula* and *A. parva* suggests that this may be a useful generic characteristic. Further species in Australia need to be compared before the value of this character is known, but an ultimate comparison between the South American and Australian species would be necessary in determining the validity of a further taxonomic division.

Inter-specific comparisons were made using the morphometric characters expressed in *A. fuscula* and *A. inconspicua* imagos and nymphs. In comparisons of the male imagos only nine characteristics differed significantly between the two species. None of these characteristics displayed geographical variation, and were therefore considered valuable in supporting the species separation. However, although statistically different, in the examined populations, the amount of overlap of character expression was very high, with only the fore tibial length/fore femur length values almost discrete. The statistically different characters are listed in Table II.17 but the amount of variation limits their value as specific characters.

Comparison of the quantitative nymphal characters revealed that 18 of the 27 analysed features were statistically different, but of these only five did not display either sexual or geographical variation, or both. The amount of overlap in variation of character expression in the sexually and/or geographically variable characters, and the inconsistency of their expression, deemed them of little value as specific

Fig. II.17. Triangular graph indicating the length of the mesosternum (a), width of mesobasisternum (b) and width of the mesofurcasternum (c) of two species of *Atalonella*, and two species of *Atalophlebia*, illustrating the discrete separation of the two genera, but not of the individual species within each genus.



■ Atalonella inconspicua
□ Atalonella fuscula
● Atalophlebia australis
○ Atalophlebia australasica
%
80
60
(a)
40
20
20
40
(c)
60
80
%
80
60
40
20
%
(b)

TABLE II.17. Morphometric characters which are useful in distinguishing the two species *Atalonella inconspicua* and *A. fuscula* in South Australia.

Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

	A. inconspicua			*A. fuscula*					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
Male Imagos.									
AD/CL	1.20	0.09	1.04-1.31	1.09	0.06	1.03-1.21	18	2.85	*
FWL/FWW	3.29	0.30	2.59-3.78	3.11	0.11	2.81-3.28	36	2.63	*
FT_iL/FFL	1.46	0.08	1.28-1.55	1.27	0.06	1.17-1.34	21	6.55	***
FT_4L/FFL	0.33	0.03	0.26-0.35	0.29	0.03	0.24-0.33	21	3.91	***
MT_2L/MFL	0.08	0.01	0.06-0.09	0.11	0.01	0.09-0.12	24	5.76	***
MT_3L/MFL	0.08	0.01	0.07-0.10	0.09	0.01	0.08-0.10	24	2.71	*
MT_4L/MFL	0.07	0.01	0.04-0.10	0.09	0.01	0.07-0.10	24	3.64	**
HT_2L/HFL	0.08	0.01	0.07-0.10	0.09	0.01	0.08-0.11	20	3.52	**
HT_4L/HFL	0.07	0.01	0.06-0.08	0.09	0.01	0.08-0.09	20	3.93	**
MBSL/MFSL	0.88	0.08	0.77-1.00	0.97	0.09	0.87-1.09	18	2.33	*

Continued ....

Table II.17. (Cont.)

		A. inconspicua			*A. fuscula*				
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
Nymphs.									
MFL/FFL	0.99	0.04	0.80-1.05	1.03	0.03	0.98-1.09	50	3.17	**
HFL/FFL	1.08	0.03	1.00-1.15	1.21	0.04	1.11-1.29	49	11.91	***
Labial palpi :									
BL/BW	1.96	0.17	1.67-2.57	1.56	0.06	1.44-1.67	66	8.97	***
AL/BL	0.61	0.06	0.47-0.73	0.70	0.04	0.63-0.79	65	5.15	***
Maxillary palpi :									
ML/BL	0.89	0.09	0.73-1.09	0.67	0.07	0.54-0.78	61	8.80	***

characteristics. The characters which are consistently expressed, both sexually and geographically, are included in Table II.17.

The thoracic morphological comparisons made by Tsui and Peters (1972) were analysed and were found to be not significantly different. The only morphological comparison which differed was the mesobasisternum length/mesofurcasternum length ratio (Table II.17). A triangular scatter diagram comparing the length of the mesosternum, width of mesobasisternum and width of mesofurcasternum was constructed using *Atalonella spp.* and *Atalophlebia spp.* which illustrates the value of these characteristics at the generic level (Fig. II.17) not as was suggested by Tsui and Peters (1972), at the specific level. The genera are discretely placed, but, there is much overlap of each species within the generic groupings.

As was concluded in the discussion of the *Atalophlebia* character expression, the morphometric characteristics may be useful in supporting species separations made using qualitative characters.

II.4.3 Genus *Jappa* Harker 1954.

Harker, 1954 : 257

Riek, 1970a : 239

Tsui and Peters, 1975 : 538-540

Male Imago Characteristics. Fore wings 3.5 - 5 x longer than wide, with numerous cross veins, those in subcostal space are upright and parallel. Hind wing with long narrow costal region with numerous cross veins, MA forked, single intercalary present or absent. Tarsal claws dissimilar, one blunt club shaped, one long, slender, hooked distally. Forceps three segmented, basal segment very long. Penes as long as basal segment of forceps, or much shorter. Cerci longer than appendix dorsalis.

Mature Nymph Characteristics. Head large with or without two tusk-like projections arising from the gena and extending forward on either side of the labrum, labrum with a small convex projection on mid anterior margin. Maxillary palpi three segmented, distal segment very small (or two segmented with distal segment large and rectangular). Gills broad, ovate, with apical tracheal filament fringed with long fine hairs. Body and legs fringed with long fine setae.

History and Discussion.

Jappa was described by Harker (1954) and included two species, *J. kutera*, the genotype, from northern New South Wales and southern Queensland, and *J. tristis* from Cradle Mountain, Tasmania. The nymph of the genotype was described earlier by Harker (1950a) and it possessed large tusk-like projections on either side of the labrum, but, as noted by Riek (1970a), the nymphs of other species in the eastern states lack the frontal horns. Harker (1950a) also recorded only two segmented maxillary and labial palpi, although her illustration of the labium suggests a three segmented palp. Although Harker's material has not been examined, adults of a *Jappa* sp. from two Victorian catchments (the La Trobe and Thomson Rivers) are consistent with Harker's description of *J. kutera*. The associated nymphs are also similar to Harker's description, but the maxillary and labial palpi are definitely three segmented, with a very small distal segment.

The species found in South Australia lacks the frontal horns, and has three segmented maxillary and labial palpi, and therefore the generic criteria have been modified. Until the nymph described by Harker is also examined some doubt must exist on both the number of palpal segments of the maxillae and labium, and the identification of the Victorian *Jappa* sp. Therefore the presence of two segmented palpi is still included in the generic criteria. Adult characteristics of *Jappa pipinna* sp. nov. have also been incorporated into the modified generic characterization.

II.4.3.1 *Jappa pipinna* sp. nov.

Holotype Male Imago

Body Length	9.44mm
Notal Length	2.54mm
Pronotal Width	0.92mm
Mesonotal Width	1.33mm
Fore Wing Length	9.31mm
Hind Wing Length	2.03mm
Cerci Length	14.10mm
Appendix Dorsalis Length	11.97mm

Body colour reddish-brown, abdomen darker dorsally.

Head : dark brown, with a white patch between ocelli. Dorsal compound eyes raised, grey brown, lateral eyes black. Antennae short, 1mm long, basal segment twice as long as wide, flagella 0.87mm long.

Thorax : light brown dorsally with white patches on scutoscutellum, laterally with patches of white and pink. Legs light brown, femora with two dark bands, one distally, and one at 2/3 of length, T_1 partially fused to tibia, join apparent. Tarsal claws dissimilar with one blunt, and one sharply hooked claw, apex of blunt lobe with a short terminal tooth (Fig. II.18h). Middle and hind tarsal segments 1-4 with distal spine. Ratios of leg segments;

fore leg 1.00 : 1.74 : 0.07 : 0.65 : 0.60 : 0.47 : 0.19 (1.84mm)

middle leg 1.00 : 1.28 : 0.04 : 0.09 : 0.09 : 0.06 : 0.20 (1.49mm)

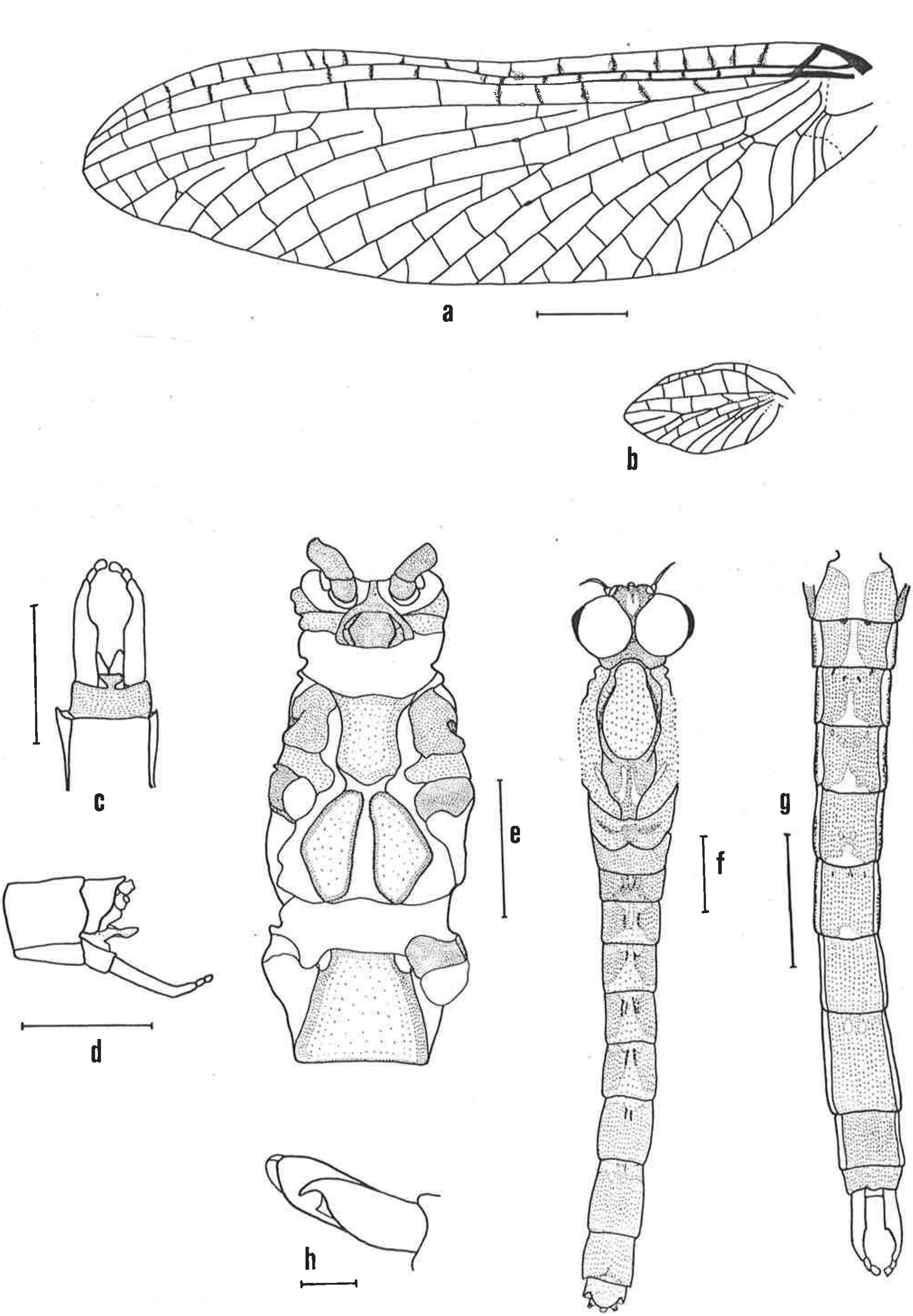
hind leg 1.00 : 1.09 : 0.04 : 0.08 : 0.06 : 0.06 : 0.15 (1.80mm).

Sternum dark brown (Fig. II.18e). Prosternum with heavily sclerotized base. Mesosternum; basisternum length 1.46 x width, 0.79 x furcasternum length, posterior margin rounded, furcasternum length 0.87 x width, lateral margins of median longitudinal invagination divergent posteriorly, posterior margin slightly concave.

Wings : hyaline. Fore wing (Fig. II.18a), length 3.5 x width, cross veins in pterostigmal region simple, costal cross veins extending along entire length, slightly shaded with grey, cross veins of subcostal space also shaded with grey, cross

Fig. II.18. *Jappa pipinna*, male imago: a, fore wing; b, hind wing; c, genitalia, ventral view; d, genitalia, lateral view; e, thoracic sterna; f, dorsal colour pattern; g, ventral abdominal colour pattern; h, fore claws.

Scale lines : a – g 1mm.
h 0.5mm.


a
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h

vein system almost complete, but anal and cubital regions with only a few. Three bullae present, one in each of R_2, $R_{4\ \&\ 5}$ and MP. Hind wing (Fig. II.18b), length 2 x width, costal hump not exaggerated, C and Sc join about 4/5 of wing length, with 5 cross veins distally. R_1 straight, Rs joins MA in centre of wing, MA straight, MP branched in proximal half of wing, anal region without cross veins.

Abdomen : dark reddish-brown. Dorsally with lighter brown markings on segments 2-8, each marking with two short, black longitudinal stripes, segments 1, 9 and 10 not marked (Fig. II.18f), ventrally segments 1-5 with central white marking, segment seven with a pair of anterior white spots, segments 6, 8, 9 dark red/brown (Fig. II.18g). Cerci long, reddish-brown at base, appendix dorsalis shorter than cerci.

Genitalia : forceps light brown, proximal segment long, 0.74mm, broad at base, narrows approximately half way along length, second segment almost square, distal segment longer, narrow proximally. Penes paired, very short, extending half way to narrowing of proximal segment of forceps, separate, mesal margins divergent, lobes simple (Figs. II.18c, d; 20a, b).

Mature Female Nymph (Fig. II.21).

Head Width	1.96mm
Notal Length	3.12mm
Pronotal Width	2.32mm
Mesonotal Width	2.36mm
Cerci Length	8.25mm
Appendix Dorsalis Length	9.71mm

Head : prognathous, brown. Lateral eyes black, lateral ocelli black. Antennae 3.08mm long with whorls of setae at apex of each segment. Tentorial body; width 2.33 x length.

Thorax : brown. Pronotum width 1.18 x head width, brown with black/brown median marking, lateral margins lined with long fine setae. Mesonotum width 1.2 x head width, light brown, wing sheaths extend posteriorly to the middle of the fourth abdominal segment. Legs brown, with one mid and one distal black band on femora; tibiae and tarsi not banded, margins of segments lined with long fine setae, ventral margin of tibiae lined with short spines (Fig. II.19a), hind leg with spines on dorsal margin of tibia. Tarsal claws short and curved, with 12-16 small rounded ventral denticles (Fig. II.19b). Femora of fore and middle legs almost equal in length, hind leg longest, 1.34 x fore femur length. Ratios of leg segments;

fore leg 1.00 : 1.04 : 0.37 (1.66mm)
middle leg 1.00 : 0.94 : 0.33 (1.60mm)
hind leg 1.00 : 0.87 : 0.26 (2.14mm).

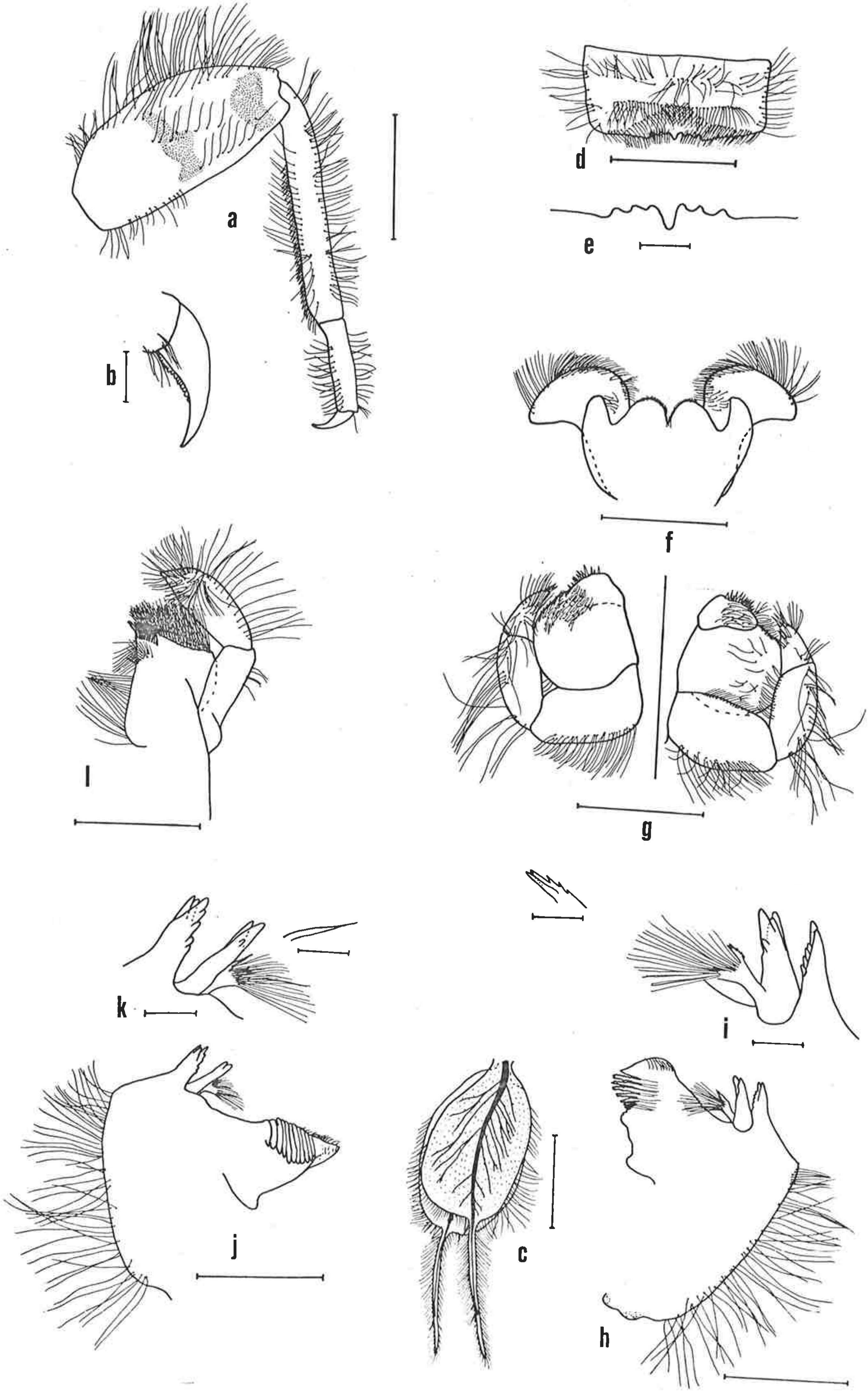
Femur length to width ratios; fore leg 2.18, middle leg 2.22, hind leg 2.68. Sternum; prosternum triangular with apex truncated, sternacostal suture absent. Mesosternum; basisternum, almost square, length 0.92 x width, and equal to furcasternum length, sternacostal suture present. Metasternum; basisternum narrower than mesofurcasternum, width 4.75 x length.

Abdomen : dark brown with light central stripe on segments 4-7, segments 8, 9, and 10 dark brown (Fig. II.21). Segments 6-9 with postero-lateral margins produced into backward pointing projections, all segments with long fine setae dorsally. Caudal filaments well developed, appendix dorsalis longer than cerci. Gills, 7 pairs on segments 1-7, each consisting of a pair of broad lamellae with one apical tracheal filament, lined with long fine setae, dorsal lamella grey (Fig. II.19c).

Mouthparts : labrum (Fig. II.19d), 2.12 x wider than long, lateral margins angular lined with long fine setae, mid anterior margin with seven tubercles, three tubercles on each side of a large sharp central projection (Fig. II.19e), anterior margin lined with long setae, dorsal surface covered with long setae. Left mandible (Fig. II.19h); lateral margin lined with long setae, incisors displaced mesally, outer incisors with two large teeth and four smaller teeth on mesal margin, inner incisors with three apical teeth and one small lateral tubercle, prostheca narrow with six spines, covered by a brush of setae inserted at base (Fig. II.19i), molar region of 7-8 rows of raised ridges. Right mandible (Fig. II.19j); outer margin lined with long setae, incisors displaced mesally, outer incisors rugose, with three apical teeth, with four lateral tubercles, inner incisors with two apical teeth and one lateral tubercle, prostheca long, spinous (Fig. II.19k), molar region with rows of grinding ridges. Hypopharynx (Fig. II.19f), simple, median lobe divided, with lateral processes, paragnaths large, convex, anterior margins lined with long setae. Maxillae (Fig. II.19*l*); galeo-lacinia rectangular, apical surface with a dense brush of setae, row of sixteen rake setae on ventral surface, rake of setae also interspersed within apical brush; mesal corner with one large rake spine, inner margin lined with long fine pinnate setae; palpi three segmented, longer than galeo-lacinia,

Fig. II.19. *Jappa pipinna*, mature nymph: a, fore leg; b, fore claw; c, third abdominal gill; d, labrum, dorsal view; e, antero-median emargination of labrum, enlarged; f, hypopharynx; g, labium, dorsal (left) and ventral views; h, left mandible, ventral view; i, left incisors and prostheca, enlarged and prostheca, enlarged; j, right mandible, ventral view; k, right incisors and prostheca, enlarged and prostheca, enlarged; l, left maxilla, ventral view.

Scale lines :		
	a,c,d,f,g,h,j,l	0.5mm.
	b,e,i,k	0.1mm.
	prostheca	0.05mm.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proximal segment 2.33 x longer than wide, second segment long and broad, 1.88 x longer than wide, lateral margin lined with long setae, distal segment very short, triangular, covered with long setae, apex with two short spines, segment ratios 1.00 : 0.94 : 0.29 (0.36mm). Labium (Fig. II.19g); palpi three segmented, proximal segment 1.71 x longer than wide, outer margin lined with long setae, mesal margin lined with short spines, second segment outer margins lined with very long, fine setae, mesal margin with short setae, distal segment covered with setae, apex with four spines, segment ratios 1.00 : 0.65 : 0.58 (0.41mm), paraglossae broad, rectangular, lined with short blunt spines, glossae with large lateral process ventrally, extending over paraglossae, anterior margin lined with short setae.

Female Imago : unknown.

Subimago : unknown.

Male Nymph : unknown.

Diagnostic Characteristics.

1. Genitalia of male imago, penes very short (Figs. II.18c, d; 20a, b).

2. Wing length 3.5 x width, (Fig. II.18a).

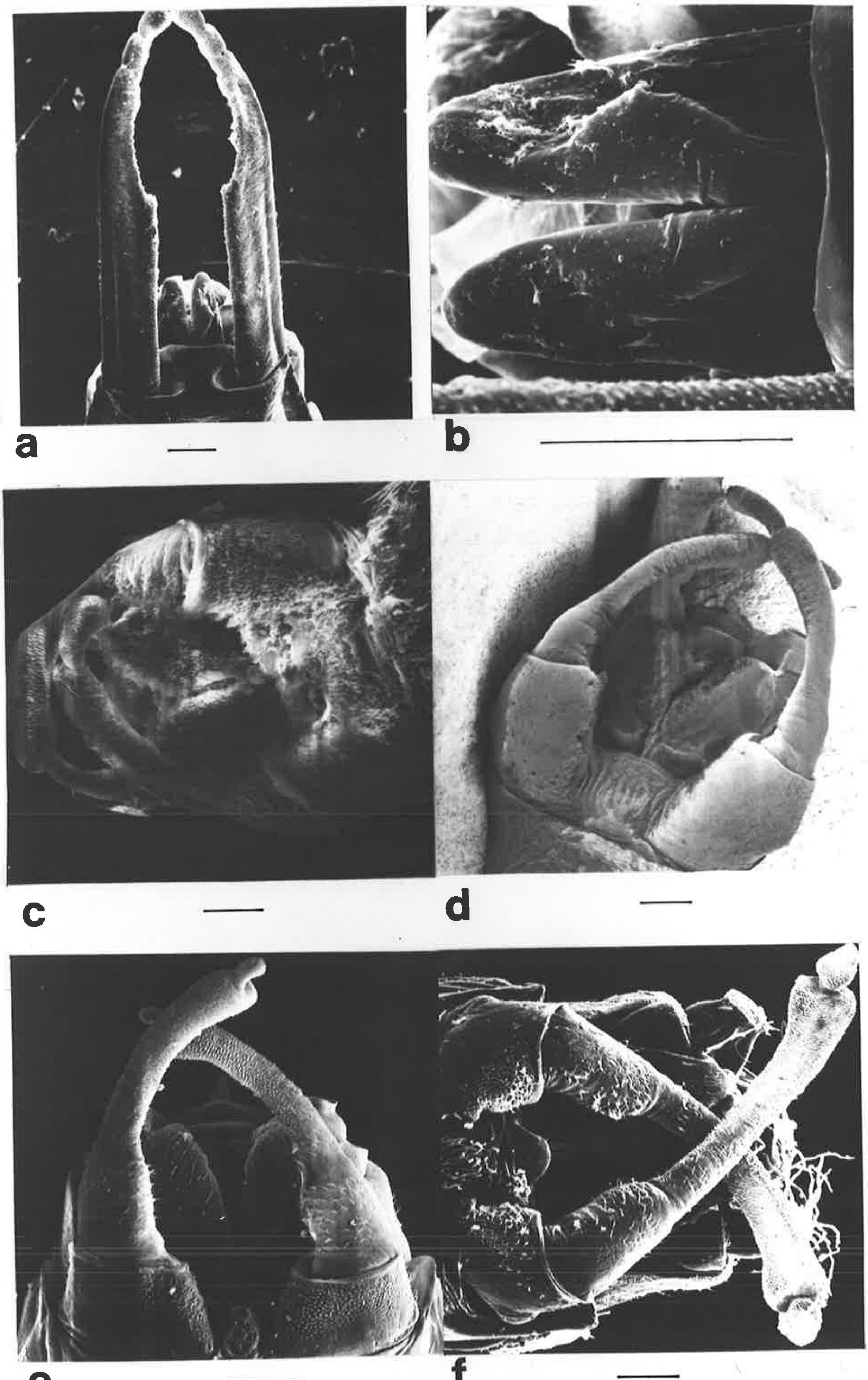
3. Femora of imago with two black bands.

4. Nymph without frontal lobes (Fig. II.21).

5. Labrum with one mid anterior projection and three denticles on each side (Figs. II.19d, e).

Fig. II.20. SEM micrographs of some South Australian mayflies. a - b, *Jappa pipinna*: a, genitalia, ventral view; b, penes, ventral view, enlarged. c - e, genitalia, ventral view of *Baetis soror* (c); *Centroptilum elongatum* (d); *Cloeon fluviatile* (e); and *Cloeon paradieniensis* (f).

Scale lines : 100μm.


a
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e
f

6. Maxillary palpi three segmented (Fig. II.19*l*).

7. Lateral projection of glossae of labium. (Fig. II.19g).

8. Mandibles, shape and form of incisors and prosthecae (Figs.II.19h-k).

Type Locality.

Second Wannon River, Grampian Mountains, Victoria, Grid Reference on 1:250,000 map series Ballarat Sheet 547396. Collected 25th November, 1977 by P. J. and D. N. Suter.

Type Specimens.

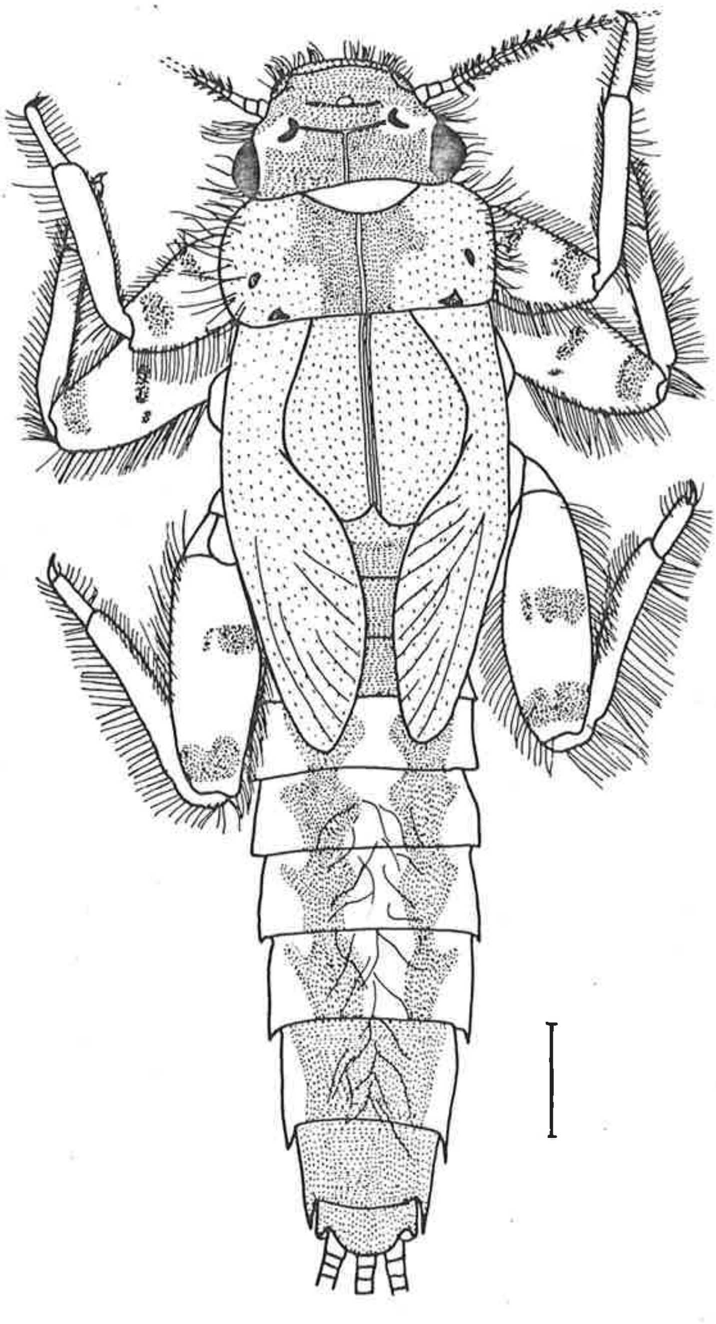
The holotype male is deposited in the National Museum of Victoria. Two paratype imagos are also placed in the National Museum of Victoria. The wings and legs of the holotype male are mounted on slides, and the genitalia and body are in ethanol. The female nymph is mounted on slides.

Type Habitat.

The Second Wannon River in the Grampian Mountains, where the holotype male was collected, is a moderately fast flowing stream over large cobble size rocks. The nymphs were collected using a kick sample technique, and therefore there is no certainty of the habitat being occupied by this species. Riek (1970a) records that the nymphs are "found burrowing below rocks in the slower-flowing streams", but there is no evidence that this is so with *J. pipinna*.

Fig. II.21. Dorsal colour pattern of mature female nymph of *Jappa pipinna*.

Scale line : 1mm.



Etymology of Specific Epithet

The two species of *Jappa* described by Harker (1954), *J. tristis* and *J. kutera* possessed very long penes, extending well beyond the constriction of the first segment of the forceps. In contrast the penes of *J. pipinna* are very short, and hence the specific epithet *pipinna* (L) for small penes.

Affinities

Although the male imago of *J. pipinna* resembles the species described by Harker (1954) in the generic characteristics, it can be distinguished by the short penes, and the relatively short fore wings, being only 3.5 x longer than wide, in contrast to the generic designation of "about 5 times as long as wide" (Harker, 1954). The nymph of *J. pipinna* is distinctly different to that of *J. kutera*, as described by Harker (1950a), in lacking the frontal horns, and in possessing maxillary and labial palpi with three segments. The gills, general structure of the labrum, maxillae and mandibles, and the presence of long fine setae on most parts of the body confirm the generic affinity of these two species. The generic characterization of *Jappa* has therefore been altered to include these new characters.

Material Examined. South Australia : South East; Cress Ck., Eight Mile Ck., Hitchcocks Drain. Victoria : Crawford R., Fitzroy R., Fyans Ck., Shaw R., Wannon R., Second Wannon R.

II.5 Systematics : Family BAETIDAE

This family occurs on every continent, and is represented in Australia by the genera *Baetis* Leach, *Bungona* Harker, *Centroptilum* Eaton, *Cloeon* Leach and *Pseudocloeon* Klapálek. Riek (1970a) included these genera in the subfamily Baetinae, which, with the subfamily Siphlonurinae, formed the family Baetidae. In a subsequent paper Riek (1973) accepted the families Baetidae and Siphlonuridae with reservation, considering the Baetidae as a possible subfamily of the Siphlonuridae. Edmunds (1973) and Landa (1973) both placed the Baetidae and Siphlonuridae as separate families. The more recent reviews of the phylogeny of Ephemeroptera by Edmunds (1975) and Edmunds, Jensen and Berner (1976) have recognised the Baetidae and Siphlonuridae as distinct families, and it is this classification which has been adopted in the present study.

The following characterization of the Baetidae is after Edmunds, Jensen and Berner (1976).

Male Imago Characteristics. "Eyes of male divided, upper portion turbinate. Fore wings with veins IMA, MA_2, IMP, and MP_2 detached basally. Interspaces between veins at outer margin of fore wing with short single or paired intercalaries. Hind wings reduced, with or without veins, with 1-3 longitudinal veins, or with hind wings absent. Two caudal filaments only. Penes of male membranous and retractable ... " (Edmunds, Jensen and Berner, 1976).

Mature Nymph Characteristics. "Body streamlined, minnowlike. Head hypognathous. Antennae long, usually two or more times as long as width of head. Labium with glossae and paraglossae long and narrow. Gills on abdominal segments 1-7, 1-5, or 2-7. Abdominal segments without postero-lateral projections except in *Callibaetis*, *Cloeon* and some *Centroptilum* species, in which they may be moderately developed" (Edmunds, Jensen and Berner, 1976).

II.5.1 Genus *Baetis* Leach 1815.

Leach, 1815 : 137
Burmeister, 1839 : 800 (*B. costalis* later placed in *Atalophlebia*)
Pictet, 1843 : 189-191 (*B. australasica* later placed in *Atalophlebia*)

Walker, 1853 : 559-561 (*B. australasica, B. costalis*)
Eaton, 1871 : 110
1881 : 196
1885 : 156-158
Ulmer, 1908 : 44-45
Tillyard, 1926 : 64
1936 : 50-53
Harker, 1950a : 21-24, 29
1954 : 263-264, 266
Scholes, 1961 : 36-38
Riek, 1970a : 235

Male Imago Characteristics. Fore wings with reduced cross vein system, marginal intercalaries in pairs. Hind wings greatly reduced, long and narrow with or without an acute costal projection, with one, two or three longitudinal veins. Forceps four segmented.

Mature Nymph Characteristics. Labrum oval with a shallow, square, median notch. Mandibles with two separate groups of incisors, prosthecae with a basal brush of setae. Labial palpi three segmented, distal segment round, second segment enlarged distally on mesal surface. Tarsal claws short with many ventral denticles. Metathoracic wing (hind wing) sheaths present. Gills plate-like on abdominal segments 1-7, single on all segments. Three caudal filaments, appendix dorsalis only slightly shorter than cerci (in Australian material) or reduced, fringed on lateral margins with long fine setae, cerci fringed on mesal margin.

History and Discussion.

Since *Baetis* is a cosmopolitan genus the discussion of its world wide history would be beyond the scope of this study. Müller-Liebenau (1969) revised the European species, and Edmunds, Jensen and Berner (1976) list the species recorded in North and Central America.

Leach (1815) initially erected the genus *Baetis* to include *B. bioculatis* (Linn. Fabr.) and Burmeister (1839) placed *B. costalis* from Australia in this genus. Pictet (1843) described *B. australasica*, and Walker, (1853) listed these three species in the "Catalogue of the species of Neuropterous Insects in the Collection of the British Museum". Eaton (1871) placed both the Australian species (*B. costalis* and *B. australasica*) in the genus *Leptophlebia* and subsequently (1884) in the genus *Atalophlebia*.

The first record of *Baetis* from Australia was made by Ulmer (1908) when *B. soror* was described from Western Australia. Tillyard (1936) described *B. frater* from Tasmania, and Harker (1950a) added two further species *B. baddamsae* and *B. confluens* from New South Wales. In 1954, Harker described *B. sogerensis* from Port Moresby, New Guinea, but this species has not been recorded on the Australian mainland.

Müller-Liebenau (1969, 1973) recorded and discussed the characteristics used in the revision of the European species of *Baetis*; these characteristics have been found to be useful in the present study. The following redescription of the male adult, and the original description of the nymph of *B. soror* Ulmer, include the characteristics which Müller-Liebenau (1969, 1973) found to be species specific.

II.5.1.1 *Baetis soror* Ulmer 1908

Baetis soror Ulmer, 1908 : 44-45
Tillyard, 1926 : 64
Harker, 1950a : 29
1954 : 266

Male Imago.

	$\bar{x}$	SD	n	Range
Body Length	5.45	0.45	18	4.40 - 6.00
Notal Length	1.59	0.21	14	1.36 - 2.00
Mesonotal Width	0.88	0.08	12	0.74 - 1.00
Pronotal Width	0.62	0.08	12	0.54 - 0.76
Fore Wing Length	4.93	0.51	30	4.20 - 5.82
Hind Wing Length	1.01	0.16	30	0.80 - 1.26
Cerci Length	11.57	0.92	5	10.25 - 12.50

General colour brown.

Head : dark brown. Antennae brown, basal segment darker brown. Dorsal turbinate eyes yellow, oval, lateral eyes black. Ocelli white.

Thorax : light brown. Pronotum narrower than head. Mesonotum humped with black mesonotal suture, areas near posterior margins of scutoscutellum white. Legs; buff, slender. Fore legs longer than middle and hind legs, fore leg femur length 1.23 x middle leg femur length, and 1.25 x hind leg femur length, middle and hind legs with four tarsal segments. Ratios of leg segments;

fore leg 1.00 : 1.80 : 0.08 : 0.78 : 0.62 : 0.37 : 0.18 (0.93mm)

middle leg 1.00 : 0.98 : 0.16 : 0.13 : 0.07 : 0.20 : - (0.75mm)

hind leg 1.00 : 0.97 : 0.16 : 0.13 : 0.07 : 0.20 : - (0.76mm).

Tarsal claws dissimilar, one blunt, club shaped, one slender with a terminal hook. Sternum; light brown. Prosternum rectangular, 1.25 x wider than long, with concave lateral margins. Mesosternum brown, basisternum rectangular 2 x longer than wide, furcasternal length 0.88 x width, median longitudinal invagination wide with smoothly concave posterior margin.

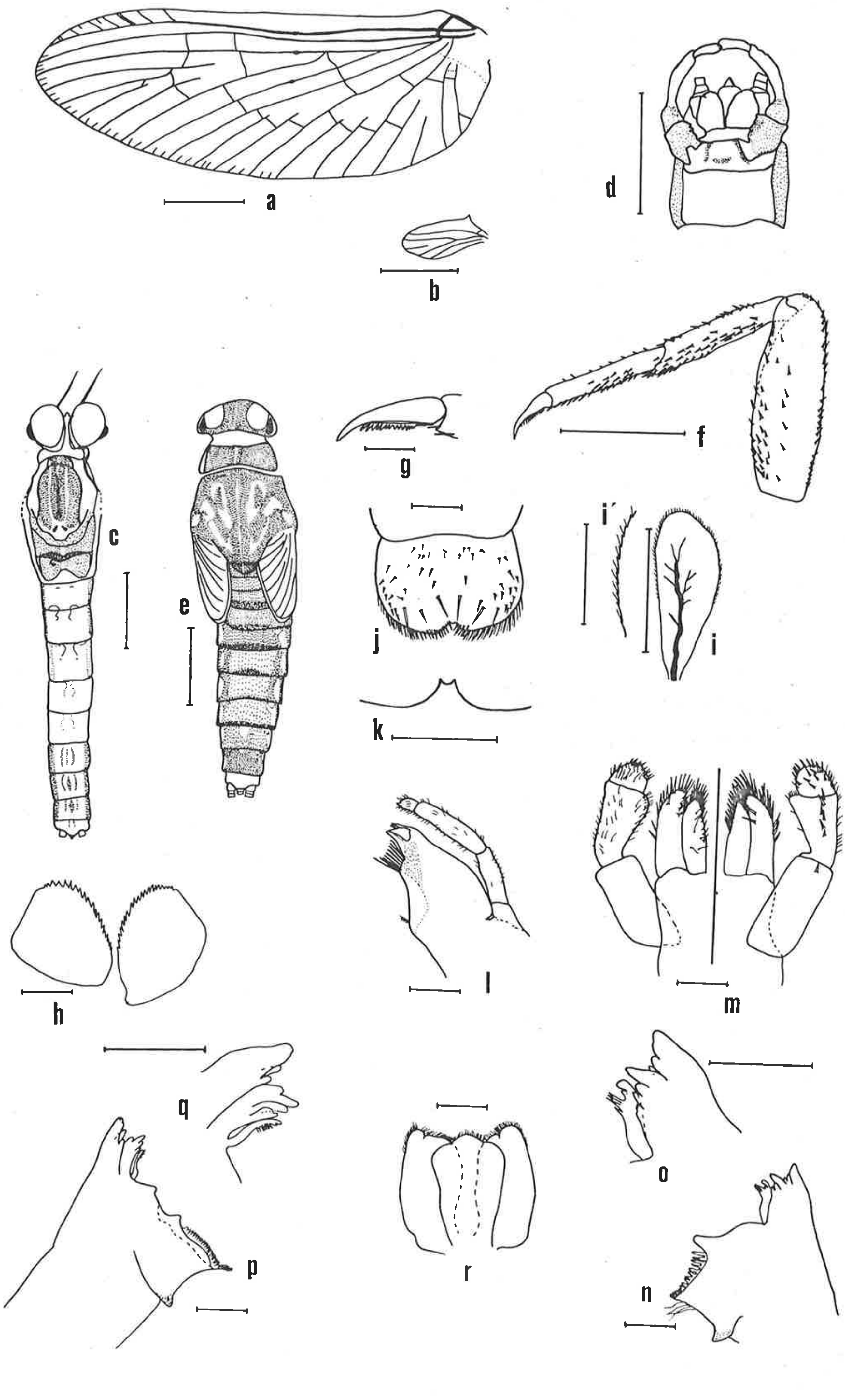
Wings : fore and hind wings hyaline with light brown venation. Fore wing (Fig. II.22a), 2.67 x longer than wide, pterostigmal region slightly opaque (milky) with 7-10 cross veins, anastomosed, branched or incomplete, proximal region of costal space without cross veins. Three bullae present, one in Sc, one in each branch of Rs fork (R_2 and $R_{4 \& 5}$). Marginal intercalaries paired. Hind wing with triangular costal projection, three longitudinal veins, second forked with one intercalary, one proximally located cross vein in costal space (Fig. II.22b).

Abdomen : brown, with black marking just apparent on segments 3-6, but more obvious on segments 7-9 (Fig. II.22c). Cerci long, well developed, light brown, appendix dorsalis reduced to a basal stump.

Genitalia : forceps four segmented, proximal segment cylindrical, second segment bulbous, fused to third segment, third segment long and slender, distal segment short but 3 x longer than wide, rounded, bulbous distally. Covers of penes broad, extending beyond bulbous second segment of forceps, bluntly pointed with divergent apices (Fig. II.22d; 20c).

Fig. II.22. *Baetis soror*. a – d, male imago: a, fore wing; b, hind wing; c, dorsal colour pattern; d, genitalia, ventral view. e – r, mature nymph: e, dorsal colour pattern; f, fore leg; g, fore claw; h, paraprocts, ventral view; i, third abdominal gill; i′, margin of gill, enlarged; j, labrum, dorsal view; k, antero-median emargination of labrum, enlarged; l, left maxilla, ventral view; m, labium, dorsal (left) and ventral views; n, left mandible, ventral view; o, left incisors and prostheca, enlarged; p, right mandible, ventral view; q, right incisors and prostheca, enlarged; r, hypopharynx.

Scale lines :	a,b,c,e	1mm.
	d,f,i	0.5mm.
	g,h,i′,j-r	0.1mm.


a
b
c
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r

Mature Male Nymph (Fig. II.22e).

	$\bar{x}$	SD	n	Range
Head Width	0.97	0.07	22	0.86 - 1.06
Notal Length	1.50	0.14	17	1.30 - 1.74
Mesonotal Width	1.27	0.13	17	1.06 - 1.46
Pronotal Width	0.87	0.09	17	0.76 - 1.00
Cerci Length	3.43	0.50	7	2.60 - 4.16
Appendix Dorsalis Length	2.29	0.24	7	2.00 - 2.60

Body cylindrical, light brown.

Head : hypognathous, brown with buff epicranial sutures. Dorsal compound eyes sepia, lateral eyes black. Ocelli black. Antennae long without apical projection on basal segment.

Thorax : pronotum width 0.90 x head width, brown with triangular light patches near lateral margins. Mesonotum width 1.31 x head width, brown with an oxbow shaped white marking beside mesonotal suture, wing sheaths black, extending to mid third abdominal segment. Legs buff/grey with darker femur/tibia joint, lined with short spine setae on margins (Fig. II.22f). Tarsal claws short curved with ventral peg like denticles (Fig. II.22g). Ratios of leg segments;

fore leg	1.00 : 0.72 : 0.64	(0.77mm)
middle leg	1.00 : 0.71 : 0.58	(0.79mm)
hind leg	1.00 : 0.68 : 0.54	(0.82mm).

Femur length to width ratios; fore leg 3.15, middle leg 3.45, hind leg 3.70.

Abdomen : brown, without definite markings, lateral regions lighter. Posterior margins of terga with short sharp spines. Paraprocts curved, lined with 17 - 24 spines (Figs. II.22h; 23a, b). Three caudal filaments, lateral margins of appendix dorsalis and inner margins of lateral cerci lined with long fine setae, cerci longer than appendix dorsalis (appendix dorsalis transparent in last instar). Gills; seven pairs of single flat lamellae (Fig. II.22i) on segments 1 - 7, margins serrated with one fine bristle alternating with each serration (Fig. II.22i), first gill small without clear trachea, gills 2 - 7 with black branched trachea, 3, 4, 5 largest, ovate, 1, 7 narrower.

Mouthparts : labrum (Fig. II.22j) ovoid, length 0.58 x width, with deep concavity in centre of anterior margin (Fig. II.22k), two small median denticles within concavity, one long spine setae on each side of median line, with two similar setae laterally, and a group of short stout spine setae near lateral margin, anterior margin lined with fine setae. Left mandible (Fig. II.22n) outer incisors with three teeth, outer tooth broad and robust, inner incisors with one long central tooth and three shorter lateral teeth, prostheca robust with one large curved apical tooth with 3 - 4 spines in concavity of tooth (Fig. II.22o); molar region of numerous grinding ridges with 3 - 4 long setae on inner margin. Right mandible (Fig. II.22p); outer incisors with first tooth robust with two small inner teeth, inner incisors with 1 - 2 long central teeth with two (one each side) lateral teeth, prostheca long and narrow with outer margin lined with 6 - 7 setae (Fig. II.22q).

Hypopharynx rectangular, median lobe with slightly pointed apex, paragnaths constricted on anterior margin, lined with short fine setae (Fig. II.22r). Maxillae (Fig. II.22*l*); galeo-lacinia long and narrow with pointed apex, lined with four stout teeth, ventrally with a line of pinnate setae and a line of nine curved setae just below teeth, palpi longer than galeo-lacinia, three segmented, segment ratios 1.00 : 1.45 : 0.36 (0.10mm), distal segment with a short tooth, all segments with short fine setae. Labium (Fig. II.22m); palpi three segmented, length of proximal segment 2.06 x width, inner margin of second segment produced forming a lobe, segment ratios 1.00 : 0.71 : 0.33 (0.19mm); glossae shorter than paraglossae, paraglossae outer margin convex curving over glossae, margins of both lined with spine setae.

Female Imago : wings similar, lacking dorsal compound eyes, fore legs shorter than male, body colour cream, abdomen broad.

Female Nymph : similar to male, lacking dorsal compound eyes, lateral eyes black.

Sexual Variation of Nymphs.

Last instar female nymphs have much narrower heads than similar stage males, and consequently comparisons of thoracic and limb measurements compared with the head width tend to be statistically different. The length/width ratio of the proximal segment of the labial palpi, and paraglossae and the length of the distal segment of the labial palpi/proximal segment length were also found to differ between the sexes (Table II.18). Of the 27 characters compared only ten were statistically different, and each character showed a wide range of expression in the examined population (Table II.18). The non-significant characters are given in Appendix 9.

Diagnostic Characteristics

1. Hind wings with three longitudinal veins, second forked (Fig. II.22b).
2. Third and fourth segments of forceps elongated (Fig. II.22d; and Fig. II.20c).
3. Dorsal compound eye yellow.
4. Incisors and prosthecae of left and right mandibles (Figs. II.22n-q).
5. Number of spines on paraprocts (Figs. II.22h; 23a, b).

History and Discussion

Ulmer (1908) described *Baetis soror* from south-west Western Australia. This species resembles the South Australian species in hind wing venation and forceps structure. Ulmer recorded that "the costal and subcostal region of the fore wings are weakly tanned (browned)" [*sic*. translation from Ulmer, 1908], but the South Australian specimens possess a milky costal and subcostal region. Müller-Liebenau (1973) stated "However, the colour of the pterostigma can be useful, especially when one separates two related species in the same material". This colour difference is usually associated with other character differences, (genitalia and hind wing venation) and is not used as a primary specific character. Until further material from Western Australia is made available, it is

Fig. II.23. SEM micrographs of the paraprocts of nymphs of *Baetis soror* (a, b); *Centroptilum elongatum* (c, d) and *Tasmanophlebia lacus-coerulei* (e, f).

Scale lines : 100µm.

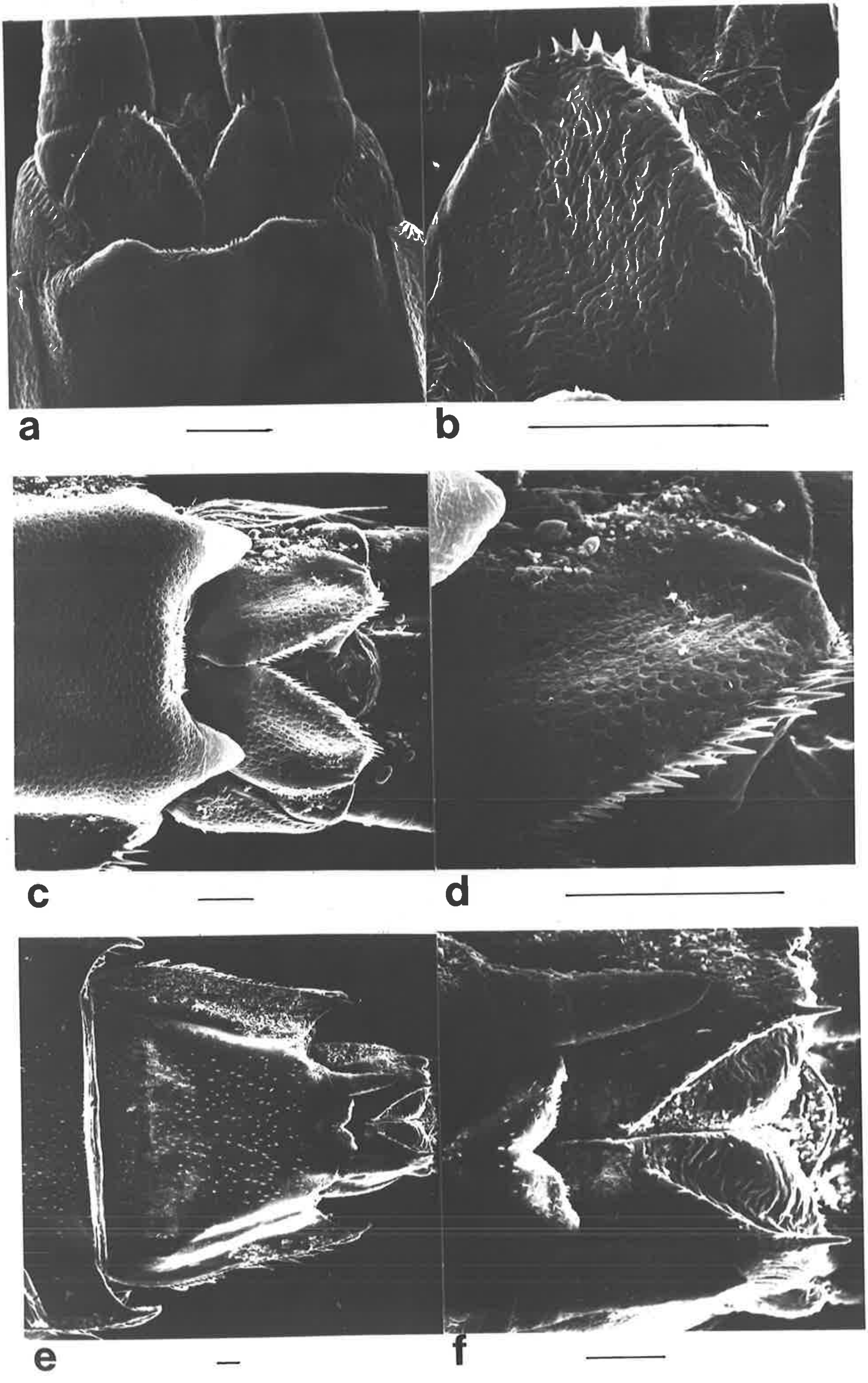

a
b
c
d
e
f

TABLE II.18. Morphometric characters of *Baetis soror* nymphs in which males differ from females.

Data refers to last instar nymphs from Deep Creek, Mt. Lofty Ranges, South Australia. Abbreviations as for Tables II.1 and II.4. * $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Character	Males $\bar{x}$	Males S.D.	Males Range	Females $\bar{x}$	Females S.D.	Females Range	d.f.	t	
NL/HW	1.51	0.09	1.40-1.66	1.89	0.16	1.68-2.15	16	6.37	***
MNW/HW	1.26	0.06	1.15-1.33	1.46	0.13	1.30-1.65	16	4.29	***
PNW/HW	0.87	0.06	0.76-0.96	1.10	0.05	1.05-1.16	16	9.43	***
FFL/HW	0.79	0.04	0.75-0.85	0.94	0.04	0.89-1.00	16	8.64	***
MFL/HW	0.82	0.03	0.76-0.85	0.98	0.08	0.78-1.05	16	5.75	***
HFL/HW	0.85	0.04	0.79-0.90	1.04	0.02	1.00-1.07	14	11.77	***
MT_aL/MFL	0.60	0.05	0.54-0.71	0.56	0.02	0.53-0.60	23	2.62	*
Labial palpi :									
BL/BW	2.17	0.20	2.00-2.50	1.97	0.14	1.80-2.25	18	2.63	*
AL/AW	0.32	0.04	0.27-0.40	0.37	0.04	0.30-0.40	19	2.30	*
Paraglossae L/W	3.16	0.28	2.80-3.60	2.78	0.21	2.67-3.20	20	3.64	**

considered that this single feature which differs from the type description is not enough to validate erection of a new species for the South Australian material. This material is therefore designated as *Baetis soror* Ulmer.

Variation of Character Expression.

Male imagos and nymphs of both sexes were analysed for geographically variable character expression by comparing populations from Deep Creek, Mt. Lofty Ranges and Spring Creek, Southern Flinders Ranges.

The comparison of the male imagos revealed twelve of the 30 characters compared were statistically different, being thoracic, limb and fore wing characteristics. The statistical parameters are given in Table II.19. The nymphal comparison also revealed a high degree of geographical variation with fifteen of the 25 analysed characters significantly different. Of these five were also sexually variable. Of the ten characters which showed relatively consistent geographical expression in the nymphs five showed sexual variation, therefore leaving only five morphometric characters which did not show geographical or sexual variation. These characters were fore leg; femur length/width, and tibia length/femur length, middle and hind femora length/fore femur length, and labium length/width. Table II.20 lists the statistical parameters of the morphometric characters of the nymphs of *Baetis soror* which displays differences between the two geographical populations. All characters show extensive overlap, even though the mean values are statistically different. All

TABLE II.19. Geographical variation in some morphometric characters of *Baetis soror* male imagos from Deep Creek, Mt. Lofty Ranges, and Spring Creek, Southern Flinders Ranges, South Australia.

Abbreviations as for Tables II.1 and II.4. * $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.01$.

	Deep Creek Population			Spring Creek Population					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
NL/BL	0.28	0.03	0.25-0.32	0.32	0.02	0.28-0.35	12	3.21	**
PNW/BL	0.11	0.01	0.10-0.13	0.13	0.01	0.12-0.15	10	3.12	*
FWL/BL	0.87	0.06	0.80-0.96	0.98	0.07	0.90-1.10	26	4.43	***
HWL/BL	0.17	0.02	0.14-0.20	0.21	0.02	0.19-0.24	26	6.80	***
FFL/BL	0.15	0.01	0.14-0.16	0.19	0.02	0.17-0.21	15	5.91	***
MFL/BL	0.12	0.01	0.11-0.14	0.15	0.01	0.13-0.16	21	5.23	***
HFL/BL	0.12	0.01	0.11-0.14	0.15	0.01	0.13-0.17	21	5.05	***
FT$_3$L/FFL	0.67	0.04	0.63-0.73	0.57	0.07	0.44-0.67	14	3.59	**
FT$_4$L/FFL	0.39	0.02	0.36-0.42	0.35	0.03	0.30-0.40	14	2.73	*
FT$_5$L/FFL	0.19	0.01	0.18-0.20	0.17	0.01	0.14-0.19	14	3.30	**
MT$_4$L/MFL	0.21	0.02	0.18-0.23	0.19	0.03	0.14-0.25	21	2.31	*
HT$_4$L/HFL	0.21	0.02	0.19-0.24	0.19	0.02	0.17-0.23	19	3.02	**

Table II.20. Geographical variation of morphometric characters of *B. soror* nymphs from Deep Creek, Mt. Lofty Ranges and Spring Creek, Southern Flinders Ranges, South Australia.

Abbreviations as for Tables II.1 and II.4. Characters marked (S) also exhibit sexual variations.

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

	Deep Creek Population			Spring Creek Population					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
NL/MNW	1.24	0.11	1.40-2.15	1.16	0.07	1.51-2.18	32	2.77	**
MNW/PNW	1.41	0.15	1.21-1.74	1.53	0.14	1.35-1.64	32	2.51	*
FT$_a$L/FFL	0.63	0.04	0.56-0.69	0.58	0.04	0.51-0.67	37	3.12	**
MFL/MFW	3.57	0.34	3.00-4.09	3.27	0.24	3.00-3.58	39	3.00	**
MT$_i$L/MFL	0.70	0.03	0.66-0.76	0.73	0.04	0.64-0.79	39	2.76	**
HFL/HFW	3.81	0.36	3.08-4.44	3.54	0.18	3.21-3.77	33	2.38	*
HT$_i$L/HFL	0.66	0.03	0.62-0.76	0.71	0.02	0.67-0.74	33	4.36	***
HT$_a$L/HFL	0.55	0.03	0.49-0.61	0.49	0.08	0.43-0.68	33	3.12	**
Labial palpi :									
ML/BL	0.70	0.05	0.60-0.80	0.74	0.08	0.64-0.90	36	2.01	*
glossae L/W	3.57	0.19	3.25-4.00	2.84	0.38	2.25-3.40	33	7.56	***
NL/HW(S)	1.68	0.22	1.38-2.15	1.88	0.27	1.51-2.18	31	2.35	*
MNW/HW(S)	1.35	0.14	1.15-1.65	1.65	0.26	1.24-2.04	32	4.26	***
PNW/HW(S)	0.97	0.13	0.76-1.16	1.07	0.12	0.93-1.24	32	2.42	*
MT$_a$L/MFL(S)	0.58	0.04	0.53-0.71	0.53	0.06	0.47-0.65	38	3.46	**
paraglossae L/W(S)	2.95	0.30	2.67-3.75	3.27	0.26	2.80-3.33	33	3.09	**

characters analysed but which were not statistically different are presented in Appendix 10.

Since *Baetis soror* is the only species of this genus in South Australia, no inter-specific comparisons could be made, and, therefore, no evaluation of the morphometric characters in specific determinations was made. Müller-Liebenau (1969, 1973) confined her study to qualitative characters and found these valuable in the specific separation of species. A similar conclusion has been drawn with the study of *B. soror*. The hind wing venation, colour of the turbinate eyes, and the genitalia distinguish the male imago, while the paraprocts, mouthparts, setation of the legs, and dorsal colour pattern distinguish the nymphs from other species in the genus.

Material Examined. South Australia : South East; Eight Mile Ck., Deep Ck., Jerusalem Ck., Mosquito Ck., Hitchcock Drain. Mt. Lofty Ranges; Deep Ck., Little Para R. Fleurieu Peninsula; The Deep Ck (Delamere), Finnis R., Hindmarsh R., Inman R., Tookayerta Ck., Yankalilla R. Southern Flinders Ranges; Nectar Brook Ck., Spring Creek. Northern Flinders Ranges; Balcanoona Ck., Brachina Ck., Bunyeroo Ck., Elatina Ck., Emu Ck., Wirrealpa Ck. Victoria : Crawford R., Darlots Ck., Eumarella R., Fitzroy R., Gawkers Ck., Glenelg R., Jimmy's Ck., Mt. Emu Ck., Trib. Mt. Zero Channel, Pidgeon Hole Ck., Shaw R., Stokes R., Stony Ck., Wando R., Wannon R., Wennicott R.

II.5.2. Genus *Centroptilum* Eaton 1869

Eaton, 1869 : 131-132
1871 : 107-108
1885 : 174-175
Harker, 1957 : 75-76
Riek, 1970a : 235

Male Imago Characteristics.

Fore wings with reduced cross vein system, marginal intercalaries single. Hind wings small, long and slender with hooked costal projection present or absent. Tarsal claws dissimilar, one blunt club shaped, one long and sharp.

Mature Nymph Characteristics.

Head hypognathous. Labrum broad, square, with a wide, deep V shaped median notch. Mandibles with two separate groups of incisors, prostheca with a basal brush of setae. Tarsal claws very long and slender, almost half as long as tarsus, with or without fine denticles. Seven pairs of flat plate like abdominal gills on segments 1-7. Three caudal filaments, appendix dorsalis well developed with long fine setae on lateral margins, cerci with long fine setae on mesal margin only.

History and Discussion.

Centroptilum is also a cosmopolitan genus, but it was not until Harker (1957) described *C. collendum* from Kuringae Chase, New South Wales, that an Australian species was recognised.

Eaton (1869) erected the genus *Centroptilum* to include *C. luteolum* (Müller) which originally was described in *Ephemera* by Müller in 1776. Although numerous species have been recorded from North America and Europe since the erection of this genus, *C. collendum* Harker is the only recorded Australian representative. A new species *C. elongatum* sp. nov. which is recorded in South Australia, is described from associated material from the Wannon River, Victoria. *C.elongatum* has a limited distribution in South Australia (see Chapter 6) and although many nymphs are present in the collections there are relatively few adult specimens. Consequently the type series was taken from a much larger collection made in Victoria, from which some assessment of variation of character expression could be made.

II.5.2.1 *Centroptilum elongatum* sp. nov.

Holotype Male

Body Length	8.20mm
Notal Length	2.01mm
Mesonotal Width	1.33mm
Pronotal Width	0.95mm
Fore Wing Length	7.05mm
Hind Wing Length	1.72mm
Cerci Length	14.02mm

Appendix dorsalis absent.

Head : light brown. Antennae brown, basal segment long, flagellum 0.62mm, total antennal length less than 1mm. Dorsal compound eyes turbinate, upper portion brown/orange, oval, lateral eyes grey. Ocelli white.

Thorax : pronotum brown, narrower than head. Scutum of mesonotum grey, lateral and posterior regions of scutoscutellum dark brown, median suture edged in black with white patches at posterior edge of scutellum. Metanotum dark brown with median backward produced projection (Fig. II.24c). Legs; fore leg femur light brown, tibia and tarsal segments darker brown, middle and hind legs light brown, tarsal segments darker brown. T_1 fused to tibia in all legs. Fore leg longer than middle and hind legs, fore leg femur length 1.19 x middle leg femur length, and 1.16 x hind leg femur length. Ratios of leg segments (second value is the combined tibia + T_1 length to femur length);

fore leg 1.00 : 1.18 : - : 0.50 : 0.44 : 0.26 : 0.16 (1.60mm)

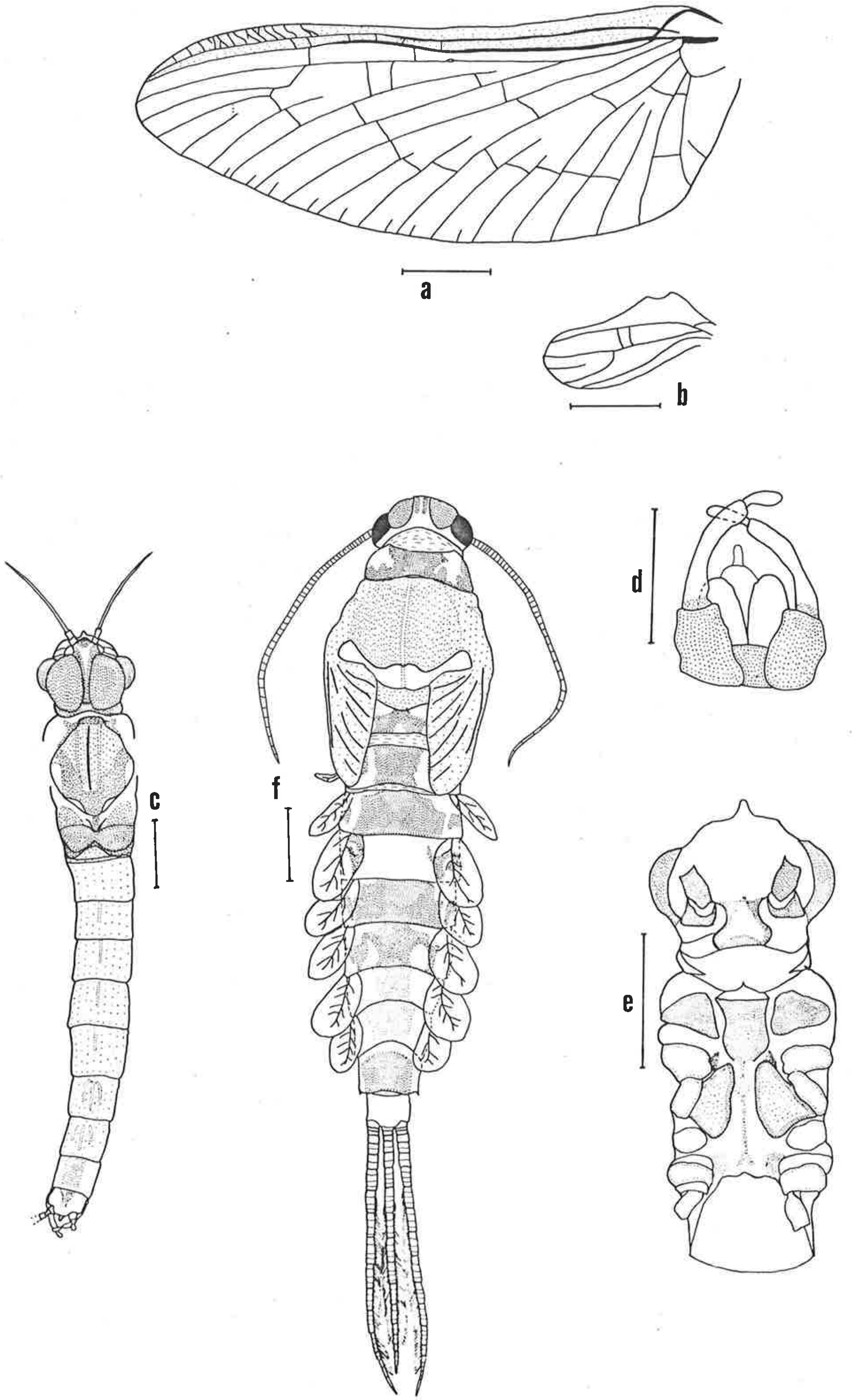
middle leg 1.00 : 0.75 : - : 0.19 : 0.10 : 0.08 : 0.16 (1.34mm)

hind leg 1.00 : 0.74 : - : 0.19 : 0.10 : 0.07 : 0.16 (1.38mm).

Tarsal claws dissimilar, one blunt, club shaped, one slender with terminal hook. Sternum light brown (Fig. II.24e). Prosternum dark brown. Mesosternum brown, lateral regions and coxae dark brown, basisternal length 1.28 x width, furcasternum length 0.5 x width, and equal to basisternal length, median longitudinal invagination broad with parallel margins divergent posteriorly. Metasternum light brown.

Fig. II.24. *Centroptilum elongatum*. a - e, male imago: a, fore wing; b, hind wing; c, dorsal colour pattern; d, genitalia, ventral view; e, thoracic sterna. f, mature nymph: dorsal colour pattern.

Scale lines : a,b,c,e,f 1mm.
d 0.5mm.


a
b
c
d
e
f

Wings : hyaline. Fore wing (Fig. II.24a); 2.78 x longer than wide, costal and subcostal spaces shaded with yellow, pterostigma with 10-14 cross veins, some forked, one faint cross vein in costal space present or absent, subcostal space with six cross veins. Bulla on R_1. Marginal intercalaries single, but faint. Hind wing (Fig. II.24b); 2.15 x longer than wide, with a curved costal projection, three longitudinal veins, second forked with one intercalary, two cross veins between first and second longitudinal veins.

Abdomen : brown dorsally with red tinges in patches on segments, 2, 3, 4, 6, 7, 8 and 9, segment 1 dark brown (Fig. II.24c). Light brown ventrally with paired brown markings on each side of median line. Cerci long, segments 1-26 dark brown, 27-49 lighter, appendix dorsalis absent.

Genitalia : (Fig. II.24d; Fig. II.20d); forceps four segmented, proximal segment rectangular 1.6 x longer than wide, second segment fused to third segment, third segment long and slender, bowed slightly, distal segment shorter, rounded apically. Pene covers paired, rectangular, rounded apically, divergent, extending beyond apex of proximal segment of forceps.

Mature Male Nymph (Fig. II.24f)

Body Length	7.68mm
Head Width	1.32mm
Notal Length	2.12mm
Mesonotal Width	1.68mm
Pronotal Width	1.16mm
Cerci Length	4.20mm
Appendix Dorsalis Length	3.44mm

Body cylindrical, general colour brown.

Head : hypognathous, brown. Dorsal compound eyes red/brown, lateral eyes black. Antennae 3.9mm long.

Thorax : pronotum width 0.88 x head width, brown with light lateral markings. Mesonotum width 1.27 x head width, brown without distinct markings, wing sheaths darker extending beyond anterior margin of second abdominal segment. Legs yellow/brown with black patches distally on femur about 2/3 of length (Fig. II.25a); tibia and tarsi yellow/brown, not marked. Tarsal claws very long and slender, half tarsal length, lined proximally with 13-20 fine denticles, distal half smooth and tapering. Ratios of leg segments;

fore leg	1.00 :	0.63 :	0.66	(1.28mm)
middle leg	1.00 :	0.62 :	0.54	(1.30mm)
hind leg	1.00 :	0.62 :	0.52	(1.30mm).

Femur length width ratios; fore leg 4.92, middle and hind leg 5.42.

Abdomen : brown, with tinges of red brown, segment 3 darker brown, segment 4 light red brown without dark markings, segment 5 darker (saddle-like), segments 6-9 light brown, segment 10 without dark markings, lateral flanges of segments 1-8 with an anteriorly directed V-shaped dark marking. Posterior margin of tergites with long spines and smaller minute spines between them. Hind margin of sternites similarly lined with long spines and only minute inner basal spines. Paraprocts rounded, with 25 large spines on internal and apical margins (Fig. II.25c; Fig. II.23d); hind margins of ninth sternite with developing forceps, separated by a concave depression with 24 spines

(Fig. II.25b; II.23c). Cerci well developed, mesal margins fringed with long fine setae, apices of segment groups dark brown, appendix dorsalis shorter, lateral margins lined with long fine setae. Gills on segments 1-7, single, plate-like with black, branched trachea (Fig. II.25d), first gill smallest, half moon shaped, second wider and longer, third and fourth larger, fifth and sixth largest, seventh larger than second, margins serrated with one short fine bristle in each depression.

Mouthparts : labrum rectangular (Fig. II.25e), length 0.77 x width, with a broad, deep, V-shaped concavity, with truncated apex, and lateral denticles near apex (Fig. II.25f), anterior margin lined with long setae on antero-lateral processes, and pinnate setae along sides of concavity. Left mandible (Fig. II.25i), outer incisors with four large teeth apically and four smaller teeth along inner margin, outer margin with one long spine, inner incisors with three large apical teeth and 3-4 small tubercles on inner basal margin, prostheca long, broadest proximally with paired apical projections, one long and slender with one apical spine seta , the other shorter, curved and blunt, with a sharp opposing tooth (similar to a bottle opener) (Fig. II.25j), molar region with 20 rows of grinding ridges. Right mandible (Fig. II.25k); outer incisors with three large teeth, outer margin with one long tapering spine, inner incisors with two contiguous teeth, prostheca strap-like, long and slender with 2-3 minute spines on apex, and two long setae near mid region (Fig. II.25*l*), molar region with two rows of 30-40 teeth. Hypopharynx simple, median lobe with a large, bulbous, apical tubercle, paragnaths ovate (Fig. II.25h). Maxillae (Fig. II.25m); galeo-lacinia broad, inner margin lined with rake setae, apex with long spine setae, palpi three segmented, longer than galeo-lacinia, basal segment long and slender, 3.67 x longer than wide, lined with short fine setae, segment ratios 1.00 : 0.55 : 1.09 (0.22mm). Labrum (Fig. II.25e); palpi three segmented proximal segment 2.43 x longer than wide, second segment narrow proximally, broad distally, distal segment short, broad with concave apical margin, lined with long spine setae, segment ratios 1.00 : 0.71 : 0.35 (0.34mm); glossae shorter than paraglossae, inner margin lined with spine setae, paraglossae curved over glossae, external margin lined with long fine setae, ventrally apex densely covered with setae.

Female Imago : resembles male, but lacks dorsal turbinate eyes, lateral eyes black. Body length 7.95mm, fore wing length 7.54mm, hind wing length 2.87mm. Thorax grey, abdomen red/brown. Costal margin of fore wing brown. Fore leg shorter than in male. Sub-anal plate with paraprocts lacking spines.

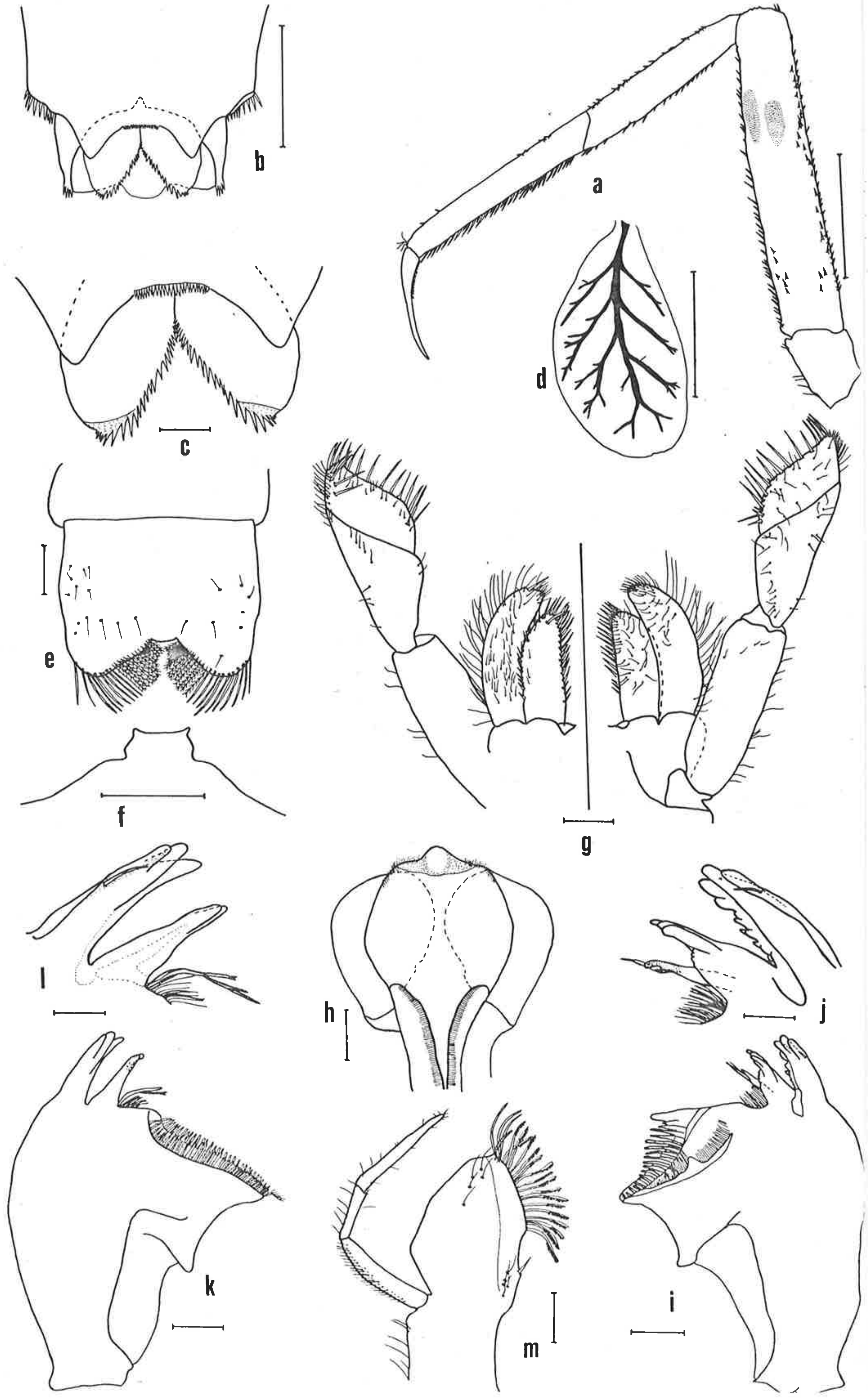
Female Nymph : similar to male, lacking dorsal compound eyes, lateral eyes black. Ninth abdominal sternite hind margin square and lined with spines.

Diagnostic Characters.

1. Genitalia, shape of last segment of forceps (Fig. II.24d; Fig. II.20c).
2. Hind wing lacks acute costal projection (Fig. II.24b).

Fig. II.25. *Centroptilum elongatum*, mature nymph: a, fore leg; b, paraprocts, ventral view; c, paraprocts, enlarged; d, third abdominal gill; e, labrum, dorsal view; f, antero-median emargination of labrum, enlarged; g, labium, dorsal (left) and ventral views; h, hypopharynx; i, left mandible, ventral view; j, left incisors and prostheca, enlarged; k, right mandible, ventral view; l, right incisors and prostheca, enlarged; m, right maxilla, ventral view.

Scale lines :	a,b,d	0.5mm.
	c,d,e,f,g,h,i,k,m	0.1mm.
	j,l	0.05mm.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3. Number of spines on paraprocts of nymphs (Figs.II.25b, c; 32c, d).

4. Incisors and prosthecae of mandibles (Figs. II.25i-*l*).

5. Labrum shape (Fig. II.25e).

6. Saddle-like colour pattern on abdomen (Fig. II.24f).

Type Locality : Wannon River just above Wannon Falls, near Wannon, Western Victoria, Grid reference 1:250,000 map series Hamilton Sheet 353482.
Collected 30th October, 1977 by P. Suter and A. Wells.

Type Specimens.

The Holotype male and nymphal type are located in the National Museum of Victoria. Five paratype male imagos and paratype nymphs are also placed in the National Museum of Victoria and five paratype males and nymphs are placed in the South Australian Museum.

Type Habitat.

The nymphs were found in fast flowing water about 500m above the Wannon Falls. Adult males and females were swarming in the afternoon sun above a grass covered bank about 10m above the water's edge.

The habitat records of this species in South Australia are quite variable, but may reflect only the season and flow conditions of the streams from which the collections were made. On Kangaroo Island, collections were made in September, 1976 (W. D. Williams) and November 1977 (J. E. Bishop) and *C. elongatum* nymphs were found occupying the flowing water, similar to the type habitat records. Collections from Mosquito Creek in south east South Australia in November 1977 (D. N. and P. J. Suter) were from a similar habitat to those occupied in Victoria and on Kangaroo Island. In Carrickalinga Creek on the Fleurieu Peninsula, South Australia, the collection was made in November 1977 when the creek was in the process of drying, and pools were being formed. It was from one of these stationary *Juncus* lined pools, that the only record of *C. elongatum* on the Fleurieu Peninsula, was made. At times of higher water levels and discharge, *C. elongatum* may be found occupying the faster flowing waters, rather than the stationary pool habitat recorded in November 1977. A more detailed discussion of the distribution of this species is given in Chapter 6.

Etymology of Specific Epithet

The specific epithet *elongatum* refers to the elongated distal segment of the forceps of the male imago. This long segment distinguishes *C. elongatum* from *C. collendum* Harker, the only other species in this genus described from Australia.

Affinities

Of the diagnostic features, the genitalia and hind wing characteristics clearly distinguish *C. elongatum* from *C. collendum* Harker. Harker's (1957) description records that the nymphs of *C. collendum* have long tarsal claws "about equal in length to the tarsus itself". *C. elongatum* has much shorter tarsal claws, being about half the tarsal length. Other differences between the nymphs are not obvious from Harker's description, and the nymphal morphotype of *C. collendum* has not been examined.

Material Examined. South Australia : South East; Mosquito Ck. Fleurieu Peninsula; Carrickalinga Ck. Kangaroo Island; Breakneck R., De Mole R., Rocky R., South West R., Stunsail Boom R., Western R. Victoria : Jimmy's Ck., Mt. Emu Ck., Wannon R.

II.5.3 Genus *Cloeon* Leach 1815

Leach, 1815 : 137
Eaton, 1868 : 87-88
1871 : 102
1885 : 179-181
Klapálek, 1905 : 106-107
Ulmer, 1916 : 17
1919 : 54
Tillyard, 1926 : 64
1936 : 53-55
Harker, 1950a : 24, 29
1954 : 266
1957 : 72-73
Scholes, 1961 : 38-39
Riek, 1970a : 236

Male Imago Characteristics.

Fore wings with reduced cross vein system, marginal intercalaries single; costal and subcostal region opaque or coloured. Hind wing absent. Forceps four segmented, second and third segments almost entirely fused.

Mature Nymph Characteristics.

Labrum broader than long with a shallow median notch. Mandibles with two separate groups of incisors, prosthecae with a basal brush of setae. Labial palpi three segmented, distal segment truncated at apex. Tarsal claws long and narrow, at least half as long as tarsi, with or without small denticles. Metathoracic wing (hind wing) sheaths absent. Gills on abdominal segments 1-7, flat plate-like, usually with double lamellae, (Edmunds, Jensen and Berner, 1976, record double and single). Three caudal filaments, cerci with (mesal) margin fringed with long fine setae, appendix dorsalis fringed on lateral margins.

History and Discussion

The genus *Cloeon* was erected in 1815 by Leach, to include *C. dipterum* (Linn. Fabr.). Eaton (1868) noted "A species (1 specimen in British Museum) is reputed to be from S. Australia"., and in 1885 he included Australia in the distribution of this cosmopolitan genus.

The first confirmed record of *Cloeon* in Australia was made by Ulmer (1916) when he recorded *C. virens* Klapálek (incorrectly spelt as *C. viridis* Klap. by Ulmer and later by Tillyard, 1926) from the Kimberley district, N.W. Australia. This species was originally described from Java by Klapálek (1905). A further species *C. fluviatile* Ulmer was described by Ulmer (1919) from New Guinea, and was later recorded at Armidale (N.S.W.) by Harker (1950a), who added the description of the egg.

Tillyard (1936) recorded the first purely Australian species of the genus, when the male imago, female imago and subimagos of *C. tasmaniae* were described from the Macquarie River, Tasmania. Harker (1957) described the first *Cloeon* nymph in her description of *C. nandirum* from Townsville, Queensland.

The present study recognises one new species, and *C. fluviatile* Ulmer from South Australia, and the descriptions include the characteristics used by Müller-Liebenau (1969, 1973) in her revision of *Baetis*. The nymph of *C. fluviatile* is described from South Australian material.

II.5.3.1 *Cloeon fluviatile* Ulmer 1919

Cloeon fluviatile Ulmer, 1919 : 54-57
Harker, 1950a : 24, 29
1954 : 266

The following description is based on one male imago from the Third Spring on the Oratunga Loop, Flinders Ranges, South Australia, collected 9th April 1977 by P. J. Suter.

Body Length	4.12mm
Notal Length	1.40mm
Mesonotal Width	0.80mm
Pronotal Width	0.56mm
Fore Wing Length	4.32mm
Cerci Length	8.53mm

Appendix dorsalis absent.

Head : dark brown. Antennae light brown 0.72mm long, proximal and second segment dark brown, rectangular. Dorsal compound eyes turbinate, upper portion yellow/brown, lateral portion lighter brown, lateral eyes black. Ocelli light brown.

Thorax : brown, notal sutures black. Legs; buff, T_1 fused in middle and hind tibia, only partially fused in fore tibia. Ratios of leg segments;

fore leg 1.00 : 1.76 : 0.07 : 0.68 : 0.49 : 0.27 : 0.20 (0.82mm)

middle leg 1.00 : 0.82 : - : 0.28 : 0.15 : 0.08 : 0.18 (0.78mm)

hind leg 1.00 : 0.86 : - : 0.26 : 0.12 : 0.07 : 0.19 (0.86mm).

Tarsal claws dissimilar, one blunt, club shaped, one slender with terminal hook. Sternum brown. Prosternum brown, triangular, rounded, truncated. Mesosternum; basisternum rectangular, length 1.80 x width, furcasternum triangular with concave lateral margins, truncated anteriorly, furcasternum length equals width, and is 2 x basisternum length (Fig. II.26c).

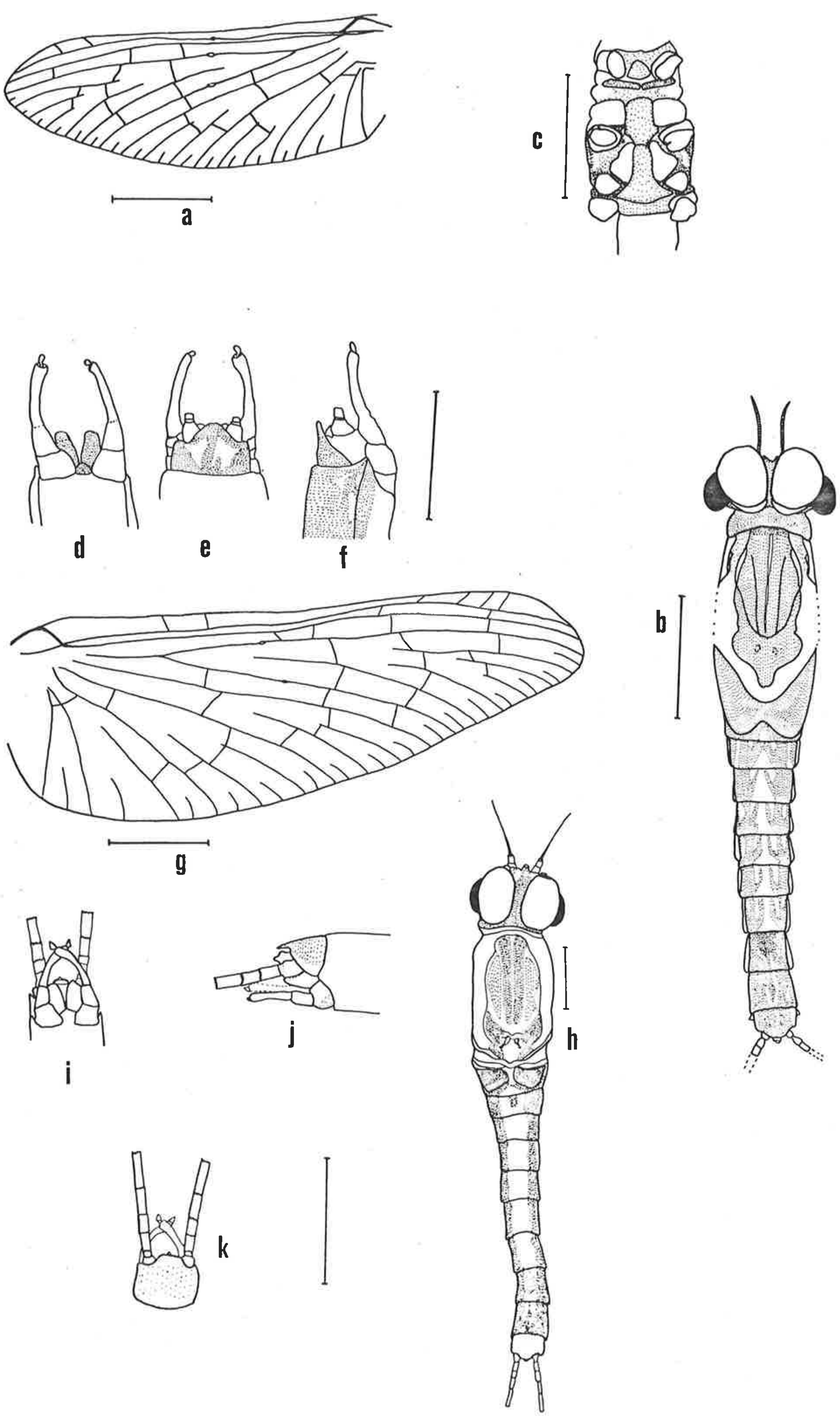
Wings : hyaline, fore wing (Fig. II.26a); length 2.70 x width, costal and subcostal region opaque, cream coloured, milky in pterostigmal region, pterostigma with 2-4 cross veins, no cross veins in proximal region of costal space, subcostal space without cross veins. Bullae on Sc, R_2 and $R_{4 \& 5}$. Marginal intercalaries single. Hind wings absent.

Abdomen : red/brown with light brown median markings on segments 1-7, segments 8, 9, 10 red/brown (Fig. II.26b). Light red/grey ventrally. Cerci long, white with red/brown joints every fourth segment, appendix dorsalis absent.

Genitalia : (Figs.II.26d-f; 20e). Forceps four segmented, proximal segment rectangular, length 0.69 x width, second segment slender, partially fused with third segment which is long and slender, distal segment short, with a basal stalk and globular apex. Penes covers large and obvious, extending to middle of second segment of forceps, separate, rectangular, apices divergent. Subgenital plate with a posterior brown projection which separates proximal segments of forceps.

Fig. II.26. *Cloeon fluviatile*. a - f, male imago: a, fore wing; b, dorsal colour pattern; c, thoracic sterna; d, genitalia, ventral view; e, genitalia, dorsal view; f, genitalia, lateral view. *Cloeon paradieniensis*. g - k, male imago: g, fore wing; h, dorsal colour pattern; i, genitalia, ventral view; j, genitalia, lateral view; k, genitalia, dorsal view.

Scale lines : a,b,c,g - k 1mm.
d,e,f 0.5mm.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Mature Male Nymph.

Body Length	5.08 - 5.60
Head Width	1.02 - 1.08
Notal Length	1.60 - 1.74
Mesonotal Width	1.38 - 1.46
Pronotal Width	0.92 - 0.98
Cerci Length	3.50 - 5.40
Appendix Dorsalis Length	1.62 - 3.80

Body cylindrical, general colour light brown.

Head : hypognathous, brown. Dorsal compound eyes red/brown, lateral eyes black. Antennae long, 3 x longer than head width.

Thorax : pronotum width 0.91 x head width, brown with light markings. Mesonotum width 1.35 x head width, uniformly light brown, wing sheaths darker extending beyond anterior margin of second abdominal segment. Metanotum without wing sheaths. Legs cream with brown banding, one band on distal 1/3 of femur, one proximally on tibia, tarsus with one proximal and one distal band (Fig. II.27a). Tarsal claws long and slender with two ventral rows of peg like denticles (Fig. II.27b).

Ratios of leg segments;

fore leg	1.00 : 0.73 : 0.63	(1.01mm)
middle leg	1.00 : 0.74 : 0.54	(1.03mm)
hind leg	1.00 : 0.68 : 0.53	(1.16mm).

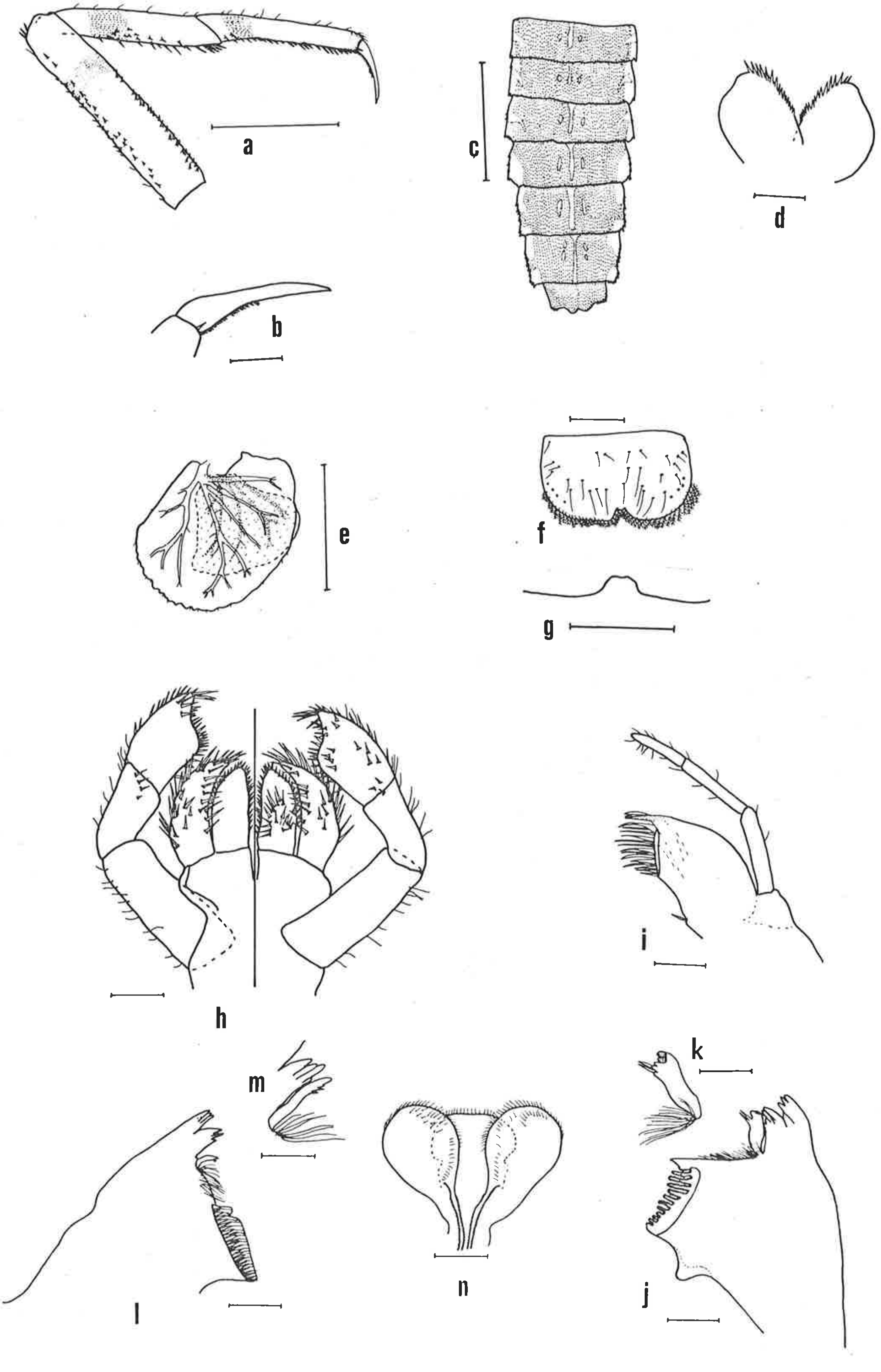
Femur length width ratios; fore leg 4.87, middle leg 5.01, and hind leg, 5.27.

Abdomen : brown, with dark brown rectangular patches on each segment, edged with light brown, a central light stripe on each segment (Fig. II.27c), lateral flanges of segments 7-10 lined with spines, 1-2 spines on postero-lateral margins. Posterior margins of tergites with large single spines. Paraprocts with 16-22 spines on inner and apical margins, largest spine at apex, smaller mesally (Fig. II.27d). Cerci long, white, apices of segment groups brown, fringed on mesal surface with long fine setae, appendix dorsalis shorter, lateral margins lined with long fine setae. Gills (Fig. II.27e), on segments 1-7, with paired lamellae on segments 1-6, single on segment 7, black branched trachea, seventh gill smallest, fifth gill largest, margins serrated with short fine bristle in each depression.

Mouthparts : labrum (Fig. II.27f); rectangular 1.94 x broader than long with a U-shaped concavity in centre of anterior margin (Fig. II.27g), fine setae on dorsal surface, anterior margin lined with pinnate setae. Left mandible (Fig. II.27j); robust, outer incisors with 3-4 large teeth, inner incisors with 4-5 teeth, prostheca with three apical denticles and two sharp spines (Fig. II.27k), molar region of grinding ridges. Right mandible (Fig. II.27*l*); robust, outer incisors with three apical teeth, inner incisors with three large and one small teeth, prostheca long and slender, mesal margin near apex with two short spines and one small denticle (Fig. II.27m). Hypopharynx (Fig. II.27n); simple, median lobe ovate, paragnaths ovate, lined with short fine setae. Maxillae (Fig. II.27i); galeo-lacinia slender, with three well developed apical teeth, lined mesally with 12-15 large spine setae, palpi three segmented, longer than galeo-

Fig. II.27. *Cloeon fluviatile*, mature nymph: a, fore leg; b, fore claw; c, dorsal abdominal colour pattern; d, paraprocts; e, third abdominal gill; f, labrum, dorsal view; g, antero-median emargination of labrum; h, labium, dorsal (left) and ventral views; i, left maxilla, ventral view; j, left mandible, ventral view; k, left prostheca, enlarged; l, right mandible, ventral view; m, left prostheca, enlarged; n, hypopharynx.

Scale lines :	c	1mm.
	a,e	0.5mm.
	b,d,f - j, l, n	0.1mm.
	k,m	0.05mm.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lacinia, proximal segment 5.83 x longer than wide, segment ratios; 1.00 : 0.80 : 0.82 (0.15mm), distal segment lacks apical spines. Labium (Fig. II.27h); palpi three segmented, length of proximal segment 2.20 x width, apical margin of distal segment concave lined with short spine setae, segment ratios; 1.00 : 0.61 : 0.80 (0.22mm); glossae shorter than paraglossae, paraglossae outer margin convex curving over glossae, margins of glossae lined with short spine setae, paraglossae margins with longer setae.

Female Imago : Lacks dorsal compound eyes, lateral eyes black, fore leg shorter than male, otherwise similar to male imago.

Female Nymph : Similar to male nymph, lacks dorsal compound eyes, lateral eyes black, thorax broad, wider than head.

Diagnostic Characteristics.

1. Distal segment of forceps minute, globular (Fig. II.26d-f; 20e).
2. Turbinate eyes yellow/brown.
3. Incisors and prostheca of left and right mandibles (Figs.II.27j-m).
4. Paraproct spination (Fig. II.27d).

History and Discussion.

C. fluviatile was described in 1919 by Ulmer from specimens from New Guinea. Harker (1950a) recorded this species from Armidale, New South Wales, and described the egg. Since the type material is held in the Berlin Museum (Ulmer, 1919) or the Stockholm Museum (Harker, 1950a, 1954) it was not available for this study. The South Australian specimens have no features which distinguish them from the species described by Ulmer, and until the type material is examined they are placed as *C. fluviatile* Ulmer.

Material Examined. South Australia : Mt. Lofty Ranges; Torrens R. Southern Flinders Ranges; Ohlenmeyer Reservoir, Rocky R., Wild Dog Ck. Northern Flinders Ranges; Balcanoona Ck., Bendieuta Ck., Brachina Ck., Elatina Ck., Emu Ck., Eregunda Ck., Kanyaka Ck., Marolana Ck., Mt. Chambers Ck., Parachilna Ck., Stubbs Waterhole, Willigan Ck., Creek in Warren Gorge.

II.5.3.2 *Cloeon paradieniensis* sp. nov.

Holotype Male

Body Length	7.80mm
Notal Length	2.96mm
Mesonotal Width	1.20mm
Pronotal Width	0.92mm
Fore Wing Length	7.05mm
Cerci Length	15.73mm

Appendix dorsalis absent.

Head : brown. Antennae short, 1.02mm, buff. Dorsal compound eyes turbinate, yellow dorsally, brown laterally, lateral eyes grey. Ocelli white.

Thorax : pronotum light brown, narrower than head. Mesonotum brown with light brown mesonotal sutures and patterns, dark brown postero-lateral regions of scutoscutellum. Legs; white-cream, fore leg longer than middle and hind legs, fore leg femur length 1.06 x middle leg femur length, and equal to hind leg femur length. T_1 of middle and hind legs fused to tibia. Ratios of leg segments;

fore leg 1.00 : 1.68 : 0.05 : 0.70 : 0.50 : 0.28 : 0.18 (1.48mm)

middle leg 1.00 : 1.01 : - : 0.29 : 0.13 : 0.06 : 0.16 (1.40mm)

hind leg 1.00 : 0.99 : - : 0.26 : 0.12 : 0.06 : 0.15 (1.46mm).

Tarsal claws dissimilar, one blunt club shaped, one slender and terminally hooked. Sternum damaged in holotype.

Wings : hyaline (Fig. II.26g); 2.89 x longer than wide, veins buff, transparent, pterostigmal region with 3-4 cross veins, well separated, proximal region of costal space with two cross veins, subcostal space with two cross veins in distal half. Three bullae present, one in each of Sc, R_2 and $R_{4\ \&\ 5}$. Marginal intercalaries single. Hind wings absent.

Abdomen : red/brown with a light brown dorsal stripe, segments 8 and 9 dark red/brown, 10 lighter (Fig. II.26h). Cerci long, appendix dorsalis reduced to a vestigial stump.

Genitalia : (Figs. II.26i-k; 20f); forceps four segmented, proximal segment short and broad, second segment short, narrower than proximal segment, almost fused with third segment, third segment long and narrow, bulbous apically, distal segment short and angular, conical. Penes covers broad, extending beyond fusion of second and third segments of forceps, bluntly pointed, divergent apices.

Mature Male Nymph

Head Width	1.31mm
Notal Length	1.96mm
Mesonotal Width	1.64mm
Pronotal Width	1.15mm
Cerci Length	6.23mm
Appendix Dorsalis Length	4.59mm

Body cylindrical, red/brown dorsally, light brown ventrally.

Head : hypognathous, brown with white epicranial sutures. Dorsal compound eyes red/brown (sepia), lateral eyes black. Ocelli black. Antennae long, 4.92mm, proximal and second segment brown, flagellae buff.

Thorax : pronotum width 0.88 x head width, brown with median longitudinal white stripe, no other markings. Mesonotum width 1.25 x head width, brown with light median longitudinal stripe, wing sheaths black extending to third abdominal segment. Metanotum dark brown, without wing sheaths. Sternum light brown, with little sclerotization. Legs buff without markings, femora lined with short spine setae, posterior margin of tibia and tarsus lined with longer spine setae, anterior margins with long fine setae (Fig. II.28a). Tarsal claws long and slender, with two ventral rows of peg-like denticles.

Ratios of leg segments;

fore leg	1.00 : 0.67 : 0.58	(1.44mm)
middle leg	1.00 : 0.67 : 0.51	(1.56mm)
hind leg	1.00 : 0.79 : 0.60	(1.68mm).

Femur length to width ratios; fore leg 5.18, middle leg 6.05, hind leg 6.51.

Abdomen : red/brown dorsally, yellow/brown ventrally, without definite colour pattern, overlap of segments darker brown. Lateral margins of segments 7-10 lined with spines, postero-lateral margins with 2-3 spines, posterior margins of tergites with large and small irregularly placed spines. Paraprocts broadly triangular, lined on mesal margin with 27-30 large spines (Fig. II.28b). Cerci long, mesal margin fringed with long fine setae, appendix dorsalis shorter, lateral margins fringed with long fine setae, every fourth segment red/brown, giving banded appearance. Gills; seven pairs, lamellae paired on segments 1-6 (Fig. II.28e), seventh single, margins of gills serrated with a single fine bristle.

Mouthparts : labrum (Fig. II.28c); rectangular, 1.5 x broader than long with a deep concavity in centre of anterior margin (Fig. II.28d), spine setae on dorsal surface, anterior margin lined with long, fine setae and pinnate setae. Left mandible robust (Fig. II.28i), outer incisors with four teeth, inner incisors with 3-4 teeth, prostheca robust with a corrugated apex of 5-6 rounded teeth and two long spines mesally (Fig. II.28j), molar region with rows of grinding ridges.

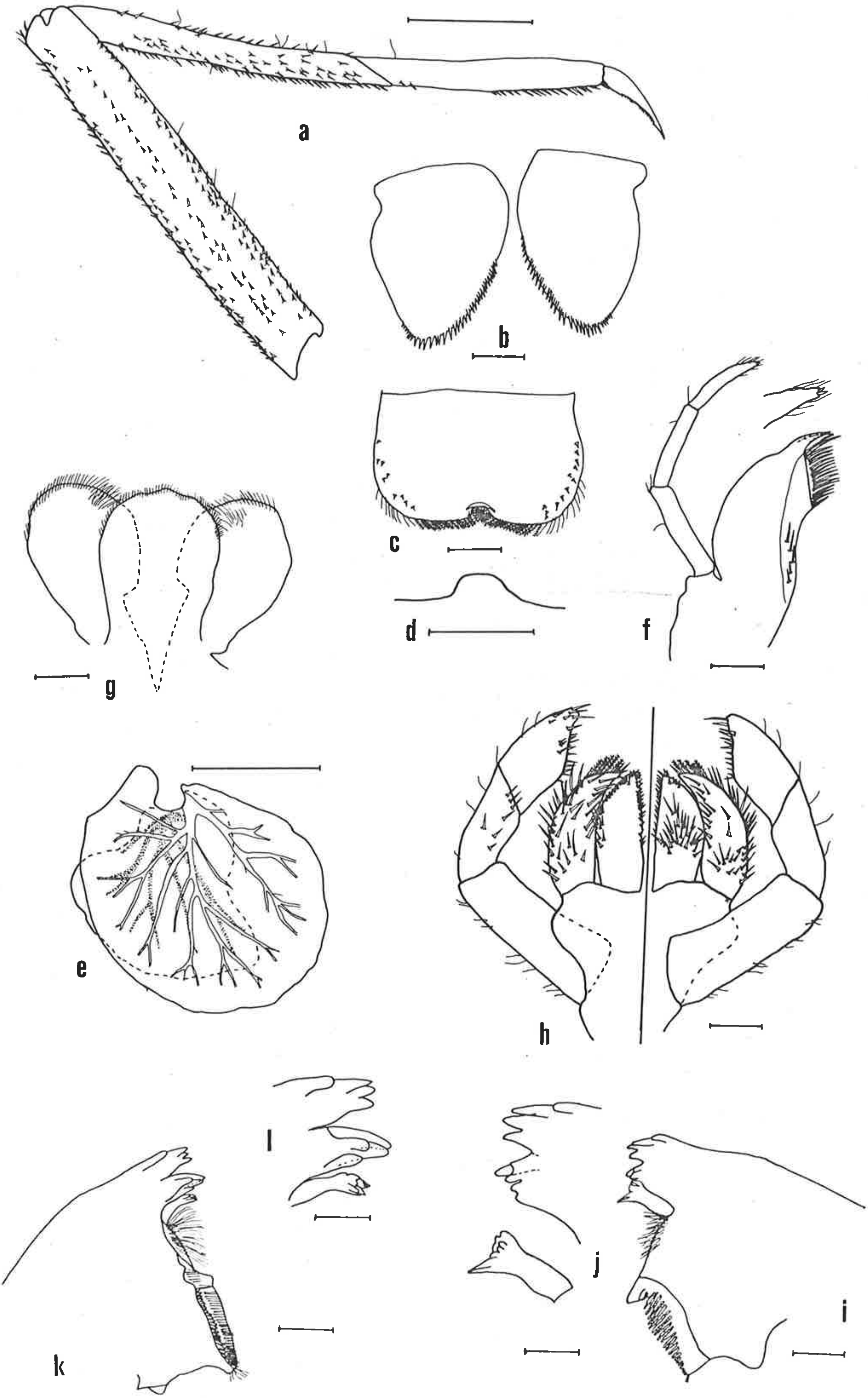
Right mandible (Fig.II.28k); robust, outer incisors with four teeth, inner incisors with two large teeth and two smaller teeth, prostheca robust with apex of 6-8 tooth-like ridges (Fig. II.28l), molar region with grinding ridges. Hypopharynx (Fig. II.28g); simple, median lobe rounded with a small median bulbous projection, paragnaths ovate, lined with short fine setae. Maxillae (Fig. II.28f); galeo-lacinia long and narrow, with three well developed sharp teeth apically, mesal margin lined with 3-4 strap-like setae fringed on one side with fine hairs, and 16 long setae, palpi three segmented, longer than galeo-lacinia, proximal segment 5.33 x longer than wide, segment ratios 1.00 : 0.69 : 0.88 (0.24mm), distal segment fringed with fine setae, and two small terminal teeth. Labium (Fig. II.28h); palpi three segmented, length of proximal segment 2.74 x width, apical margin of distal segment slightly concave, segment ratios 1.00 : 0.56 : 0.48; glossae shorter than paraglossae, paraglossae with outer margin convex curving over glossae, margins of glossae fringed with short spine setae, margins of paraglossae with long spine setae, apex with pinnate setae.

Female Imago : Without dorsal compound eyes, fore legs shorter than male. Fore wing; costal and subcostal spaces shaded with red brown, twelve cross veins in costal space. Body colour red brown.

Female Nymph : Similar to male, lacks dorsal compound eyes, lateral eyes black, thorax broader than male, pronotum wider than head.

Fig. II.28. *Cloeon paradieniensis*, mature nymph: a, fore leg; b, paraprocts; c, labrum, dorsal view; d, antero-median emargination of labrum; e, third abdominal gill; f, right maxilla, ventral view, with enlarged apex of terminal segment of the palp; g, hypopharynx; h, labium, dorsal (left) and ventral views; i, left mandible, ventral view; j, left incisors and prostheca, enlarged; k, right mandible, ventral view; l, right incisors and prostheca, enlarged.

Scale lines :		
	a,e	0.5mm.
	b - d, f - i, k	0.1mm.
	j,l	0.05mm.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Diagnostic Characteristics.

1. Distal segment of forceps conical shape (Fig II.26i-k; 20f).

2. Turbinate eyes yellow.

3. Female with costal and subcostal spaces shaded red brown.

4. Incisors and prostheca of left and right mandibles (Figs. II.28i-*l*).

5. Paraproct spination (Fig. II.28b).

6. Maxillary palpi with terminal spines on distal segment (Fig. II.28f).

Type Locality.

Little Para River at Paracombe, Mt. Lofty Ranges, South Australia, Grid Reference 1:250,000 map series, Adelaide Sheet 179695. Collected 20th October, 1976 by J. H. Diener and P. J. Suter.

Type Specimens.

Holotype male and nymphal type and allotype female are located in the National Museum of Victoria. This short type series is because this species is only known from two collections from the type locality, and one in the drain system of the South East. Further material has not been collected.

Type Habitat.

The nymphs were found in a non-flowing pool system in a culvert beside the Paracombe road. The pool was overgrown with *Nasturtium* sp. and *Lemna* sp. Adults were raised in the laboratory from mature nymphs collected from the type locality.

Etymology of the Specific Epithet.

The specific epithet *paradieniensis* refers to the river (Little Para River), and is in recognition of J. H. Diener whose collection from the Little Para River was the first of this species.

Affinities

Cloeon paradieniensis resembles all the described Australian species, but it can be readily distinguished by the conical shaped distal segment of the forceps of the male imago. The nymph can only be compared with *C. nandirum* Harker and *C. fluviatile* Ulmer, the only Australian species associated with their nymphs. The shape of the labrum clearly distinguish the nymphs of *C. paradieniensis* and *C. nandirum*, but as the type material is in the British Museum, and the description given by Harker (1957) was not comprehensive enough, no further character comparisons are possible.

The nymphs of *C. paradieniensis* can be distinguished from *C. fluviatile* Ulmer initially by size, the latter species being less than 6mm, the former greater than 8mm. The number of spines on the paraprocts, the lack of bands on the femora, spines on the distal segment of the maxillary palpi, and the shape of the prostheca of the right mandible also distinguish the two species found in South Australia. Tabulated comparisons of all Australian *Cloeon* species is given in Table II.21, with data taken from the present study, and from published descriptions by Klapálek (1905), Ulmer (1919), Tillyard (1936) and Harker (1957).

II.6 Systematics: Family SIPHLONURIDAE

This family has representatives in the temperate and cooler regions of the world, being most diverse in the Holarctic region, South America, Australia and New Zealand. The four Australian genera; *Tasmanophlebia* Tillyard, *Ameletoides* Tillyard, *Coloburiscoides* Lestage and *Mirawara* Harker, are endemic, being recorded mainly from the south-eastern region of the Great Dividing Range, and the Tasmanian highlands (*Tasmanophlebia* only), with *Mirawara* the exception, being found as far north as central Queensland.

Riek (1955, 1970a) considered the Siphlonuridae as a subfamily (Siphlonurinae) of the Baetidae, but Edmunds (1972), Riek (1973), and Edmunds, Jensen and Berner (1976) consider the Siphlonuridae as a distinct family. The Australian genera all belong to different subfamilies within the Siphlonuridae, the Siphlonurinae (*Ameletoides*), Ameletopsinae (*Mirawara*), Coloburiscinae (*Coloburiscoides*) and Oniscigastrinae (*Tasmanophlebia*), and it is the classification outlined by

TABLE II.21. Tabulated comparison of all described species of *Cloeon* in Australia. Data collected from the present study, and from published descriptions by Klapálek (1905), Ulmer (1919), Tillyard (1936) and Harker (1957).

	Cloeon fluviatile	*C. paradieniensis*	*C. nandirum*	*C. virens*	*C. tasmaniae*
MALE IMAGO :					
Body Length (mm)	4.12	7.80	7	6	7
Fore Wing Length (mm)	4.32	7.05	4	6	6
Fore Wing Width	1.60	2.44	1.6	2.27	2.4
Cerci Length	8.53	15.73	-	11-12	12
Eye Colour	Sepia	Yellow	Orange	-	Buff-pink
Pterostigmal cross veins	2-4	3-4	5	4-5	5
C/Sc basal cross veins	0	2-5	0	6	-
Sc/R cross veins	0	2-6	0	7	-
Costal Coloration	Milky	Milky	Milky	Emerald green in females	Cream
Genitalia					
Forceps, terminal segment	Short and narrow	Triangular	Long and narrow	Short and narrow	Globular
Penes Covers	Rectangular, flat apically	Pointed apically	?	?	?
NYMPH :				UNKNOWN	UNKNOWN
Body Length (mm)	5.08-5.60	-	6		
Head Width (mm)	1.02-1.08	1.31	-		
Cerci Length (mm)	3.50-5.40	6.23	-		
Appendix dorsalis Length	1.62-3.80	4.59	-		
Legs	Banded	Not banded	Not banded		
Left Mandibles					
Outer incisors	3-4 teeth	3-4 teeth	-		
Inner incisors	4-5 teeth	5-6 teeth	-		
Prostheca	3 denticles + 2 sharp spines	5-6 teeth + 2 long spines	-		
Right Mandibles					
Outer incisors	3 teeth	4 teeth	-		
Inner incisors	3 large, 1 small	2 large, 2 small	-		
Prostheca	Long and slender, 2 short spines + 1 denticle apically	robust, 6-8 tooth-like ridges	-		
Maxillary palpi	No terminal teeth	2 Terminal teeth	-		

Edmunds, Jensen and Berner (1976) that has been adopted in the present study.

Male Imago Characteristics: Wings with complete cross vein system, posterior branch of MP of fore wing attached to main MP vein. Hind wings well developed with extensive cross vein system, large, from one-third to half as long as fore wing. Eyes simple, upper portion larger than lower portion, but not distinctly separate. Hind tarsi with four segments. Forceps three or four segmented.

Mature Nymph Characteristics : Body cylindrical and streamlined. Head hypognathous to prognathous. Abdomen slightly dorso-ventrally flattened, postero-lateral margins of each segment produced backwards forming a sharp projection. Cerci with long fine setae on mesal side only, appendix dorsalis lateral margins lined with long fine setae. Gills on abdominal segments 1-4 or 1-7.

II.6.1 Genus *Tasmanophlebia* Tillyard 1921

Tillyard, 1921 : 409-412
1926 : 62
1933 : 12-13
1936 : 27
Lestage, 1935a : 132
1935b : 350-353 (in part as *Tasmanophlebioides*)
Harker, 1950a : 29
1954 : 267

Riek, 1955 : 268-269

1970a : 235

Scholes, 1961 : 21-23

Male Imago Characteristics : Fore wing with tornus at half of wing length or beyond. Hind wing about half as long as fore wing, and nearly as wide. Tarsi of middle and hind legs four segmented (five segmented in fore leg), tarsal claws dissimilar, one broad blunt, club-shaped, one long, slender and hooked. Cerci well developed, appendix dorsalis vestigial or absent.

Mature Nymph Characteristics : Body cylindrical, abdomen dorso-ventrally flattened. Head hypognathous. Abdominal segments with median dorsal crest and lateral flanges with postero-lateral projections, gills on segments 1-4, first pair operculate, covering other three which are membranous and ovoid. Cerci well developed, appendix dorsalis reduced.

History and Discussion.

The genus *Tasmanophlebia* was erected by Tillyard (1921) to include the Tasmanian species *T. lacustris*, which was recorded from lakes and streams at high altitudes.

In 1933 Tillyard described the mayflies of the Mt. Kosciusko Region, and included the descriptions of two new species of *Tasmanophlebia*, *T. lacus-coeruli* and *T. nigrescens*, both associated with their respective nymphs. Tillyard noted that *T. nigrescens* imagos resembled closely *T. lacustris* in size and habits, but distinguished the two species by the black appearance of the subimagos of *T. nigrescens* and the three segmented forceps rather than four as recorded in *T. lacustris*. The nymphs of *T. nigrescens* and *T.lacus-coerulei* differ in the dorsal abdominal crest, with the latter species having tooth-like projections on segments 1-7, and the former on segments 1-5. The nymph of *T. lacustris* described by Tillyard (1936) resembled *T. nigrescens* in possessing a dorsal abdominal crest with projections on segments 1-5, but Tillyard stated that "these are much smaller and less nodding than in *T. nigrescens*, that of seg. 1 particularly being small."

Lestage (1935b) separated the two Australian mainland species placing them in *Tasmanophlebioides*, primarily on the forking of the MP of the hind wing and on the structure of the male forceps. Tillyard (1921) described *Tasmanophlebia lacustris* as possessing forceps with four segments, whereas the mainland species had only three segments.

Harker (1950a) apparently was unaware of Lestage's (1935b) paper, and placed all species in *Tasmanophlebia* Tillyard. Subsequently, Harker (1954) recognised the classification designated by Lestage. Riek (1955) noted that "Lestage considered the forceps of *lacustris* to be 4-segmented whereas they are really only 3-segmented as in *lacus-coerulei* and *nigrescens*. The forking of MP in the hindwing varies with the individual specimen in all three species, in *lacustris* it may fork closer to the wing margin than figured by Tillyard, and in *lacus-coerulei* and *nigrescens* it may be more basad but it is always well after the middle of the vein." Consequently all described species were placed in *Tasmanophlebia* Tillyard.

Riek (1955) also noted the similarity between *T. lacustris* and *T. nigrescens*, noting the similarities in size, male genitalia and veins of the hind wing and he suggested that the darker coloration may be subspecific rather than specific. He apparently was unaware of Tillyard's (1936) description of the nymph of *T. lacustris*, as he (Riek, 1955) recorded this nymph as unknown. The similarities between the nymphs of *T. lacustris* and *T. nigrescens*, plus the similarities of the genitalia and venation suggest strongly that these species may in fact be synonymous, as darker coloration appears a meagre characteristic to separate either species or subspecies. Speculation on this point will continue until extensive collections from the known distribution of these species are compared and analysed. (A review of the Siphlonuridae is in progress by I. Campbell, pers. comm.).

All species of *Tasmanophlebia* were recorded as high altitude species and appeared to have similar habitat requirements. Riek (1970a) noted that they are semi-burrowers in sand, and all published localities from which they are recorded have sandy substrates. However, one species has been found in South Australia at an altitude of only 120m above sea level. This species, *T. lacus-coerulei*, was previously only recorded from Blue Lake, Mt. Kosciusko at an altitude of 6200ft. These extremes of altitude, plus evidence from collections made during this study (Chapter 6) suggest that sandy substrate and still, or slow flowing water are the most important habitat requirements of this genus, rather than the high altitude with which they have been previously correlated.

II.6.1.1 *Tasmanophlebia lacus-coerulei* Tillyard 1933.

Tasmanophlebia lacus-coerulei Tillyard, 1933 : 13-17
Tasmanophlebioides lacus-coerulei Lestage 1935b : 351-353
Tasmanophlebia lacus-coerulei Harker, 1950a : 29
Tasmanophlebioides lacus-coerulei Harker, 1954 : 267
Tasmanophlebia lacus-coerulei Riek, 1955 : 270

Tillyard (1933) described the species from all stages. The following description is of one male imago from Tookayerta Creek, Fleurieu Peninsula, South Australia. Adult specimens are rare in collections from South Australia, and for this reason the mean, ranges and standard deviations are based on only three animals.

	$\bar{x}$	SD	n	Range
Body Length	10.40	1.03	3	9.40 - 11.46
Fore Wing Length	9.54	0.90	3	8.53 - 10.26
Fore Wing Width	2.90	0.43	3	2.42 - 3.25
Hind Wing Length	4.53	0.61	3	3.86 - 5.06
Hind Wing Width	2.51	0.26	3	2.23 - 2.74
Cerci Length	4.71	(other cerci damaged)		
Appendix Dorsalis Length	0.24	0.14	3	0.08 - 0.32

Head : light brown. Dorsal region of compound eyes burgundy, lateral region brown. Antennae 0.96mm long, proximal segment short (0.04mm), second segment 0.12mm long, flagellae long, 0.76mm, light brown.

Thorax : pronotum, mesonotum, brown. Legs with numerous spines and tubercles on all, except distal, tarsal segments, spines largest on tarsi of middle and hind legs. Fore leg dark brown, longer than middle and hind legs, fore leg femur length 2.11 x middle leg femur length and 1.87 x hind femur length. Middle and hind legs light brown, first tarsal segment fused to tibia. Ratios of leg segments;

fore leg 1.00 : 0.67 : 0.63 : 0.47 : 0.52 : 0.47 : 0.28 (2.24mm)

middle leg 1.00 : 0.84 : - : 0.17 : 0.17 : 0.14 : 0.29 (1.06mm)

hind leg 1.00 : 0.80 : - : 0.17 : 0.17 : 0.12 : 0.28 (1.20mm).

Tarsal claws dissimilar, one blunt club-shaped, one slender and terminally hooked (Fig. II.29f). Sternum brown. Prosternum heavily sclerotized with concave longitudinal sutures that diverge anteriorly and posteriorly. Mesosternum lightly sclerotized, basisternum long, narrow, wedge-shaped, length 1.25 x anterior width, furcasternum length equal to width, 1.14 x basisternum length, median longitudinal invagination narrow with smoothly convex posterior margin.

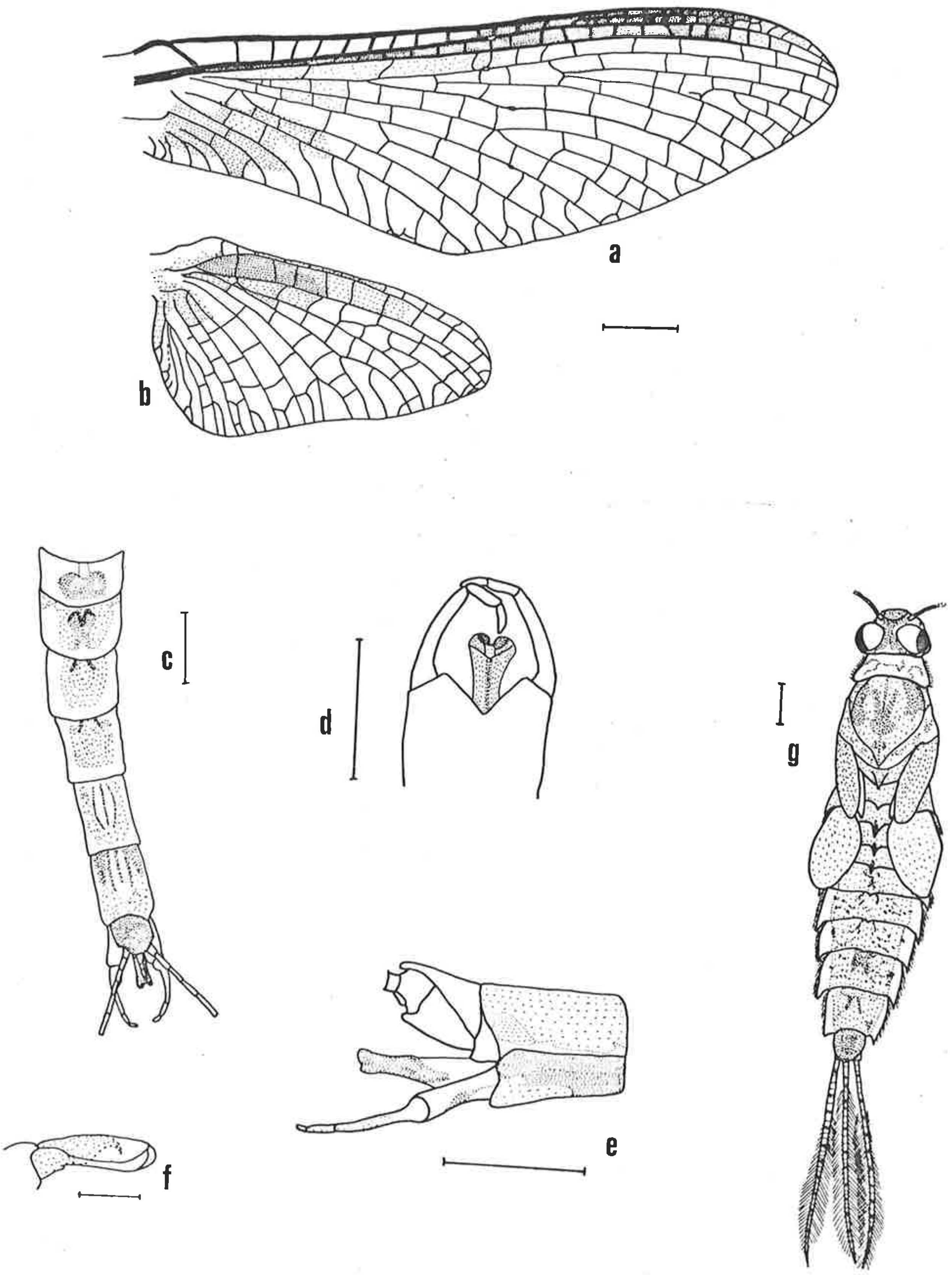
Wings : fore and hind wings hyaline, tinged with yellow, veins brown. Fore wing (Fig. II.29a); 3.31 x longer than wide, costal and subcostal region shaded with brown, radial and proximal regions of median, cubital and anal veins tinged with yellow, pterostigmal region with numerous anastomosed cross veins, four bullae present, one in each of Sc, R_2, $R_{4 \& 5}$ and MA_1. Hind wing (Fig. II.29b); 1.79 x longer than wide, half as long as forewing (0.47 x), subcostal space shaded with brown, costal, subcostal and proximal regions of the radial and anal veins tinged with yellow, cross veins brown, and numerous.

Abdomen : brown, speckled with black, segments 8 and 9 with median black stripe and two convex lateral stripes, segment 10 black (Fig. II.29c). Cerci long, dark brown, appendix dorsalis vestigial, of 1-4 segments.

Genitalia : (Fig. II.29d, e; 31a, b); forceps three segmented, subgenital plate broad forming forceps base, proximal segment very long and narrow, middle segment shorter, but elongated, distal segment just shorter than middle, rounded apically. Penes long, narrow, extending to mid proximal segment of forceps, lobes tubular, almost fused, rounded at apices.

Fig. II.29. *Tasmanophlebia lacus-coerulei*. a - f, male imago: a, fore wing; b, hind wing; c, dorsal abdominal colour pattern; d, genitalia, ventral view; e, genitalia, lateral view; f, fore claws. g, mature nymph: dorsal colour pattern.

Scale lines : a - e, g 1mm.
f 0.1mm.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Mature Male Nymph (Fig. II.29g)

	$\bar{x}$	SD	n	Range
Head Width	1.71	0.12	6	1.52 - 1.84
Body Length	12.64	1.00	4	11.18 - 13.40
Notal Length	2.91	0.21	6	2.58 - 3.20
Pronotal Width	1.77	0.12	6	1.58 - 1.88
Mesonotal Width	2.26	0.16	6	2.00 - 2.44
Cerci Length	5.09	0.29	3	4.71 - 5.41
Appendix Dorsalis Length	4.68	0.13	3	4.52 - 4.83

Thorax cylindrical, abdomen dorso-ventrally flattened, general colour mottled sandy brown.

Head : small, hypognathous, light brown. Compound eyes large, red/brown dorsally, black laterally. Antennae 1.30mm long.

Thorax : pronotum as wide as head, mottled grey brown. Mesonotum width 1.32 x head width, mottled brown, posterior margin of scutoscutellum produced posteriorly, pointed, wing sheaths long, extending beyond first gill base. Metathoracic wing sheaths shorter, reaching base of first gill. Sternum; prosternum triangular, sterna-costal suture present. Mesosternum, basisternum rectangular 1.25 x longer than wide, furcasternum widest at posterior margin length 0.60 x width, and 0.78 x basisternum length. Metasternum separated from mesosternum by a membranous region, basisternum square, with a sterna-costal suture. Legs yellow brown, femora with a brown patch on posterior margin, joints of tibia and tarsi dark brown, tarsi with brown bands along length, equivalent to tarsal segments of adult (Fig. II.30a). Tarsal claws long and slender 0.50-0.71 x length of tarsus, smooth without denticles. Ratios of leg segments;

fore leg 1.00 : 0.46 : 0.85 (1.25mm)
middle leg 1.00 : 0.41 : 0.67 (1.30mm)
hind leg 1.00 : 0.44 : 0.74 (1.32mm).

Femur length to width ratios similar; fore leg 3.44, middle leg 3.25, hind leg 3.56.

Abdomen : dorso-ventrally flattened, with medial dorsal crest of curved posteriorly directed projections on segments 1-7; process on segment 1 small, 2, 3 largest, becoming less prominent from segment 4-7 (Fig. II.29g). Lateral flanges of each abdominal segment semi-transparent, postero-lateral margin sharply produced. Paraprocts separate, smooth, developing forceps large (Figs. II.23e, f). Caudal filaments well developed, banded every second segment with dark brown, mesal margin of cerci fringed with long fine setae, distal half of external margin also fringed, appendix dorsalis shorter, fringed laterally with long fine setae. Gills; on segments 1-4, first pair broadly ovoid, operculate, extending to posterior margin of fourth abdominal segment, other three pairs with paired lamellae, transparent, with well developed tracheae, gill lamellae lined with fine setae (Figs. II.30b-e).

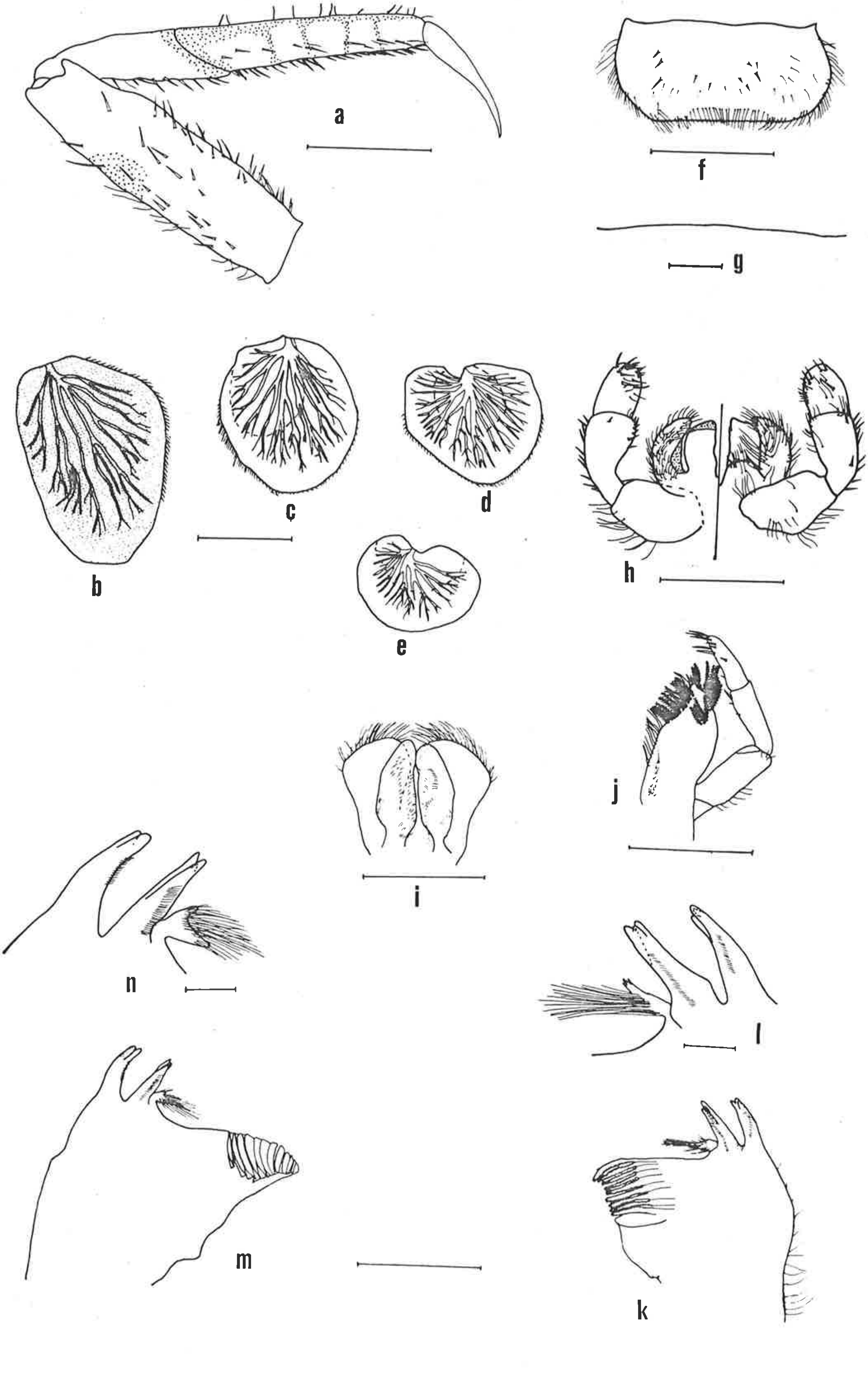
Mouthparts : labrum (Fig. II.30f); rectangular, length 0.44 x width, anterior margin smooth (Fig. II.30g) with a row of setae, lateral margins fringed with setae. Left mandible (Fig. II.30k); robust, incisors widely separate, outer group with three apical teeth, and a ventral row of short setae, inner incisors with three apical teeth and a row of short setae, prostheca broad at base, anterior margin tapers to form a long narrow projection with 3-4 short spines (Fig. II.30*l*), lined with fine setae, molar region of grinding ridges. Right mandible (Fig. II.30m); robust, incisors widely separate, outer group with two apical teeth, and a ventral row of short setae, inner incisors with three apical teeth and a ventral row of short setae, prostheca broad at base, curved, apex divided into two separate lobes, posterior lobe largest, covered with fine setae (Fig. II.30n), molar region of grinding plates. Hypopharynx (Fig. II.30i); median lobe deeply bifid, paragnaths broader, lined with long setae on distal margin. Maxillae (Fig. II.30j); galeo-lacinia lined apically and mesally with pinnate setae, apical angle with three or four spine setae, palpi three segmented, longer than galeo-lacinia, distal segment with long spine setae at apex, segment ratios; 1.00 : 0.86 : 0.77 (0.35mm). Labium (Fig. II.30h); palpi three segmented, length of proximal segment 1.3 x width, second segment constricted proximally, curved, broad apically, distal segment short, rounded apically, with spine setae dorsally, segment ratios; 1.00 : 0.86 : 0.51 (0.37mm); glossae shorter than paraglossae, glossae rectangular without setae, one small pointed tubercle distally, paragnaths curved over glossae, lined with fine setae.

Female Imago : Similar to male, compound eye smaller, fore, middle and hind legs similar, thorax more robust, abdomen without evidence of ovipositor.

Female Nymph : Similar to male, compound eye smaller, black, thorax wider than head, paraprocts smooth, lacking forcep buds.

Fig. II.30. *Tasmanophlebia lacus-coerulei*, mature nymph: a, fore leg; b, first abdominal gill; c, second abdominal gill; d, third abdominal gill; e, fourth abdominal gill; f, labrum, dorsal view; g, antero-median emargination, enlarged; h, labium, dorsal (left) and ventral views; i, hypopharynx; j, left maxilla, ventral view; k, left mandible, ventral view; l, left incisors and prostheca, enlarged; m, right mandible, ventral view; n, right incisors and prostheca, enlarged.

Scale lines :	b - e	1mm.
	a,f,h - k,m	0.5mm.
	g,l,n	0.1mm.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Diagnostic Characteristics.

1. Genitalia; shape of forceps and penes (Figs. II.29d, e; 31a, b).

2. Dorsal crest of nymph with curved posteriorly directed projections on abdominal segments 1-7 (cf. 1-5 in *T. lacustris* and *T. nigrescens*) (Fig. II.29g).

3. First abdominal gill ovoid, rounded posteriorly (cf. pointed posteriorly in *T. lacustris*) (Fig. II.30b).

4. Lateral flanges of abdominal segments narrow (cf. broad development in *T. lacustris*).

5. Shape of incisors and prosthecae of mandibles (Figs. II.30k-m).

History and Discussion.

T. lacus-coerulei was described by Tillyard (1933) from material collected at Blue Lake, Mt. Kosciusko, at an altitude of 6,200 ft. This species was distinguished from *T. lacustris* and *T. nigrescens* by its large size, and long fore wings, 13-16mm, the distinctive dorsal crest of median projections on segments 1-7 of the nymph, and the bicolorous wings of the subimagos. Riek (1955) also used these characters to distinguish this species.

The size of the species appears to be of little value, with the South Australian specimens smaller than *T. lacustris* and *T. nigrescens*. This smaller size may be accounted for by the relatively warm temperature of Tookayerta Creek, and the

Yankalilla River in South Australia (the only two localities in South Australia from which this species is recorded) compared with the high altitude Blue Lake on Mt. Kosciusko.

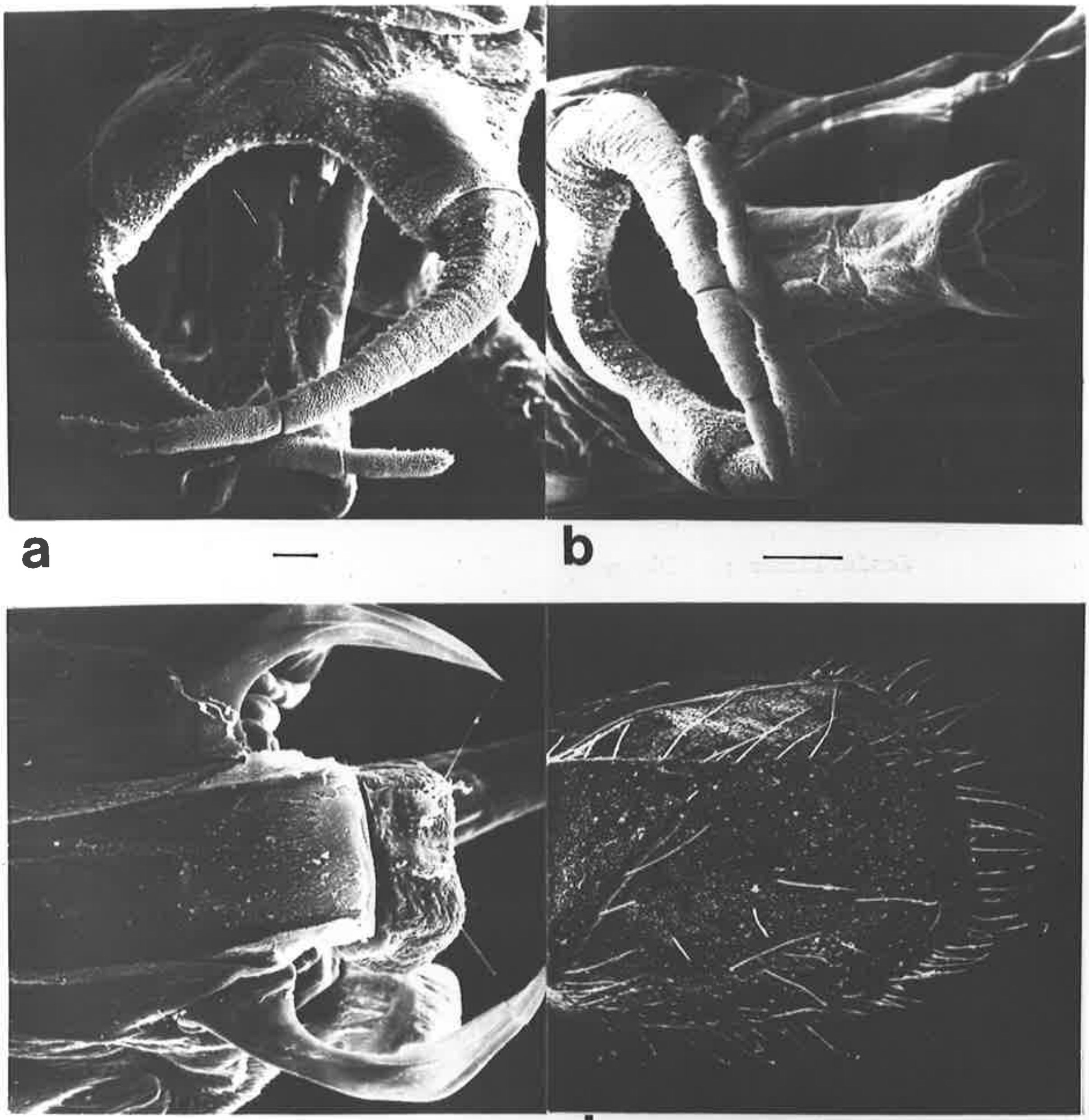
The nymphs, although smaller, have the same characteristic median dorsal crest on the abdomen which distinguish them from *T. lacustris* and *T. nigrescens*. Nymphs of *T. lacus-coerulei* and *T. lacustris* have been compared, and *T. lacustris* was found to have longer, more pointed operculate gills, broader, and generally larger lateral flanges on the abdominal segments, and larger projections on the postero-lateral margins. The incisors and prosthecae also were different.

Although this genus has previously been recorded in the highland lakes and streams, the lowland record in South Australia, and similar records in Victoria and Tasmania suggest that the distribution of the genus is much wider than previously recorded. *T. lacus-coerulei*, previously known from Blue Lake, Mt. Kosciusko, has during this study been recorded also in south-west Victoria and north-east Tasmania. A full discussion of distribution follows in Chapter 6.

Material Examined. South Australia : Fleurieu Peninsula; Tookayerta Ck., Yankalilla R. Victoria : Gawkers Ck., Stokes Ck., Tanjil R., La Trobe R. Tasmania : George R., North George R., Powers Rivulet, Ringarooma R., Scamander R., Weld R.

Fig. II.31. SEM micrographs of *Tasmanophlebia lacus-coerulei* and *Tasmanocoenis tillyardi*. *Tasmanophlebia lacus-coerulei*. a,b, genitalia of male imago, ventral views. *Tasmanocoenis tillyardi*. c, genitalia of male imago, ventral view; d, second gill of mature nymph.

Scale lines : 100μm.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II.7 Systematics Family CAENIDAE.

The Caenidae was recognised as a distinct group of mayflies by Eaton (1883) when he included the genera *Tricorythus*, *Leptohyphes* and *Caenis* in Section 7 of his Revisional Monograph. Banks (1900) erected the tribe Caenini and Thew (1960) states that "according to the Copenhagen decision of the International Commission on Zoological Nomenclature, Banks should be credited with the authorship of the family."

Lestage (1930, 1938) refers to the Caenidae as the Brachycercidae, but with the exception of Demoulin (1955b), the Brachycercidae has not been recognised by authors working on the Australian Ephemeroptera. Tillyard (1936), Harker (1950a, 1954, 1957), Thew (1960), Riek (1970a), Soldan (1978) and Suter (1979) have all recognised the family Caenidae.

In 1978 Soldan described a new genus of caenid from Australia (*Pseudocaenis*) from nymphal material only. Until that description, *Tasmanocoenis* was the only recorded genus of the F. Caenidae in Australia.

Male Imago Characteristics : Eyes of both sexes small, lateral. Thorax robust, abdomen small, contracted. Metathoracic wings absent, mesothoracic wings short and broad with reduced cross venation, anal region broad, hind margin of wing with setae. Legs of male and female similar, tarsi with five segments. Forceps one segmented, lobes of penes separate or fused. Caudal filaments very long.

Mature Nymph Characteristics : Thorax robust, abdomen dorso-ventrally flattened, metathoracic wing sheaths absent. Postero-lateral margins of abdominal segments produced as spines or plates. Gill on first abdominal segment a single filament, or absent, second abdominal segment with an operculate gill, covering gills on segments 3-6. Cerci and appendix dorsalis well developed.

II.7.1 Genus *Tasmanocoenis* Lestage 1930

Lestage, 1930 : 53-54

Tillyard, 1936 : 56 (Part in *Caenis*)

Harker, 1950a : 24-26, 29 (referred to as *Caenis*)

1954 : 266 (referred to as *Tasmanocaenis*, part in *Caenis*)

Demoulin, 1955b : 1-7

Harker, 1957 : 76

van Bruggen, 1957 :32-33

Thew, 1960 : 202

Riek, 1970a : 238

Puthz, 1975 : 412

Soldan, 1978 : 128

Suter, 1979 : 82

Male Imago Characteristics : forceps strongly bowed, sharp distally, lobes of penes fused entirely, or with an apical indentation. Prosternum longer than broad.

Mature Nymph Characteristics : head smooth, lacking tubercles. Mandibles stout, with marginal setae, incisors separate. Labium and maxillae with three segmented palpi. First abdominal gill 2-4 segments, second gill operculate with a triangular dorsal ridge, fringed marginally with setae, gill cover fringed with setae, gills on segments 3-6 lamellate with apical tracheal filaments, single, bifid or trifid. Male and female nymphs similar.

History and Discussion.

The genus *Tasmanocoenis* was erected by Lestage (1930) to include a species from Geeveston, Tasmania. This species, *T. tonnoiri*, was designated the genotype for the new genus. The description of *T. tonnoiri* was unillustrated, and Tillyard (1936) experienced difficulty in picturing what the insect was like. However, he described a second species in the Caenidae, *Caenis scotti* separating the two Tasmanian genera (*Tasmanocoenis* and *Caenis*) on the ratio of the length to breadth of the wings, with *Tasmanocoenis* having a ratio of 3:1 and *Caenis* 2:1.

Lestage noted in 1938 that the specific name *C. scotti* was preoccupied, and renamed Tillyard's Tasmanian species as *Coenis tillyardi*. (The generic spelling of *Caenis* was altered by Lestage (1930) to *Coenis*. Tillyard (1936) did not accept this change and maintained the original spelling of *Caenis*).

Harker (1950a) maintained the specific name *Caenis scotti* for the species described by Tillyard , and described a nymph and female imago which she assigned to this species. However, she states "The imago has not been found at all in Australia [here referring to the Australian mainland only], and the five specimens taken were unfortunately placed in spirit and not allowed to undergo their final ecdysis". The nymphs also were not associated with a male adult, "it is the only nymph which has not been able to be bred through in the laboratory" (Harker, 1950a). Some doubt therefore must be cast on the true identification of the nymph described by Harker (1950a). In a subsequent paper Harker (1954) refers to Lestage's (1938) alteration of *C. scotti* and refers to *C. tillyardi* and *Tasmanocaenis tonnoiri*, incorrectly spelling the generic name of the latter species.

In 1955b, Demoulin reviewed the Australian Brachycercidae (Caenidae) and re-described, with illustrations, the genotype *Tasmanocoenis tonnoiri*. He also recognised that "*C. tillyardi* est en réalité aussi un *Tasmanocoenis*. Ce genre est ainsi le seul réprésentant des Brachycercidae dans la faune australienne" (Demoulin, 1955b).

Demoulin (1955b) also presented a key to the genera of Brachycercidae for adults and nymphs. For the adults Demoulin based the generic separation on the length and width of the prosternum, the antennal pedicel length, length of leg segments, especially the comparative length of the fore tibia and fore tarsi. The nymphs of *Tasmanocoenis* were distinguished from other genera by having a three or four segmented first gill.

Other characters were mentioned by Demoulin as interpreted from Harker's (1950a) illustrations. The nymphal characteristics were therefore established not from actual specimens of *T. tillyardi* nymphs, but from Harker's illustrations and description.

Harker (1957) accepted the generic classification of the Australian Caenidae, and described the male imago and nymph of *T. jillongi* from Kuringae Chase, New South Wales. Harker noted that the adult characteristics suggested this species belonged to the genus *Tasmanocoenis*, but noted that the nymphal characters differed greatly from the nymph she described as *T. tillyardi* (described as *Caenis scotti*, 1950a). Also in 1957 van Bruggen described *T. novaeguineae* from the Wessel Lakes, central New Guinea, noting short, straight forceps with terminal spines which distinguish this species from all the known Australian species.

In 1960 Thew revised the genera of the Caenidae, comparing adult taxonomic characters and their value in the classification of this family. He presented evidence to show the variations observed in the ratios of leg segments, and concluded that these were "not valid critera for genera" (Thew, 1960). Wing venation was also considered "unwise" to be used as a generic or specific characteristic because of the "considerable amount of variation". Characters which Thew found to be reliable, and therefore valid critera, were the prosternum length to width ratio, and the form of the penes and forceps. Thew's final classification placed van Bruggen's species from New Guinea in the genus *Caenomedea* (previously recorded from Africa only) and the Australian species remained in *Tasmanocoenis*. (*T. jillongi* Harker was not mentioned by Thew, nor is Harker (1957) mentioned in his references, but this species based on adult male characters is correctly placed in *Tasmanocoenis*).

As discussed previously, in 1978 Soldan erected a new genus of Australian Caenidae, based on nymphal material only. This new genus *Pseudocaenis* included two new species *P. queenslandica* and *P. rieki*. Suter (1979) recognised only *Tasmanocoenis* in Australia, but this paper was submitted for publication before the new generic description was published.

Thew (1960) distinguished *Tasmanocoenis* nymphs from all other caenid genera by a series of characteristics, including; mandibles lacking marginal fringe on both sides; maxillae with only a few hairs, no thick spines; labrum lacking marginal fringe of hairs; gill covers without triangular ridge and without marginal fringe of hairs; first gill three or four segmented and lamellate gills with fringe of single or bifid tracheal filaments. Soldan also noted these characters. From associated material of *T. tillyardi* from South Australia, and Tasmania, it was evident that all of the above criteria failed to characterize the nymphs of *Tasmanocoenis*. The adult reared belonged in the genus *Tasmanocoenis*, but the nymph did not fit the characterization given by Harker (1950a), Demoulin (1955b), Thew (1960), nor Soldan (1978), instead it agreed closely with the recently described genus *Pseudocaenis*, erected by Soldan (1978). To solve this anomoly, nymphs of *T. tonnoiri*, the genotype from Tasmania were sought, but no specimens were located from the type locality of Geeveston. Paratype material of *Pseudocaenis* deposited in the National

Museum of Victoria by Soldan were examined, and they closely resembled the nymphs of *Tasmanocoenis tillyardi*. No caenid material examined during the present study possess the characters listed by Thew (1960) and Soldan (1978) and it is difficult to understand how these inaccurate designations have been perpetuated in published works. Harker (1950a) described a nymph designated as *Caenis scotti*. The description was not associated with a male imago, and therefore some doubt must exist on the identification. However, her description and illustrations of these nymphs were simple and did not record any of the characters used in distingishing the genera of the Caenidae. A later description of *T. jillongi* nymphs (Harker, 1957) was also over-simplified and setation, gill ridges, and tracheal bifurcations were not mentioned or illustrated. These two descriptions and illustrations of nymphs ascribed to the genus *Tasmanocoenis* are inadequate, and the illustrations are over-simplified. The generic criteria given by Thew and Soldan are consistent with these descriptions, suggesting that they were not based on extensive examination of nymphal material, but on Harker's illustrations and descriptions.

Examination of nymphal material of *T. tillyardi* and paratype material of *Pseudocaenis queenslandica* (the genotype) and *P. rieki* suggest that the generic criteria by Thew (1960) and Soldan (1978) are incorrect, and it is probable that *Pseudocaenis* is a synonym of *Tasmanocoenis*. Until associated nymphs and adults of *T. tonnoiri* are examined the two genera must remain. However the anomalous situation of the adult in one genus and the nymph in another suggests that the two genera are synonymous.

In the present study both genera are accepted with reservation pending examination of further material.

II.7.1.1. *Tasmanocoenis tillyardi* (Lestage) 1938

Caenis scotti Tillyard, 1936 : 56-58

Coenis tillyardi Lestage, 1938 : 320

Caenis scotti Harker, 1950a : 24-26, 29

Caenis tillyardi Harker, 1954 : 266

Tasmanocoenis tillyardi Demoulin, 1955b : 4
Harker, 1957 : 77
van Bruggen, 1957 : 33
Thew, 1960 : 202
Scholes, 1961 : 39-41

"Caenis" scotti Williams, 1968 : 169

Male Imago.

	x̄	SD	n	Range
Body Length	3.25	0.14	7	3.12 - 3.52
Notal Length	1.45	0.07	7	1.32 - 1.52
Mesonotal Width	0.84	0.08	7	0.67 - 0.90
Pronotal Width	0.68	0.06	7	0.55 - 0.72
Fore Wing Length	3.15	0.14	7	2.96 - 3.36
Cerci Length	11.30	-	-	-
Appendix Dorsalis Length	12.00	-	-	-

Colour, dark black/brown.

Head : brown, with light brown epicranial sutures. Compound eyes lateral, black. Dorso-lateral ocelli raised, black, median ocellus small, black. Antennal base brown, one segmented, flagellae long, 0.54mm.

Thorax : robust, dark black/brown (Fig. II.32b). Pronotum narrower than head. Mesonotum strongly humped, median notal suture black with a white elongate marking in anterior half, wider than head. Legs; slender, pale brown/grey. Fore legs longer than middle and hind legs, fore leg femur 1.15 x middle leg femur length and 1.28 x hind leg femur length. Ratios of leg segments;

fore leg 1.00 : 1.93 : 0.09 : 0.57 : 0.26 : 0.25 : 0.16 (0.69mm)

middle leg 1.00 : 0.55 : 0.08 : 0.05 : 0.05 : 0.07 : 0.08 (0.60mm)

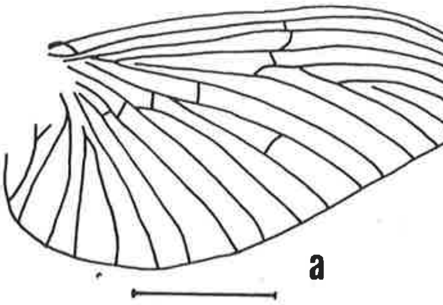
hind leg 1.00 : 0.61 : 0.08 : 0.05 : 0.05 : 0.07 : 0.08 (0.54mm).

Tarsal claws similar in fore leg, both blunt, club-shaped, dissimilar in middle and hind legs, one blunt club-shaped, one slender and sharp. Sternum (Fig. II.32c); prosternum triangular, apex truncated, lateral margins separated anteriorly, slightly longer than broad. Mesosternum dark black/brown, basisternum narrowest anteriorly, margins diverge to widest central region, then converge slightly at posterior margin, length 1.19 x maximum width, sterna-costal suture well developed, furcasternum length 0.65 x width, and 0.65 x basisternum length, posterior margin straight.

Wings (Fig. II.32a) : short and broad, length 1.72 x width, hyaline with milky-opaque pterostigma, venation reduced, simple, almost lacking cross veins, posterior margins may be lined with fine setae.

Fig. II.32. *Tasmanocoenis tillyardi*. a - d, male imago: a, fore wing; b, dorsal colour pattern; c, thoracic sterna; d, genitalia, ventral view. e, mature nymph: dorsal colour pattern.

Scale lines : a - c, e 1mm.
d 0.1mm.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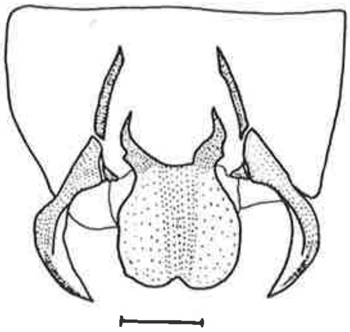
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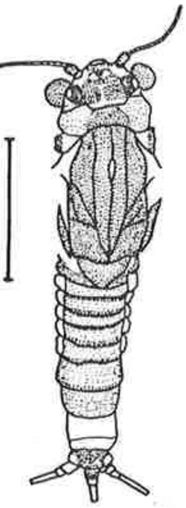
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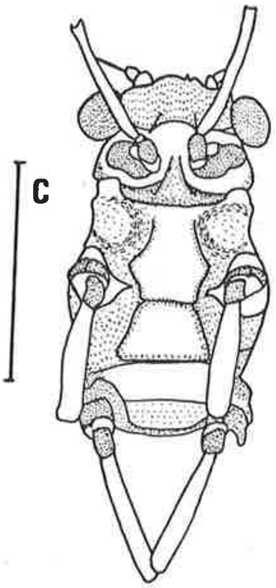
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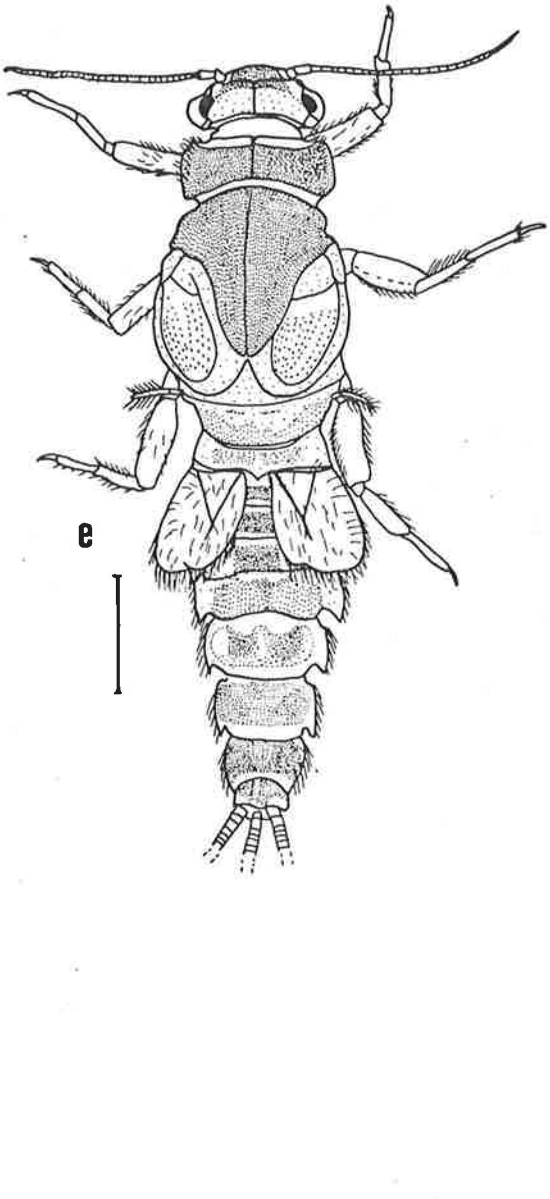
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Abdomen : short, cylindrical, segments 1-5 very short, light brown, and speckled with black, segments 8 and 9 lighter. Cerci long, transparent, appendix dorsalis longer, both tipped with long fine setae.

Genitalia (Figs.II.32d; 31c); forceps one segmented, bowed, sharply pointed with ventral mesal groove, penes lobed, fused with a small apical indentation, sclerotized basally.

Mature Male Nymph (Fig. II.32e).

	$\bar{x}$	SD	n	Range
Head Width	0.96	0.04	21	0.90 - 1.04
Notal Length	1.62	0.10	21	1.40 - 1.76
Mesonotal Width	1.14	0.05	21	1.00 - 1.20
Pronotal Width	1.00	0.06	21	0.78 - 1.04
Cerci Length	3.03	0.16	3	2.92 - 3.22
Appendix Dorsalis Length	3.39	0.18	3	3.28 - 3.60

Body colour brown.

Head : dark brown, smooth, prognathous. Lateral compound eyes black. Ocelli brown. Antennae light brown, basal segment 0.16mm long, flagellum 1.46mm (Fig. II.33e). Tentorial body rectangular, length 0.79 x width.

Thorax : pronotum brown, lateral flanges lighter, semi-transparent, anterior margins with spine setae, 0.96 x wider than the head. Mesonotum dark brown, edge of wing sheaths black, short, reaching edge of metathorax, posterior margins rounded, with a short median indentation. Legs light brown, margins lined with spine setae (Fig. II.33a). Tarsal claws short, curved with 4-6 small ventral denticles, otherwise smooth. Ratios of leg segments;

fore leg	1.00 : 0.73 : 0.65	(0.68mm)
middle leg	1.00 : 0.70 : 0.59	(0.68mm)
hind leg	1.00 : 0.76 : 0.60	(0.74mm).

Femur length to width ratios; fore leg 2.81, middle leg 2.86, and hind leg 2.95. Sternum light brown, prosternum triangular, apex rounder, slightly broader than long. Metasternum; basisternum wider than long, sterna-costal suture absent, furcasternum shorter than basisternum.

Abdomen : brown, with square patterns of brown on each side of median line. Operculate gill of second segment covers segments 3-5, segment two with median backward projecting spine, postero-lateral margins produced forming backward pointing projections. Cerci and appendix dorsalis dark brown, well developed. Gills; six pairs, on segments 1-6, first pair single, filamentous with indistinct segments, lined with fine setae (Fig. II.33b), second pair operculate with raised triangular region dorsally, mesal ridge with few setae, outer ridge not reaching posterior margin of gill covers, margins lined with long setae (Figs. II.33c; 31d); third-sixth pairs laminate with 40-50 tracheal fringes, single or bifid, few trifid, third gill largest (Fig. II.33d), progressively smaller posteriorly.

Mouthparts : labrum (Fig. II.33f); rectangular, width 2.34 x length, anterior margin with slight median concavity with 2-3 small denticles (Fig. II.33g), lateral margin and anterior margin with spine setae. Left mandible (Fig. II.33j); outer incisors with three apical teeth and one shorter mesal tooth, inner incisors with three apical teeth, prostheca robust with apical brush of setae (Fig. II.33k), molar region of transverse grinding ridges. Right mandible (Fig. II.33*l*); outer incisors with 2-3 apical teeth, inner with two, prostheca robust with apical brush of setae (Fig. II.33m), molar region of transverse grinding ridges. Hypopharynx (Fig. II.33i); with square median lobe, slightly concave anteriorly, paragnaths longer, rounded apically, lined with short setae. Maxillae (Fig. II.33n); galeo-lacinia short and narrow, with 3-4 robust apical spines, anterior margin lined with fine setae, mesal margin lined with stout spine setae, palpi three segmented, longer than galeo-lacinia, segment ratios 1.00 : 0.70 : 1.07 (0.12mm), distal segment lined with spine setae. Labium (Fig. II.33h); palpi three segmented, proximal segment length 1.47 x width, second segment curved, distal segment rounded, lined mesally with spine setae, segment ratios 1.00 : 0.78 : 0.53 (0.13mm); glossae rectangular, rounded apically with fine setae, paraglossae curved, inserted below glossae, apex not reaching apex of glossae, lined with fine setae.

Female Imago : Similar to male, sternum and notum broader, tarsi four segmented, tarsal claws, each pair dissimilar, one blunt, club-shaped, one curved and sharp.

Female Nymph : Body shape similar to male, more robust than male, i.e. head width of last instar greater than male, wing sheaths longer, second abdominal operculate gill longer, covering segments 3-6, fore, middle and hind femora longer.

Fig. II.33. *Tasmanocoenis tillyardi*, mature nymph: a, fore leg; b, first abdominal gill; c, second abdominal gill; d, third abdominal gill; e, basal antennal segments; f, labrum, dorsal view; g, antero-median emargination of labrum, enlarged; h, labium, dorsal (left) and ventral views; i, hypopharynx; j, left mandible, ventral view; k, left incisors and prostheca, enlarged; l, right mandible, ventral view; m, right incisors and prostheca, enlarged; n, left maxilla, ventral view.

Scale lines : a - e 0.5mm.
f - n 0.1mm.

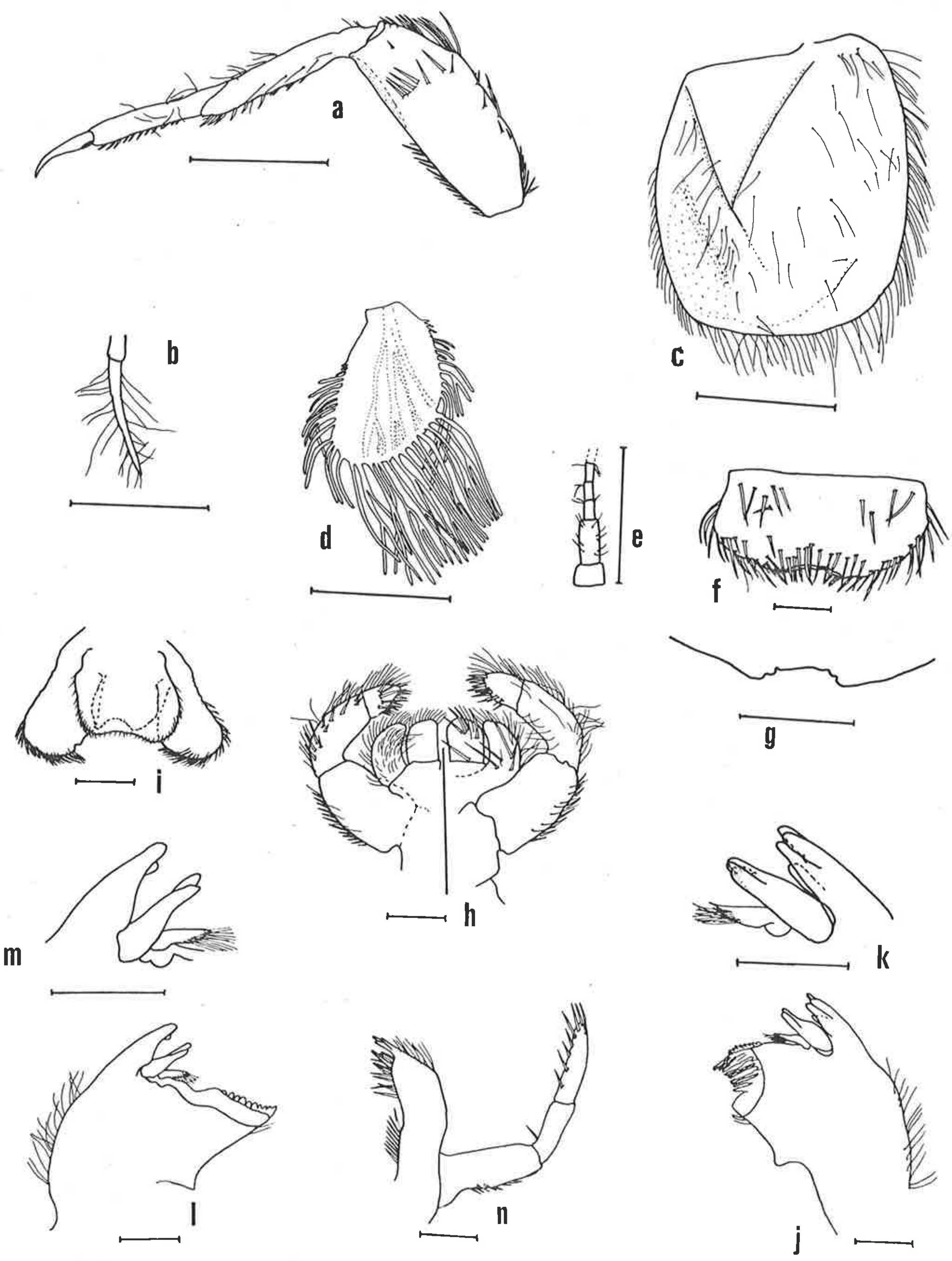
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Table II.22 lists morphometric characteristics which differ between male and female nymphs from Spring Creek, Southern Flinders Ranges. Of the 29 characters compared, only eight were statistically different. The mesonotal width/head width, wing sheath/head width and gill cover length/head width ratios are useful in the separation of the male and females of *T. tillyardi* because there is no obvious sexual differentiation in this species until late in the last instar when the adult characteristics become apparent through the nymphal cuticle (i.e. forceps and narrow mesosternum in male, eggs and broad mesosternum in female).

Diagnostic Characteristics.

1. Genitalia of male with curved sharp forceps and fused penes with a small apical indentation, not extending beyond apices of forceps (Figs. II.32d; 31c).
2. Labrum rectangular (Fig. II.33f).
3. Structure of mandibles, incisors and prosthecae (Figs. II.33j-m).

History and Discussion.

Tillyard (1936) described *Caenis scotti* from the South Esk River at Clarendon, Tasmania. Lestage (1938) noted that *C. scotti* was preoccupied by a species described by Ulmer in 1924 (referred to by Thew, 1960) and renamed the Tasmanian species *Coenis tillyardi*. Harker (1950a) apparently was unaware of this name alteration and described a nymph which

TABLE II.22. Morphometric characters which aid in distinguishing male and female nymphs of *Tasmanocoenis tillyardi* in a South Australian population.

Data is from a population of *T. tillyardi* from Spring Creek, Southern Flinders Ranges, South Australia. Abbreviations as for Tables II.1 and II.4.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

	Males			Females					
Character	$\bar{x}$	S.D.	Range	$\bar{x}$	S.D.	Range	d.f.	t	
MNW/HW	1.16	0.03	1.10-1.20	1.26	0.04	1.21-1.34	18	6.09	***
PNW/HW	1.03	0.02	1.00-1.06	1.08	0.06	0.95-1.15	18	2.49	*
NL/MNW	1.45	0.03	1.40-1.52	1.39	0.08	1.26-1.51	18	2.11	*
FFL/HW	0.68	0.03	0.60-0.70	0.71	0.03	0.67-0.74	20	2.58	*
MFL/HW	0.69	0.02	0.66-0.74	0.72	0.03	0.67-0.75	20	2.52	*
Gill cover L/HW	0.87	0.05	0.78-0.96	1.01	0.02	0.97-1.04	26	9.22	***

she assigned to *Caenis scotti*. Subsequently in 1954 she recognised the name change, and maintained the generic recognition as *Caenis*. Demoulin (1955b) reviewed the genus *Tasmanocoenis* and recognised that *Caenis tillyardi* belonged in the genus *Tasmanocoenis*, an observation validated by the review of the Caenidae by Thew (1960).

Williams (1968) noted that *Caenis* and *Tasmanocoenis* in Australia were probably synonymous, and illustrated gills of *"Caenis" scotti* after Harker (1950a). Riek (1970a) noted, as had Demoulin (1955b) and Thew (1960), that *Tasmanocoenis* was the only Australian genus in the Caenidae but records of nymphs of *Caenis* sp. have been made by Timms (1974) in a benthic study of three South Australian volcanic lakes. All specimens from South Australia belong to the one species, *T. tillyardi*.

Material Examined. South Australia : South-East; Drain L, Drain K, Eastern Division Diversion Drain, Eight Mile Ck., Hitchcock Drain, Mosquito Ck., Mt. Hope Drain, Sutherland's Drain. Mt. Lofty Ranges; Deep Ck., Eleanor R., Sturt R., Torrens R., Waite Institute Pond. Fleurieu Peninsula; Anacotilla Ck., Carrakalinga Ck., Deep Ck., Hindmarsh R., Inman R., Kangarilla Ck. Lake Alexandrina; Tookayerta Ck., Yankalilla R. Kangaroo Island; Breakneck R., Cygnet R., Grassy/Sheep Ck., North-East R., Tin Hut/Bullock Ck., South West R., South West Bay R. Southern Flinders Ranges; Broughton R., Nectar Brook Ck., Ohlenmeyer Reservoir, Rocky R., Schumacher Ck., Spring Ck. Northern Flinders Ranges; Arkaba Ck., Arkaroola Ck., Balcanoona Ck., Bendieuta Ck., Brachina Ck., Bunyeroo Ck., Elatina Ck., Emu Ck., Enorama Ck., Eregunda Ck., Hot Springs (Paralana), Kanyaka Ck., Marolana Ck., Mount Chambers Ck., Nepouie Ck., Old Wirrealpa Springs, Oraparina Ck., Oratunga Ck., Parachilna Ck., Stubbs Waterhole, Willigan Ck., Teatree Ck., Warren Gorge Ck., Wilpena Ck., Wockerawirra Ck., Woodendimna Ck. Eyre Peninsula; Old Woolshed Dam. Victoria : Crawford R., Darlots Ck., Gawkers Ck., Glenelg R., Lake Wendouree (Ballarat), Mount Emu Ck., Pigeon Hole Ck., Rocklands Reservoir, Stokes Ck., Surrey R., Wando R., Wannon R., Wennicott R. Tasmania : Elizabeth R., Lagoon of Islands, Macquarie R. Queensland : Tinaroo Pines. Western Australia : Surveyors Pool, Mitchell Plateau.

II.8 SUMMARY

In the present study 13 species of mayfly in 8 genera have been recognised and described from South Australia. The study is based on extensive collections in the Flinders Ranges, Mt. Lofty Ranges, Fleurieu Peninsula, Kangaroo Island and the south east of South Australia. Mayflies have not been recorded from the Eyre Peninsula, a region with few freshwater habitats, but records may be made at a later date. The Musgrave Ranges in South Australia's far north have not been sampled, and species not previously recorded from the State may be found there. Accessibility to these areas is limited and regrettably, collecting has not been possible.

Although 13 species are recorded at present, further records may be made from relatively inaccessible springs and waterholes in the Flinders Ranges, or from the stream and drain systems of the South East. The latter region with its close proximity to the Glenelg River system, and its obvious Glenelg River faunal affinities, may still be subject to faunal exchanges. The distribution of each species recognised from South Australia and its biogeographical relationship with the mayfly fauna of Australia is discussed in Chapter 6.

CHAPTER 3.

Habitat Comparison of South Australian Mayflies.

III.1 Introduction

The mayfly fauna of South Australia, even though consisting of 13 species, is depauperate at any one locality or in any particular stream system. The species diversity (in terms of number of species) therefore tends to be low; of the 153 freshwater localities containing mayflies, 43% had only one species, 35% two species, 16% three species, 4% four species and only 2% five species, (Table III.1). The distribution of these localities throughout the State is given in Appendix 1, and is discussed in Chapter 6. This level of diversity is lower than recorded in streams in the wetter eastern States. Six species were recorded from one locality in the Acheron River, Victoria (Suter and Williams, 1977), at least five species in Wilks Creek, seven in Chalet Creek, Victoria (Duncan 1972, unpublished thesis) and seven in the Queanbeyan River, Australian Capital Territory (Weatherley, Beevers and Lake, 1967).

In comparison with northern hemisphere records which range from four species (Kjellberg, 1972, Madsen, Bengtson and Butz, 1973) to 45 species in Wildcat Creek in South Carolina (Carlson, 1973) and with the majority greater than 10 species (e.g. Armitage, 1961, Allan, 1975, Boerger and Clifford, 1975,

TABLE III.1.

Summary of the species diversity of Ephemeroptera in freshwater localities in South Australia, noting the number of localities from which species were recorded from each of the distinct geographical regions of the State.

	Number of species					
Geographical region	1	2	3	4	5	Totals
Northern Flinders Ranges	11	13	5	-	-	29
Southern Flinders Ranges	10	8	3	2	-	23
Mt. Lofty Ranges-Fleurieu Peninsula	24	17	6	4	2	53
Kangaroo Island	8	5	4	2	-	19
South East	11	6	2	1	2	22
Total No. of Streams	64	49	20	9	4	146
Percentage record	43.84	33.56	13.70	6.16	2.74	100

Elliott 1967, Bishop and Hynes 1969a and b, Mason 1976, Macan 1957a, 1964, Nuttal and Purves 1974, Ulfstrand 1967, Vincent 1967, Ward 1975, Wilhm, Numminga and Ferraris 1978), the South Australian mayfly species richness is extremely low. Southern hemisphere records, excluding Australia, have a similar range to that of the northern hemisphere (Oliff 1959, Oliff and King 1964, Chutter 1970, Harrison and Rankin 1976, Towns 1979), with Schoonbee (1973) recording high diversity of 40 species in the Umgeni River, South Africa. In temporary streams throughout the world the mayfly species richness tends to be lower than in permanent systems; three species recorded in Moser Creek, Canada (Williams and Hynes, 1976a), five in Caldwell Hollow, Indiana (Clifford 1966) and eight in the Manwahaku stream, Rhodesia (Harrison 1966).

Hynes (1974a) and Hynes and Hynes (1975) recorded low species diversity of the Australian Plecopteran fauna and suggested "the very flexibility of life cycle that has been imposed upon most of the Australian species by the uncertain climate has probably reduced the total number of niches available on the continent". In South Australia the availability of fresh water is limited to the Flinders and Mt. Lofty Ranges, the Fleurieu Peninsula, Kangaroo Island and the south east corner of the State. In all these regions, with the exception of the south east, spatially intermittent streams form the majority of freshwater habitats, with a corresponding low mayfly diversity. The drain systems of the south east tend to be permanent, but because these are shallow and slow moving, high temperatures (and salinities), especially during the summer months, tend to limit the number of species present. The localities in which the greatest number of species occur (4 and 5), are permanent stream systems. Temperature may have a limiting effect, especially during the summer months. In the Flinders Ranges where water temperatures may exceed 28°C, no locality contains more than three species, even if permanently flowing (e.g. Parachilna Creek, Stubbs Waterhole) whereas in the cooler streams of the southern part of the State (and in fact the whole of the Continent), higher diversity is found. Hynes and Hynes (1975) suggested that the uncertainty of the Australian climate leads to a wide ecological valence. In South Australia this is particularly apt because freshwater habitats are perhaps at their limits of permanency, being often spatially and temporally intermittent because of the arid climate. The uncertainty of the climate dictates that the number of niches available will vary, depending on the existing climatic conditions. Species occupying such a capricious environment must have broad ecological tolerances to enable the utilization of the different niches available at different times.

Because of the low species diversity at any one locality, a detailed, concurrent study of the ecology of all 13 species was logistically impracticable. Therefore a comparative study of two localities, each containing three mayfly species (two common to both) was carried out in an attempt to understand the factors influencing the ecology of these species.

III.2 Materials and Methods

The two sampling localities chosen were Deep Creek (a permanent flowing stream) and Spring Creek (an intermittently flowing stream). Both streams were visited at least monthly, but the Deep Creek site was sampled fortnightly during Spring, Summer and Autumn. On each sampling date measurements of both faunal and physical characteristics were made.

III.2.1 Physical Characteristics

The physical parameters measured each collecting date were

i) air and water temperature
ii) surface water discharge
iii) pH
iv) conductivity (K_{18})
v) dissolved oxygen.

Rainfall and temperature data for each catchment were obtained from the available records of the Commonwealth of Australia, Bureau of Meteorology.

Temperature records were made using standardised maximum-minimum thermometers which were read, and reset each sampling date. Air temperature at Spring Creek was measured at ground level in a shaded area 10-15m above stream level, whereas at Deep Creek continuous vandalism of the air thermometers made measurement impossible. Morrissy (1967) found positive correlation between Adelaide air temperature and air temperature at Deep Creek. The difference between the two was usually less than 1°C, and therefore the Adelaide air temperature was considered to give a good estimate of the Deep Creek air temperature. Water temperatures were measured beneath the cobbles of the substrate in pools in both streams. The thermometers were enclosed in a PVC casing, open at each end, that allowed direct contact with the water, and provided protection from breakage during periods of substrate movement.

Surface discharge (Q) was determined by taking depth (D) and velocity (v) measurements at each 1/10th stream width. Velocity was measured using a Pitot tube at a depth of 0.6 x the total depth, giving a mean velocity measure (Hynes 1970a). Using the transformation of the formula $Q = vA$ (Morisawa 1968) where A = cross-sectional area for each measurement, the summation gives the discharge

$$\text{i.e. } Q = \Sigma vA$$

$$= \Sigma vWD$$

(For the Pitot tube $v = 2gh$ where g = gravitational constant and h = height of velocity head in the tube).

Water samples were collected and returned to the laboratory where pH and conductivity were measured within 24 hours of collection. pH was measured electrometrically using a Radiometer PHM 62 meter. Conductivity was determined using a Radiometer CDM 3 conductivity meter, and the readings were corrected to a standard temperature of 18°C

$(K_{18} = \frac{K_t}{1 + 0.025\ (t-18)})$ where K_{18} = conductivity at 18°C and K_t = conductivity recorded at temperature t (Bayly and Williams 1973). Salinity was calculated using the formula presented by Buckney and Tyler (1976) for fresh waters;

$$\log S = 0.921 \log K_{18} - 0.047,$$ where S = salinity (ppm)

and K_{18} is conductivity at 18°C in microsiemens per centimeter. Dissolved oxygen was measured *in situ* using a Yellow Springs Instrument 51B dissolved oxygen meter.

Substrate analysis was made once at each locality using sampling areas subjectively classified as erosional and depositional. An area of 0.1m^2, to a depth of 0.05m, was removed from the stream and stored in plastic bags. At Spring Creek the samples were taken when the stream was dry, allowing collection of dry substrate without having to use collecting nets for the finer particles. In Deep Creek, the benthos sampler, described below in the faunal techniques section, was used. The square box sampler enclosed 0.1m^2 of substrate, and the flow through system allowed collection of the disturbed substrate using a net, with a mesh aperture of 110μm, on the downstream side. This net did not collect all the very fine particles below 110m in size. The sediments were dried at 104°C to constant weight, and then manually shaken in a series of graded Wentworth scale sieves with mesh increments of 1 *phi* units (*phi* is defined as the negative log to base 2 of the particle size diameter in millimeters). The sediments in each size were weighed and the median diameter (Md) and sediment curves were determined using the Wentworth *phi* values as used by Cummins (1962) and Doeglas (1968) and recommended by Cummins (1966).

III.2.2 Faunal Techniques

Sampling of the mayfly fauna of the two streams differed in that Spring Creek was sampled at intervals of 4 weeks, whereas Deep Creek was sampled at 1-2 week intervals during the Spring, Summer and Autumn periods, and at 4 week intervals during the Winter.

Adults were collected using an Entomological Supplies aerial insect net, sampling any visible swarms in the vicinity of the stream, and by beating overhanging and riparian vegetation for newly emerged subimagos. Cobwebs under bridges, and on vegetation were also examined for adult material. Subimagos were also readily collected as they emerged from the stream and rested on emergent rocks. Light-trapping, using both ultra-violet fluorescent tubes (Black Light) and blue actinic (UV) fluorescent tubes, was only effective in collecting *Tasmanocoenis tillyardi* male and female adults, with all other species only being represented by female imagos or subimagos. Adults and subimagos were preserved in a solution of 75% ethanol and 4% glycerol.

The substrate and morphological characteristics of the two streams included in the present study were such that a Surber sampler, or samplers which use the principle of the Surber sampler (current-operated box samplers) could be used

(Hellawell,1978). Comparative studies of quantitative sampling in the lotic environment, including those by Macan (1958b), Hynes (1961), Needham and Usinger (1956), Radford and Hartland-Rowe (1971), Roby, Newbold and Erman (1978) and techniques reviewed by Cummins (1962, 1966), Hynes (1961, 1970a), Southwood (1966), Bishop (1973a) and more recently Hellawell (1978) and Resh (1979) show or record the inadequacies of the techniques. Cummins (1962) considered that techniques used should be determined by the physical conditions and the information that was sought. Bishop (1973a) concluded in his review of sampling techniques that "most analytical studies have shown that a limited number of standardised replicates, sampling a feasible substrate area, will give a reasonable assessment of faunistic composition and, within acceptable limits, an estimate of the dominant relationships of the fauna." The present study of the habitats and life histories (Chapter 4) of the mayflies at each study site was not primarily concerned with the absolute number of animals in any locality at any time, but rather with the overall trends being shown by the populations being sampled. To enable comparisons between the two study sites, standardised replicates were taken using a box sampler, based on samplers described by Mundie (1971) and used by Bishop (1973a), modified for local stream conditions.

The sampler was an open bottomed box enclosing $0.1m^2$ of stream bed (Fig. III.1). The construction was of galvanised steel with four rods (1cm diameter) at each corner and $0.1m^2$ lateral sheets (2mm gauge) enclosing the sampling area. The

Figs. III.1 (a, b). The box sampler in use at Deep Creek, showing the two net system (b) with the short coarse (480μm mesh) inner net, and long fine (110μm) outer net.

(a)

(b)

bottom edges were reinforced with a 2cm deep flange which aided in the insertion into the substrate. The front was open allowing free flow of water. The back was also open, but included a steel groove that allowed square mouthed nets to be inserted and removed without disturbing the positioned sampler. Two nets were inserted into this rear groove, an inner coarse mesh net ("Nytal" 500µm mesh aperture; actual measured aperture of 460-480µm; diagonal (maximum) aperture 678µm) and an outer fine mesh net ("Nytal" 106µm mesh aperture; actual measured aperture of 98-120µm; diagonal aperture 155µm). The coarse net inside the fine net retained the larger animals and substrate carried into it, by the stream current, and protected the fine net which retained materials down to 80µm diameter (and below).

Both nets were constructed with an opening of 31.7 x 31.7cm at the sail cloth covered net frames, but the sail cloth of the inner coarse net was only 15cm long tapering rapidly giving an effective filtering aperture of 20 x 20cm. The coarse mesh connected to the sail cloth extended a further 60cm, tapering gradually to 10 x 10cm at its closed trailing end. The sail cloth of the fine net was 30cm long, did not taper at all, and at the join with the mesh gave an effective filtering aperture of 31.7 x 31.7cm. The nylon mesh tapered gradually from this aperture to 10 x 10cm at its closed trailing end, 2m from the sail cloth. The tapering design of the two nets ensured that the inner coarse net did not come in contact with the outer net thus maintaining the sieving effectiveness of both nets in this dual net system. Also the long length of the fine net overcame one of the major problems experienced with fine mesh samplers, of blockage by fine organic and inorganic material.

The sampler, with nets in position, was rapidly inserted into the substrate with the open front facing into the current. If a good seal was not made with the bottom the procedure was repeated until a satisfactory seal was obtained ensuring minimum loss of benthos enclosed in the sampling area. The substrate was then disturbed by hand. Large rocks were hand scribbed and smaller particles were violently stirred into the current. In fast flowing riffles the sampling time was shorter than in slow flowing flats where the substrate disturbance was not as violent, and consequently a longer time was required to dislodge the benthos from the substrate. Once the sample was completed the nets were removed and the contents of each washed into separate polyethylene bags and preserved with 4% formaldehyde. The depth and velocity at the sampling site were measured. At each site four samples were taken on each sampling date (with the exception of the summer sampling dates at Spring Creek, see below) from visually selected uniform habitats (uniform in velocity, depth and substrate) broadly categorised as

(a) a slow flowing deep region (pool)
(b) a fast flowing deep pool (run)
(c) a slow to moderate flowing shallow region (flat)
and (d) a rapid, shallow region of broken water (riffle).

During the summer months Spring Creek consisted of a series of stationary pools, and in these a 2m kick sample (Hynes, 1961), using both nets together, was used to collect the benthos.

The marginal vegetation was not always effectively sampled using the benthos sampler (a problem associated with Deep Creek rather than Spring Creek), and therefore a qualitative supplementary sample was made by violently disturbing the vegetation by hand and foot, and the dislodged material collected using only the coarse (0.500μm) net. This sample was preserved as before.

The hyporheos was not effectively sampled using any technique, except when Spring Creek ceased to flow during the summer months. Attempts were made at both localities to use a sampling column (cf. Williams and Hynes, 1974), which was hammered into the stream bed, and opened at desired depths. Unfortunately the substrate was such that large rocks and cobbles made insertion a virtual impossibility. However, when Spring Creek was dry, holes were dug in the stream bed in areas dry for one, two and three months, until the water table was reached at depths of 16cm, 35cm and 71cm respectively. The water was sieved and all animals preserved in 4% formaldehyde. Substrate from each hole was collected and the percentage living space was calculated using the technique of Bishop (1973a).

In the laboratory the coarse net samples were poured into a 250μm mesh copper sieve and washed with a large volume of water. Each was then emptied into a large white "Ilford" developing tray containing water 1-2cm deep. The mayfly nymphs were hand sorted, separated into species, counted and stored in 75% ethyl alcohol containing 4% glycerol until measurements were made. The maximum head width across the eyes, of each specimen was measured using a Wild M5 dissecting microscope with a calibrated eyepiece graticule. Head width was used as the standard size measurement instead of total body length because this measurement eliminated the error encountered due to the expanded or contracted abdominal segments, depending on the amount of food in the gut and/or the effect of preservation on the nymphs. Head width, being a measure of only one rigid body somite, was considered to be a more accurate index of size than a measure of numerous, flexible body segments. The sex was also determined in specimens showing development of sexual characteristics and/or medial eye development in the male nymphs, and stage of development (after Clifford,(1970a)) was also recorded. When there were more than 300 specimens of any one species in any sample, a subsample of 1/2, 1/4, 1/8 or 1/16 was taken using a petri dish and a T-shaped divider, which gave one half and two quarter samples. Opposing halves or quarters consistently acquired half or quarter of the sample respectively. A minimum of 150 specimens were measured in these subsamples.

The fine net samples were poured into a 110μm mesh sieve, and the organic material was separated from the inorganic sediments by repeated (5 x) flotation in saturated calcium chloride solution, and elutriation through a 110μm mesh. The organic sample was then washed in water, and when the volume of material was too great to sort in its entirety subsampling was carried out using the technique used by Bishop and Hynes (1969a, b) and Bishop (1973a), which was a modification of the technique of Allanson and Kerrick (1961). The subsample was sorted in a perspex tray based on the Fenwick pattern, as described and illustrated by Hellawell (1978), using a Wild M5 dissecting microscope of 25 x magnification. Each mayfly nymph was identified, the head width measured at a magnification of 50 x, and stored in the ethanol-glycerol solution. The presence of eggs of each species was also noted.

Each sample was considered individually and the species composition gave some indication of the habitat in which each species could be found. The abundance of each species was compared with habitat type as defined by Allen (1951), Harrison and Elsworth (1958) and used by Schoonbee (1973).

Gut Analysis

The food habits of nymphs from Deep Creek and Spring Creek were determined from comparative material collected during the study. The contents of the fore and mid gut of preserved specimens were dispersed on a slide and were examined at 200 x magnification. The whole slide was scanned, and algae and detritis were identified, where possible, and relative abundance of each was recorded.

III.3 Study Sites Descriptions.

III.3.1 Deep Creek (Sixth Creek)

Deep Creek is a permanently flowing stream draining the Mt. Lofty Ranges just north of Mt. Lofty. The stream is a tributary of the River Torrens which has cut deep meandering gorges through the block faulted peneplain of the Mt. Lofty Ranges, and which flows across the Adelaide Plain to Gulf St. Vincent. The creek rises at an altitude of 560m above sea level near Summertown and flows in a northerly direction to join the River Torrens near Castambul at an altitude of 140m ASL (Fig. III.2).

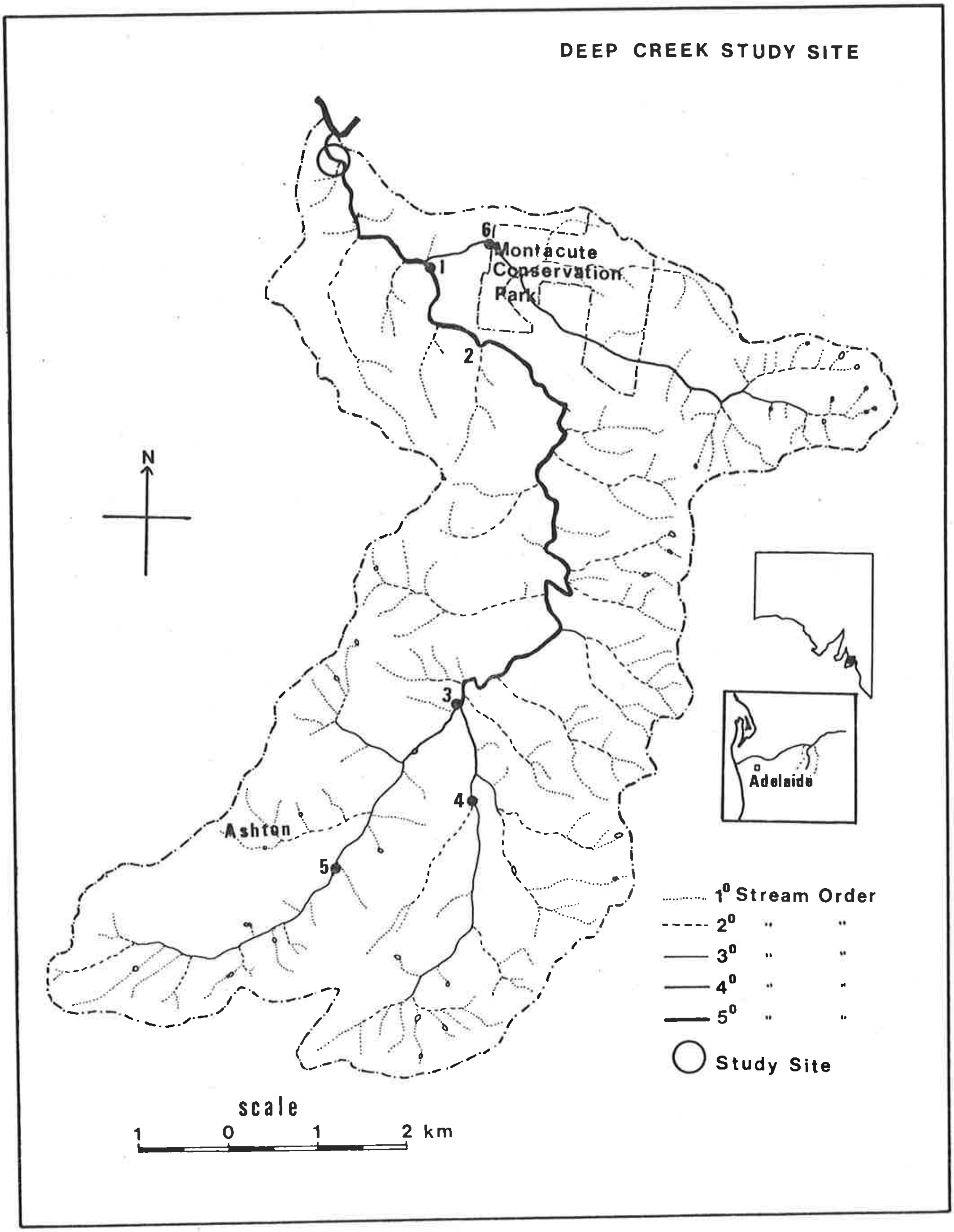
Geology and Vegetation

The geology of the area has been considered by Howchin (1904, 1906), Sprigg (1945, 1946) and a recent review was given by Daily et al (1976).

The Deep Creek catchment is of Precambrian Adelaidean Series (Burra Group) with the upper catchment underlayed by Rhynie Sandstones (Algate Sandstone) and the middle and lower catchment consists of Woolshed Flat Shales and Skillogalee dolomites respectively. The Algate Sandstone and Woolshed Flat Shales are separated by a suspected east/west fault near Marble Hill, at the confluence of the fourth order tributaries, (sensu Strahler, 1957). The lower catchment, the last 5-6km of stream channel, is of Skillogalee dolomite which includes Montacute and Castambul dolomite members. At the ford

Fig. III.2. Location of sampling sites (1 - 6) and study site in the Deep Creek Catchment, South Australia.

1. Deep Creek at ford.
2. Deep Creek at upstream ford.
3. Deep Creek on Knotts Hill Road.
4. Tributary of Deep Creek, at Hunters Road, Basket Range.
5. Deep Creek, Ashton.
6. Tributary of Deep Creek downstream of Montacute Conservation Park.


DEEP CREEK STUDY SITE
N
6
Montacute Conservation Park
1
2
3
4
5
Ashton
Adelaide
1⁰ Stream Order
2⁰ " "
3⁰ " "
4⁰ " "
5⁰ " "
Study Site
scale
1 0 1 2 km

(site 1), and 0.5km south of the ford, the catchment is traversed by two sections of a north/south fault, neither of which alter the drainage characteristics of the creek.

Associated with the geological formations are distinct soil types. Podsols are developed where the Algate Sandstones are exposed and on top of the ridges, where the rainfall is higher, leaching of the mono- and di-valent cations occurs, producing a "mature" podsol profile (Specht and Perry, 1948). In the upper reaches of the Woolshed Flat Shales, where the rainfall is also comparatively high, the nutrients of the soil have been leached, leaving a nutrient poor grey-brown podsol. The lower reaches differ by having less leached, richer grey-brown podsols. Specht and Perry (1948) correlated the nutrient levels with vegetation and stated "the savannah formation on the relatively high nutrient status, grades imperceptibly into sclerophyllous formations on the relatively low nutrient grey-brown podsols with increase in rainfall."

The vegetation of the Mt. Lofty Ranges, including the Deep Creek catchment, was studied by Specht and Perry (1948) and a review by Lange (1976) summarised the native vegetation formations of the Ranges. Deep Creek has extensive orchard development in the upper catchment, and market gardens in the richer soils of the lower catchment. Where native vegetation is still present, in the higher rainfall regions on the Mt. Lofty spine, it is dominated by stringybark *Eucalyptus obliqua* L'Herit, while the white gum *E. rubida* Deane and Maiden occupies areas "around the gully heads on highly leached grey-brown podsols with rainfall greater than 45 inches per annum."

"As the annual rainfall decreases to 35 inches the species is confined to a narrow belt of wet alluvial soil along the larger creeks" (Specht and Perry, 1948). This species is replaced along the watercourse by *E. viminalis* Labill. where the rainfall drops below 750mm (≈ 30 inches). Along the lower reaches of Deep Creek, and the study section, *E. camaldulensis* Dehnh. dominates the savanah vegetation with *Cyperus vaginatus* R. Br., *Juncus pallidus* R. Br., *J. usitatus* Johns, and *J. sarophorus* Johns the dominant riparian vegetation. In the wetter regions, introduced species may be dominant, especially blackberries *Rubus* spp., broom *Genista maderensis* (Webb and Berth), and willow, *Salix* sp.

The Influence of Man.

As mentioned above the catchment has extensive development of orchards and market gardens. With these agricultural activities there are periods of nutrient and pesticide inflow in surface runoff and groundwater flow. It is difficult to directly attribute any effects of pesticide introduction, but the high nutrient levels probably contribute to the summer blooms of the green filamentous algae, *Cladophora* sp. Water from Deep Creek is also used for irrigation during summer in indeterminant quantities, and during the study period, 3.6×10^4 l per day was pumped during February and March 1977 for use in a nearby quarry.

The Creek forms part of the South Australian Fly Fishers' Association trout fry hatchery, and is zealously protected by by members of the association in efforts to maintain the self sustaining stream populations of brown trout, *Salmon trutta* L. and rainbow trout, *S. gairdnerii* Richardson. A study of this hatchery was carried out by Morrissy (1967) but only partially published (Morrissy, 1971).

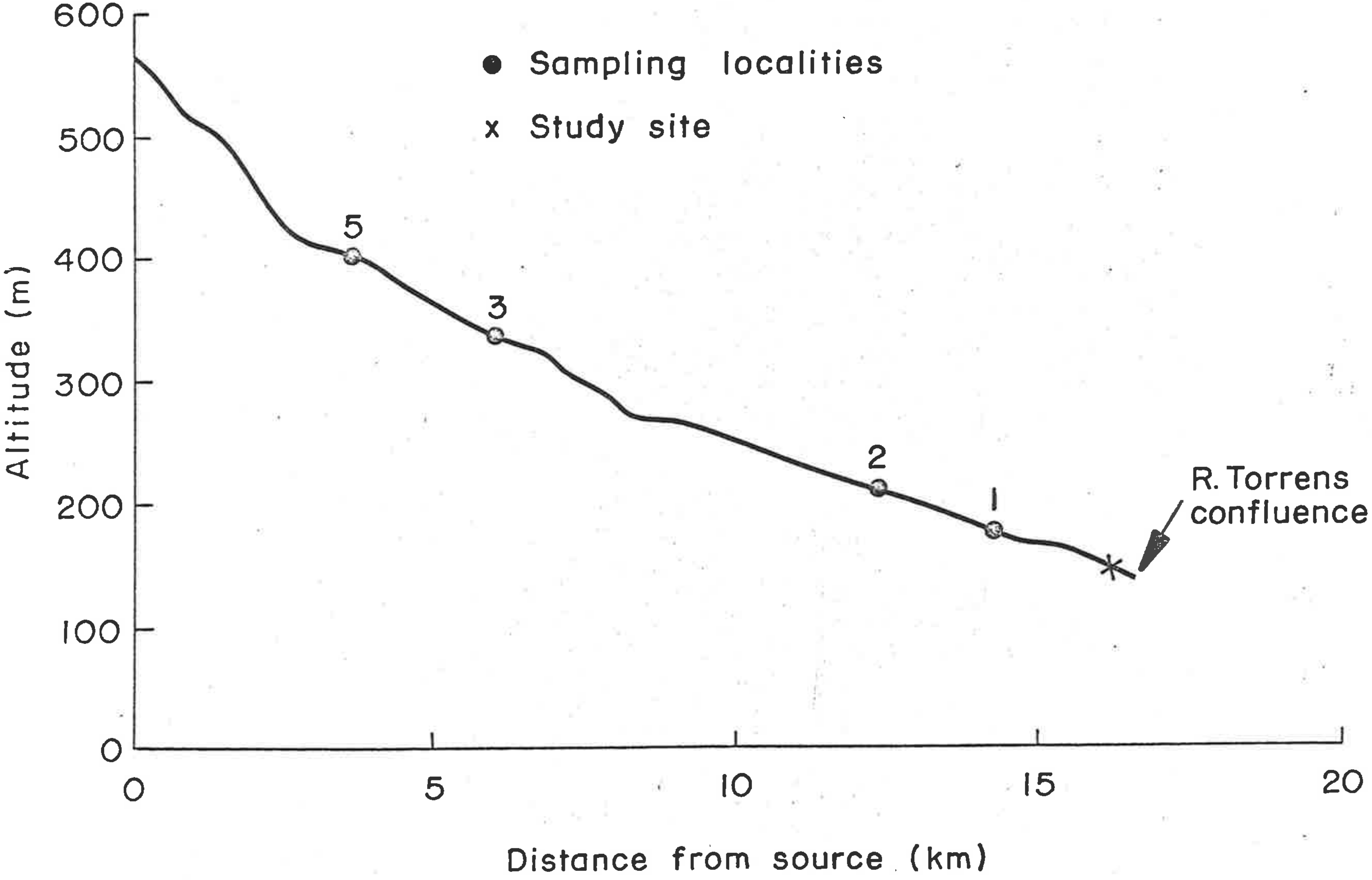
Morphometric Features of the Catchment.

The catchment area of Deep Creek is approximately 40km^2. Total stream length from the headwaters to the confluence with the River Torrens is 16.61km In profile (Fig. III.3) the stream descends rapidly for the first 2.5km to an altitude of 425m with a gradient of 64 m/km. The stream then descends more gradually at a gradient of 27.2 m/km for 5.7km, and then descends the final 8.4km at a gradient of 15.48 m/km. The watershed characteristics of stream order, length, average length; bifurcation ratios and average stream length are summarised in Table III.2.

Climate.

The climate of the region is basically Mediterranean, but lacks the moderate summer rainfall, characteristic of this climatic type. Rainfall is orographic, closely correlated with the altitude of the Mt. Lofty Ranges. The rainfall on Mt. Lofty (720m ASL) averages nearly "four times the value recorded near the coast at Port Adelaide" (Schwerdtfeger, 1976). Rainfall gauging in the Deep Creek catchment is limited to Ashton (538m) in the upper catchment, but rainfall data from Northfield Agricultural Centre (80m) on the Adelaide Plains near the River Torrens and Adelaide City (40m) for the

Fig. III.3. Longitudinal profile of Deep Creek, South Australia.



600
500
400
300
200
100
0
Altitude (m)
● Sampling localities
x Study site
5
3
2
1
R. Torrens confluence
0
5
10
15
20
Distance from source (km)

TABLE III.2. Deep Creek Drainage Characteristics

Stream Order	Number	Total Length (km)	Average Length (km)
1°	153	58.89	0.38
2°	37	28.24	0.76
3°	7	7.48	1.07
4°	3	6.36	2.12
5°	1	10.39	10.39

Bifurcation Ratios		Average Stream Length Ratios	
1 : 2	4.14	2 : 1	2.00
2 : 3	5.29	3 : 2	1.41
3 : 4	2.33	4 : 3	1.98
4 : 5	3.00	5 : 4	4.91
mean	3.69		2.58

Main Channel Length = 16.61km

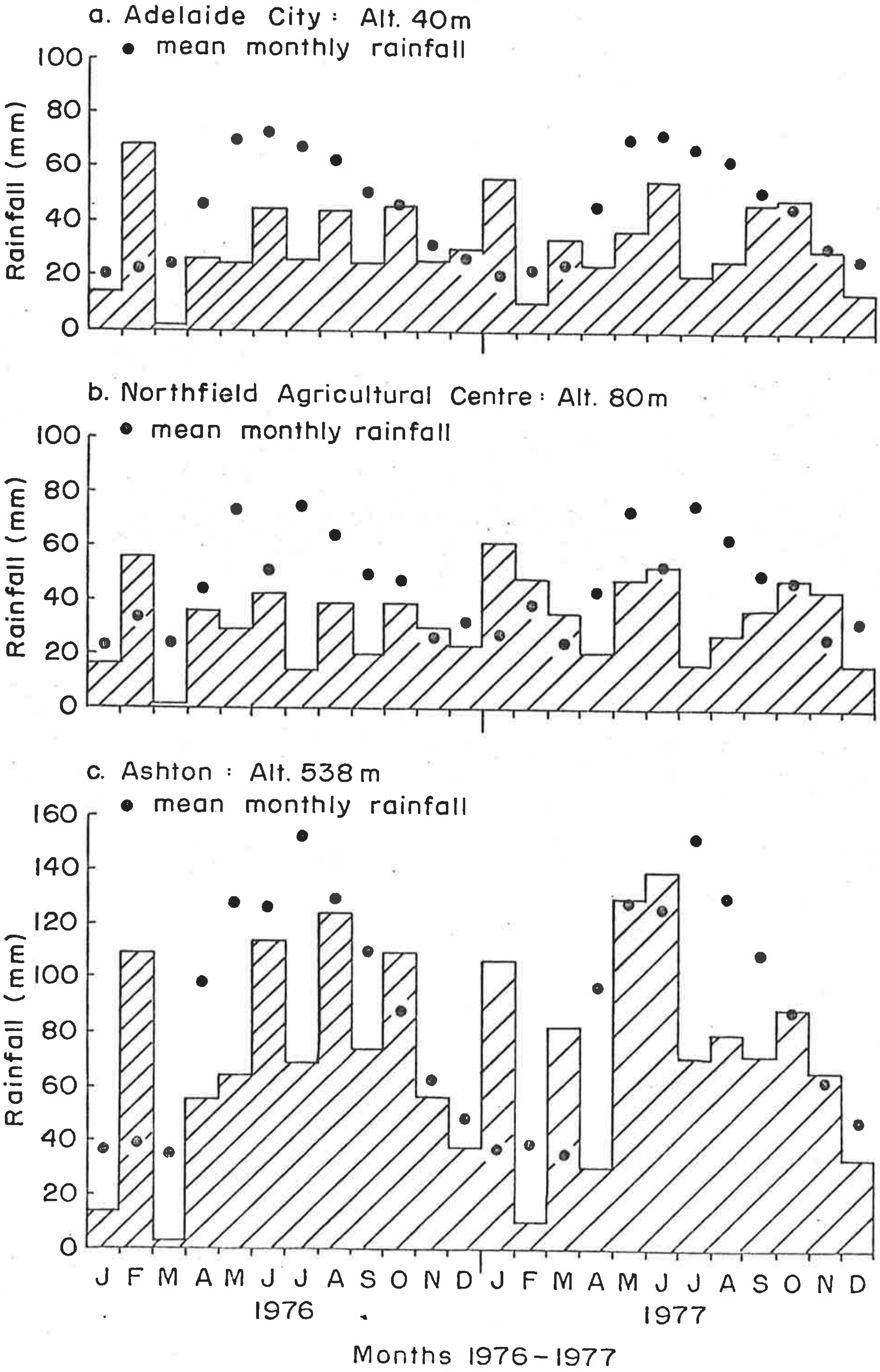
period January 1976-December 1977 are recorded in Fig. III.4, and give a reasonable estimate of rainfall for the lower part of the catchment.

Temperature recording stations are even fewer than rainfall stations. An altitude lapse-rate effect is experienced with the mean temperatures, 3.5°C cooler on Mt. Lofty than in Adelaide City; temperature contours are given by Schwerdtfeger (1976). Attempts to record air temperature at the study site were thwarted by constant interference with maximum-minimum thermometers, with these either being removed or broken. Morrissy (1967) found positive correlation between Adelaide air temperature and air temperature at Deep Creek. The regression obtained by Morrissy for the maximum temperature relationship was

$$y = 1.6103 + 0.9577\,x \quad (y = \text{Deep Creek maximum},\ x = \text{Adelaide maximum}),$$

thus suggesting that the maximum temperature at Deep Creek is fractionally warmer than in Adelaide. Since the difference between the two is usually within 1°C, it was considered that the Adelaide City air temperature was a reasonable estimate of the Deep Creek air temperature. The Adelaide monthly maxima, minima and mean air temperatures for the period January 1976 - December 1977 are given in Fig. III.5.

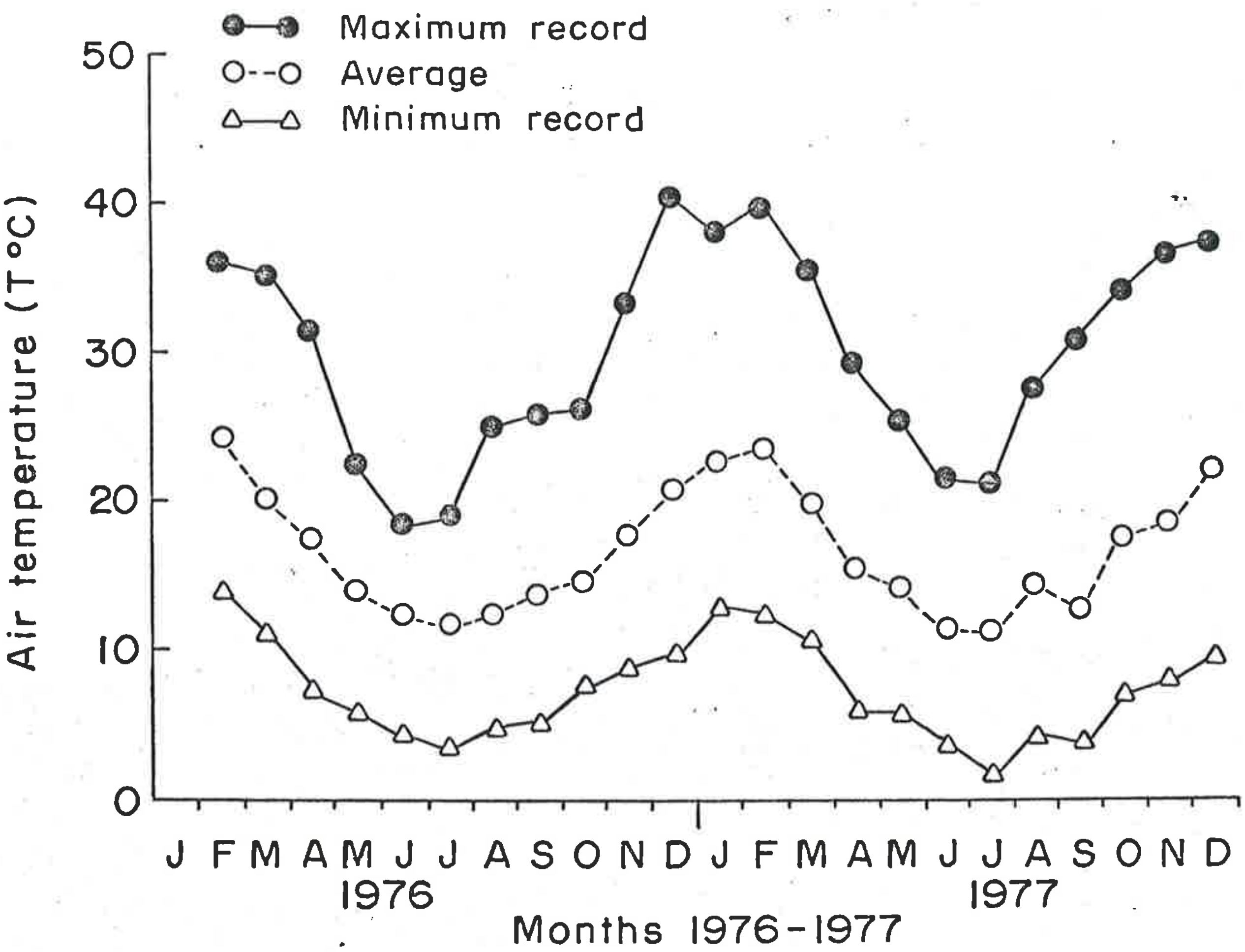
Fig. III.4. Monthly rainfall recorded in 1976 - 1977 at Adelaide City (a); Northfield Agricultural Centre (b) and Ashton (c), and compared with the mean monthly rainfall at each gauging station.



a. Adelaide City : Alt. 40m
● mean monthly rainfall
Rainfall (mm)
0
20
40
60
80
100
b. Northfield Agricultural Centre : Alt. 80m
● mean monthly rainfall
Rainfall (mm)
0
20
40
60
80
100
c. Ashton : Alt. 538 m
● mean monthly rainfall
Rainfall (mm)
0
20
40
60
80
100
120
140
160
J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
Months 1976-1977

Fig. III.5. Monthly maxima, minima and mean air temperature at Adelaide City for the period January 1976 - December 1977.

Fig. III.6. The study section of Deep Creek, South Australia, (September 1977).


Maximum record
Average
Minimum record
Air temperature (T °C)
50
40
30
20
10
0
J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
Months 1976-1977

The Study Site.

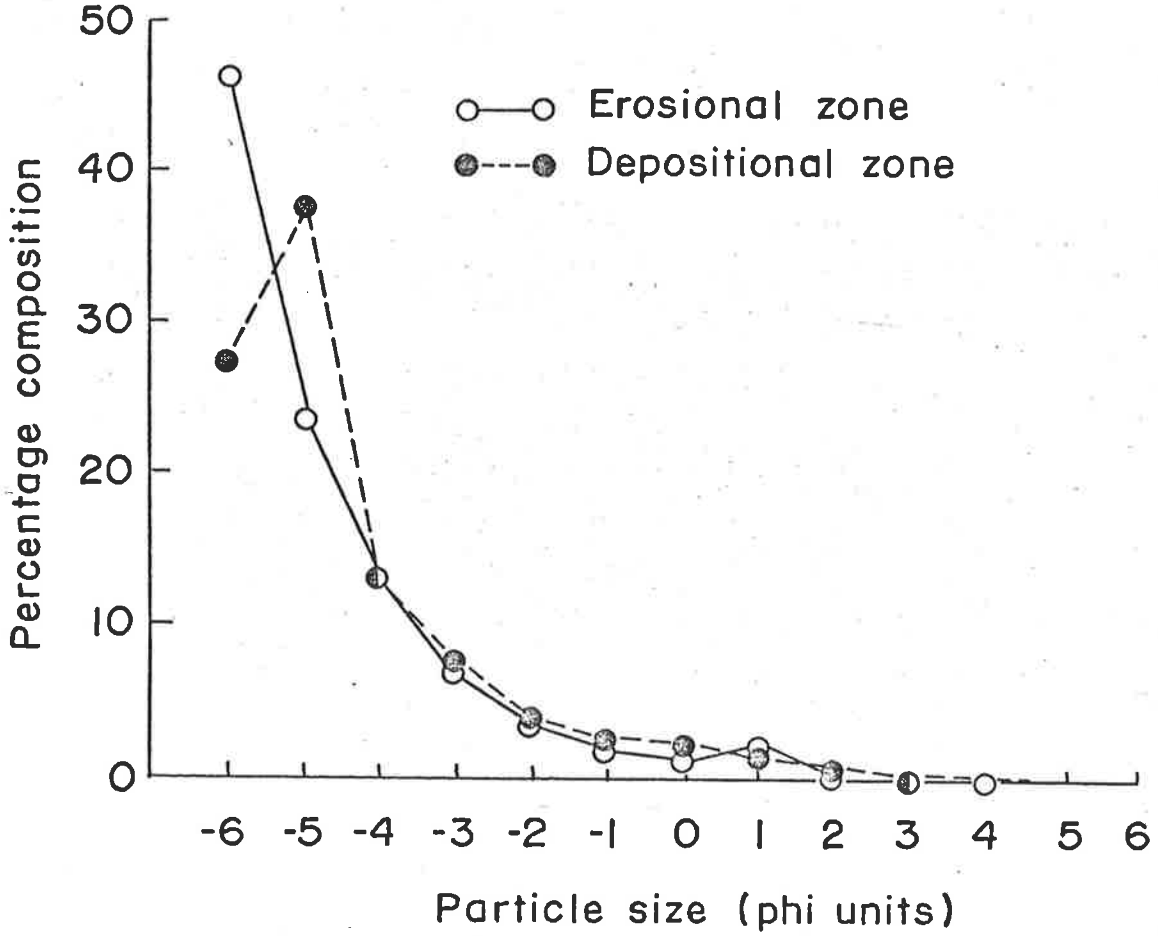
The study section was 16.5km from the source, at an elevation of 140m ASL, situated beside Corkscrew Road, Castambul, 24km from Adelaide. At the study site the stream is fifth order, and drains the entire watershed. The study section was from the confluence with the River Torrens upstream for 0.5km, grid reference, on the Onkaparinga Sheet 1:50,000 map series, 662811-388945. In this area the stream bed is 10-15m wide, and the depth varies from 0.12m in riffles to 0.42m in the deeper pools. (Fig. III.6).

A substrate analysis was carried out during the spring, when flows were moderately low. Samples from regions which were subjectively classified as depositional and erosional were taken from an area of $0.10m^2$, and to a depth of 5cm. The representation of the substrate particle size distribution is shown in Fig. III.7. The median diameter (Md) was -5.8phi and -4.5phi and the median particle size was -6phi and -5phi for the erosional and depositional samples respectively. The Q_1 and Q_3 values (Doeglas, 1968) of both samples show that the substrate can be classified as coarse to very coarse gravel with the erosional zone almost attaining small cobble size.

Physical and Chemical Features.

The discharge of Deep Creek fluctuates violently, with peaks occurring immediately after downpours of rain (Fig. III.8). An isolated summer storm occurred on January 4, 1977 causing a marked increase in the otherwise steadily decreasing discharge.

Fig. III.7. Substrate particle size distribution from depositional and erosional regions at the Deep Creek study site.


Erosional zone
Depositional zone
Percentage composition
50
40
30
20
10
0
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
Particle size (phi units)

Morrissy (1971) recorded a similar spate in December, 1965 and recorded increased temperature of the flood water, caused by the heavy rain running off warm ground. This rise in temperature (no actual value recorded) exceeded the lethal temperature of brown trout *Salmon trutta* (25-30°C). The temperature during the January 1977 flood did not exceed 23°.

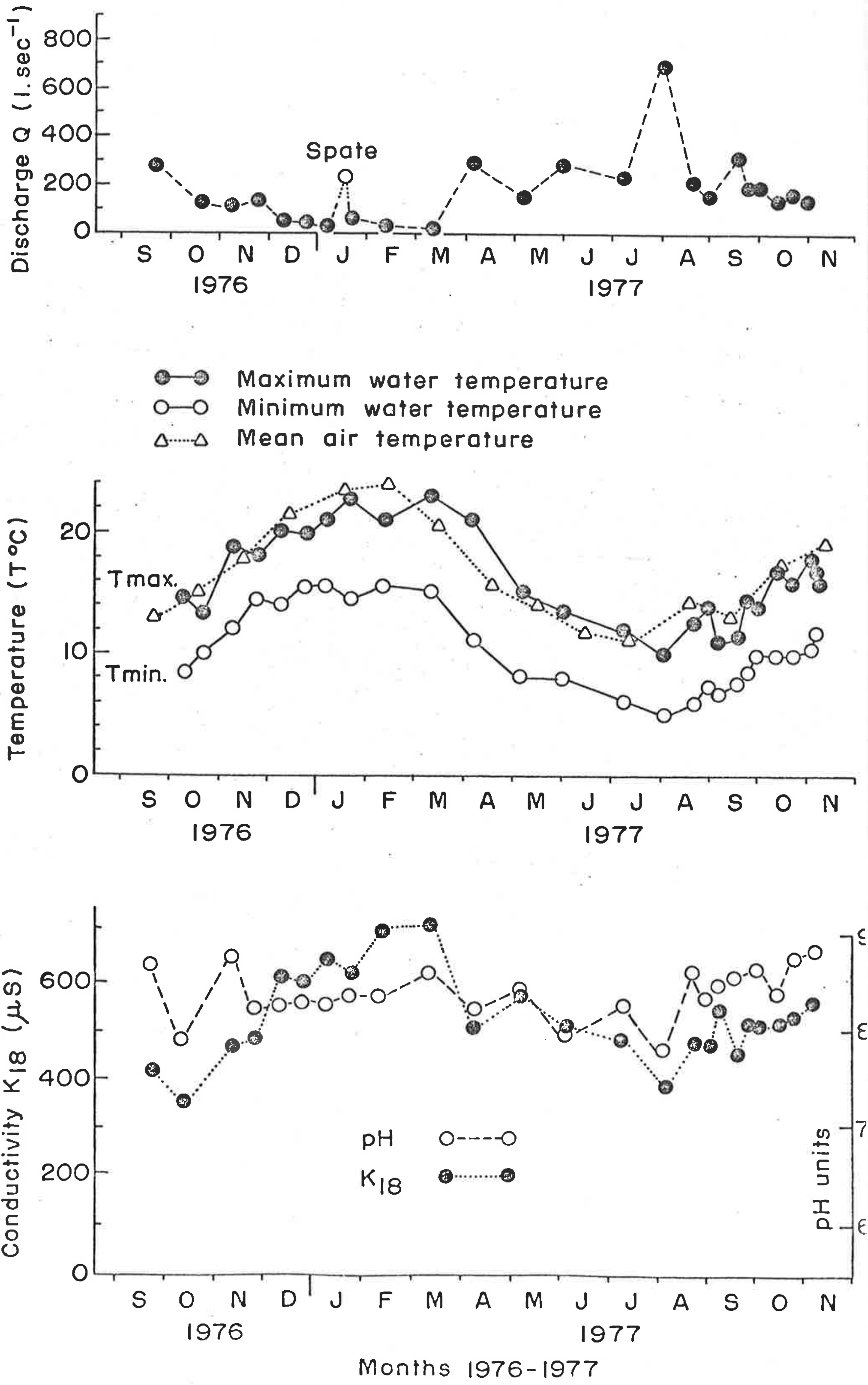
The stream temperature is closely correlated with air temperature, and Morrissy (1971) stated "daily maximum water temperature during the "spring" and "summer" months was positively correlated with the prece~~e~~ding minimum water temperature on the same day as well as with the maximum temperature. However, the day to day variations in minimum water temperature during the hotter months were not statistically dependent upon the prece~~e~~ding maximum water temperature; the daily period of cooling of the water was apparently sufficiently long for a relative degree of independence to occur. (The minimum water temperature during "winter" was negatively correlated with the maximum water temperature on the preceeding day since warm winter days with clear skies are usually followed by very cold nights, due to frosts)." The water temperature range observed during the study period was 5°C-23°C, the minimum in August 1977 and the maximum in March 1977. The recorded water temperatures and the corresponding mean Adelaide air temperature are given in Fig. III.9.

During the study period, the pH of the water always exceeded 7.75 with an observed maximum of 8.82 in October 1977. The conductivity, K_{18}, ranged from 352.4μS (Salinity of 199 ppm) in October 1976, to 708.3μS (Salinity of 378.5 ppm)

Fig. III.8. Seasonal changes of discharge ($l.sec.^{-1}$) at Deep Creek, South Australia, during the study period, September 1976 - November 1977.

Fig. III.9. Maximum and minimum water temperatures (^{o}C) recorded at Deep Creek study site, compared with mean Adelaide City air temperature from September 1976 - November 1977.

Fig. III.10. Seasonal changes of pH and conductivity (K_{18} S) at Deep Creek, South Australia during September 1976 - November 1977.



Discharge Q (l.sec^{-1})
800
600
400
200
0
Spate
S O N D J F M A M J J A S O N
1976
1977
Maximum water temperature
Minimum water temperature
Mean air temperature
Temperature (T °C)
20
10
0
Tmax.
Tmin.
S O N D J F M A M J J A S O N
1976
1977
Conductivity K_{18} (µS)
600
400
200
0
pH units
9
8
7
6
pH
K_{18}
S O N D J F M A M J J A S O N
1976
1977
Months 1976-1977

in March 1977. Conductivity was inversely proportional to discharge. pH and K_{18} data are given in Fig. III.10.

The ionic dominance of Deep Creek water is $Mg^{2+} > Na^{+} > Ca^{2+} > K^{+}$ and $HCO_3^{-} > Cl^{-} > SO_4^{2-}$. Dissolved oxygen concentration was either saturated or super-saturated throughout the year.

Stream Flora.

Deep Creek is typical of the creeks draining the Mt. Lofty Range, all of which have blooms of *Cladophora* sp. during the summer months. The bloom of this green filamentous alga begins in the riffle zones as the temperature steadily increases during spring/early summer, until it occupies all habitats and flow regimes, forming a floating mat on the pools. (Fig. III.11). Morrissy (1971) recorded mat thickness of 30cm, and during the November, 1976 - February, 1977 period the dry weight of *Cladophora* exceeded 40gm^{-2}. When the discharge was low, large areas near the banks became overgrown with *Nasturtium* sp. and locally with *Potamogeton crispus* L.. An extensive periphyton, predominantly of unicellular diatoms, developed on the *Cladophora* and *Potamogeton*. This included *Tabellaria, Caloneis, Cocconeis, Gomphoneis, Navicula, Pinnularia, Surirella* and *Chlorhormidium* (nr). A filamentous diatom, *Melosira* sp. was also recorded. During Winter, with increased flow and decreased light and temperature, this flora was greatly reduced, with very little *Cladophora, Potamogeton* and *Nasturtium,* and their attached communities, remaining.

Fig. III.11. Deep Creek, South Australia, January 6, 1977, overgrown with *Nasturtium* sp. and pools covered with *Cladophora*. Fig. III.1 also illustrates the abundance of the *Cladophora* growing at Deep Creek in Summer.

Mayfly Fauna.

Four species of mayfly were recorded in the Deep Creek catchment, *Atalophlebia australasica, Atalonella inconspicua, Baetis soror* and *Tasmanocoenis tillyardi*. In the study section of Deep Creek all species were recorded, but *Atalonella inconspicua,* although present in nearly all samples, was in very low numbers, especially after the spring of 1976. Of the 43,124 nymphs collected during the study period 70.86% were *T. tillyardi* , 18.70% were *B. soror*, 9.96% were *Atalophlebia australasica* and 0.48% were *Atalonella inconspicua.*

Collections throughout the catchment in localities other than the major study section revealed that *B. soror* was limited to the streams of the lower 4km of the catchment. Collections from the upper reaches at Knotts Hill Road (Locality 3) recorded *A. inconspicua* only, at Hunters Road, Basket Range (Locality 4) *A. inconspicua* and *T. tillyardi* and near Ashton (Locality 5) *A. inconspicua* and *Atalophlebia australasica.* The tributary flowing from the Montacute Conservation Park (Locality 6) contained all four species.

III.3.2 Spring Creek.

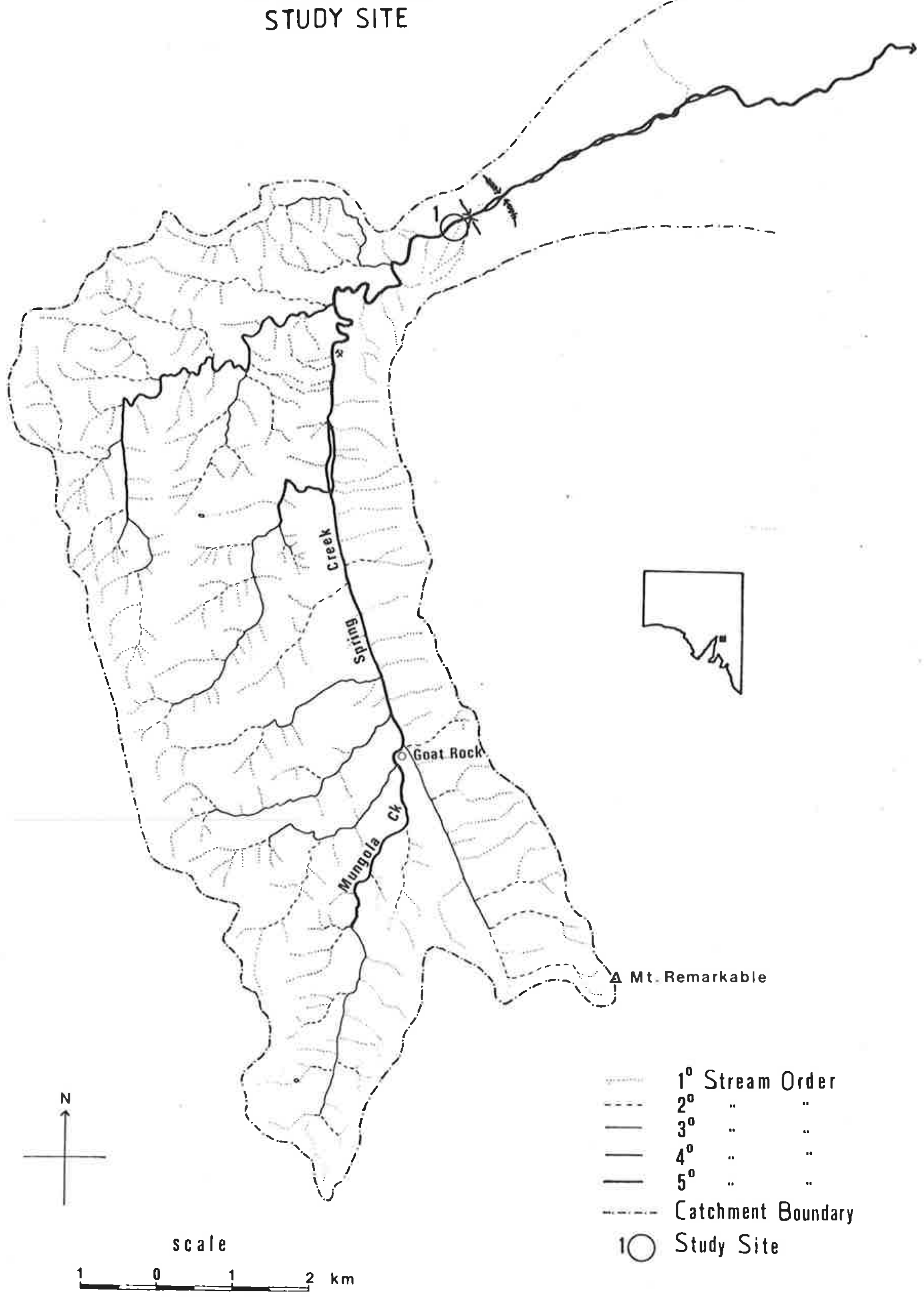
Spring Creek is an intermittent stream draining the eastern slopes of the coastal spur of the Southern Flinders Ranges, midway between Melrose and Wilmington, 280km north of Adelaide. The stream is a tributary of the Willochra Creek which is a large intermittent stream flowing northwards towards the dry salt pan of Lake Torrens. Spring Creek rises at an altitude of 895m on the northern slopes of Mt. Remarkable (960m) and flows in a northerly direction for 10km, when it turns sharply north eastwards to cut through the range and debouche onto the Willochra Plain at an altitude of 350m ASL (Fig. III.12).

Geology and Vegetation.

The geology of the Mt. Remarkable area has been studied by Howchin (1916) and Binks (1971). The Spring Creek catchment is of Cambrian age with the western ridge (Black Range) composed of ABC quartzite capping the Brachina Formation of "well bedded, red brown, ripple marked siltstone" (Binks, 1971). Below the Brachina Siltstone lies a bed of Willochra Sandstone which grades into Willochra Siltstone with a basal Limestone member. Beneath the Willochra Formation lie the Tapley Hill Siltstones with a basal member of Tindelpina Shale. Appila Tillite forms the base of the western slopes, and the Spring Creek watercourse follows the north-south lineament (unconformity?) along the boundary of the Appila Tillite and Burra Group (Rhynie Sandstones) which form the Mt. Remarkable Ridge, and the eastern slopes of the catchment. Just north of the Spring Creek Mine, the creek reaches an east-west fault line where it deviates to the north east, flowing through a folded region of Willochra Formation Sandstones and Siltstones and a Willochra Dolomite/ Limestone band. At the base of the Mt. Remarkable Range the creek flows, through Quaternary low angle slope deposits, onto the Willochra Plain.

Fig. III.12. Spring Creek Catchment and study locality, Southern Flinders Ranges, South Australia.

SPRING CREEK
STUDY SITE



The vegetation of the area has been described by Boomsma (1946) and as in all watercourses in arid and semi-arid areas of South Australia the riparian cover of Spring Creek is dominated by the river red gum, *Eucalyptus camaldulensis*. The upper reaches of Spring Creek are well grassed on the Appila Tillite, but dense shrubs of *Acacia victoriae* Benth., *A. rupicola* F. Muel. ex Benth., and *Bursaria spinosa* Cav., grow on the Tapley Hill Formation. Along the watercourse, *E. camaldulensis* is usually the only tree species except for an occasional association with *Casuarina stricta* Ait. Clumps of rushes *Juncus* sp. also often line the watercourse.

The lower reaches of the creek, flowing onto the Willochra Plain, are bordered by grazed and cultivated (wheat) land. Sheep, cattle and other stock have free access to the stream throughout the year, and during the summer months congregate near the waterholes in the creek bed adding nutrients to the pool systems.

Morphometric Features of the Catchment.

The catchment area of Spring Creek is approximately 50km^2 with the major contribution from the western slopes (Fig. III.12) off the Brachina, Willochra and Tapley Hill Formations. Total stream length is 21km, before disappearing into the Willochra Plain. In profile (Fig. III.13) the channel descends rapidly at a gradient of 89m/km for the first 5km, to an altitude of 450m, and then has a constant gradient of 11.5m/km until reaching the Willochra Plain at an elevation of 270m ASL. The longest tributary, Mungola

Fig. III.13. Longitudinal profile of Spring Creek, South Australia.

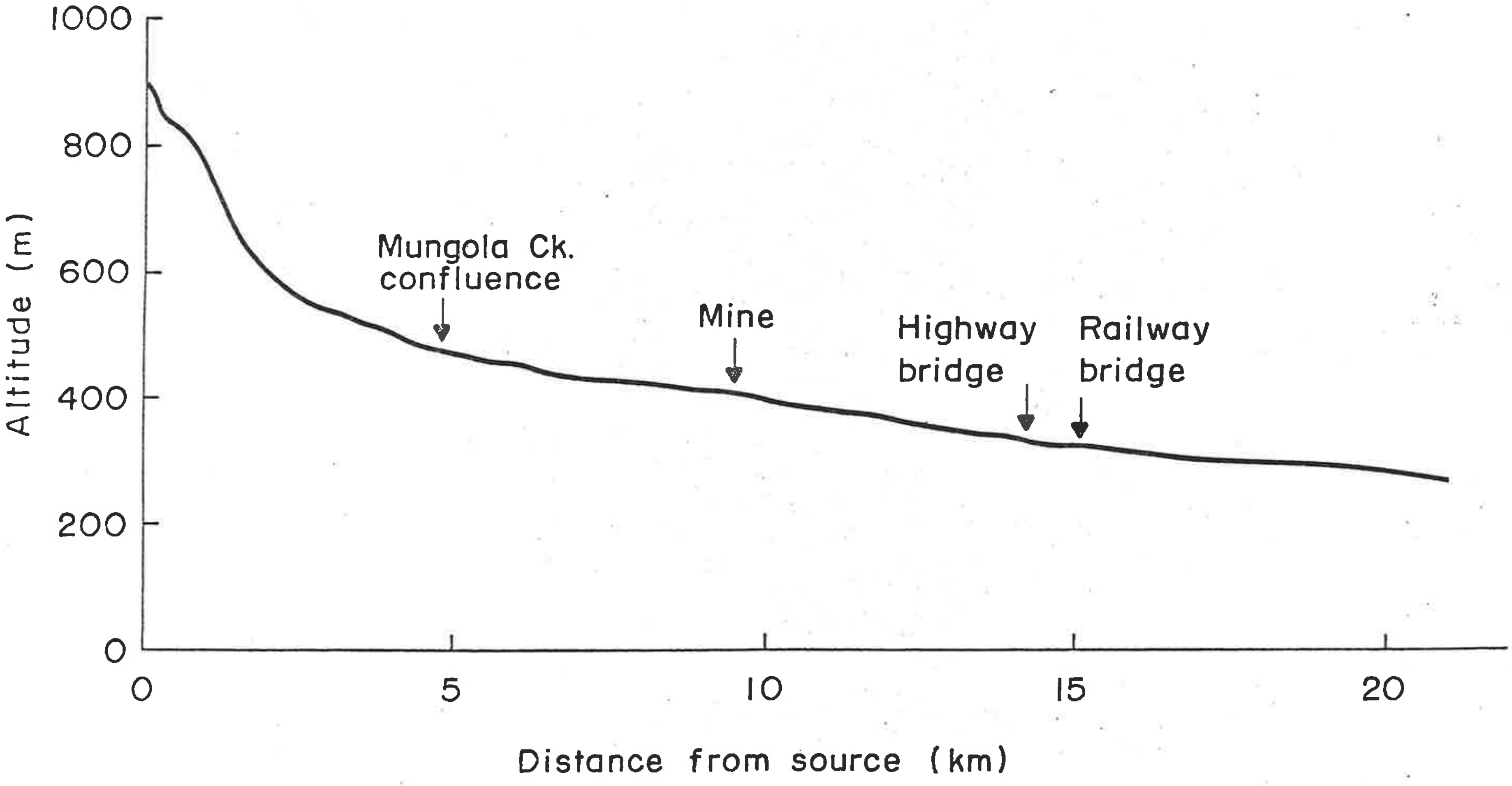

1000
800
600
400
200
0
Altitude (m)
0
5
10
15
20
Distance from source (km)
Mungola Ck. confluence
Mine
Highway bridge
Railway bridge

TABLE III.3. Spring Creek Drainage Characteristics

Stream Order	Number	Total Length (km)	Average Length (km)
1°	266	100.80	0.38
2°	54	32.80	0.61
3°	14	19.95	1.43
4°	3	14.35	4.78
5°	1	12.60	12.60

Bifurcation Ratios		Average Stream Length Ratios	
1 : 2	4.93	2 : 1	1.61
2 : 3	3.86	3 : 2	2.34
3 : 4	4.67	4 : 3	3.34
4 : 5	3.00	5 : 4	2.64
mean	4.12		2.48

Total Length of Spring Creek = 21.1km

Length of longest Tributary (Mungola Creek) and Spring Creek = 23.10km

Creek, is 2km longer than Spring Creek, but rises at an altitude of 730m ASL, and descends only 250m in its first 7km (gradient 35.7m/km) before its confluence with Spring Creek. The watershed characteristics are given in Table III.3.

Climate.

The climate is Meditteranean to semi-arid with characteristic hot, dry summers and rainfall limited to the cooler winter months. Rainfall is variable with the highest gaugings recorded near Mt. Remarkable. Melrose receives an average of 583mm per year, while Wilmington, 22km to the north, receives only 441mm per year. Mt. Remarkable creates a rain shadow for the Willochra Plains with an average of less than 150mm per year recorded near the centre of the plain. The monthly rainfall data for Melrose (Fig. III.14a) and Wilmington (Fig. III.14b) for the years 1976-1977 are compared with the monthly average rainfall for these centres. The study period September, 1976 to October, 1977 covered a dry period. No temperature recording stations are present in the immediate vicinity of the Mt. Remarkable Range, consequently no average data are available. Air temperature measurements were made at the study site and these are presented in Fig. III.15.

The Study Site.

The study section was 13.5km from the source, at an elevation of 350m ASL, and situated 8km south of Wilmington, grid reference on the Wilmington Sheet, 1:50,000 map series 323768. In the study area the creek bed is 15-30m wide,

Fig. III.14. The monthly rainfall data from 1976 - 1977 for Melrose (a) and Wilmington (b), compared with the monthly average rainfall for these centres.

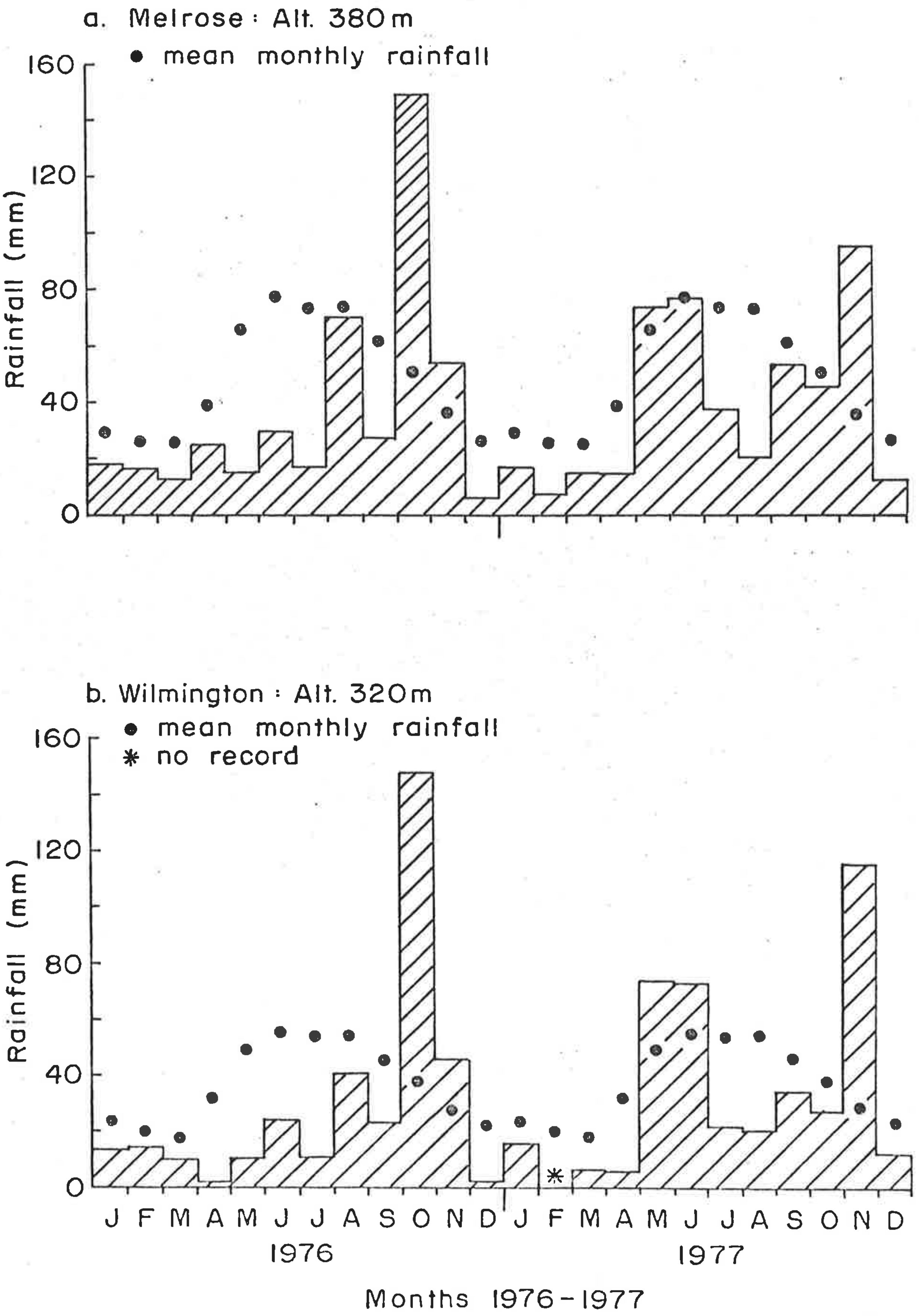
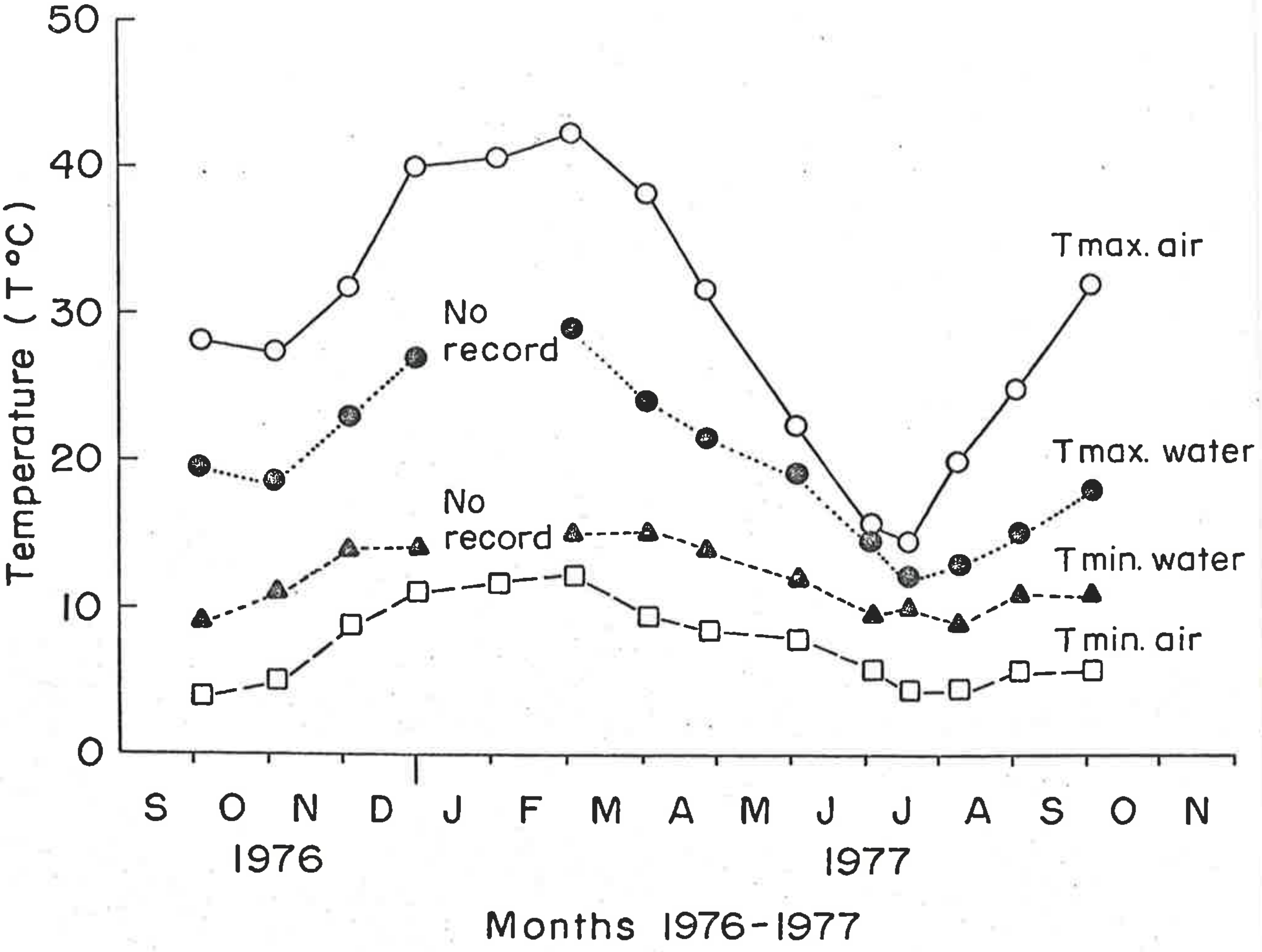
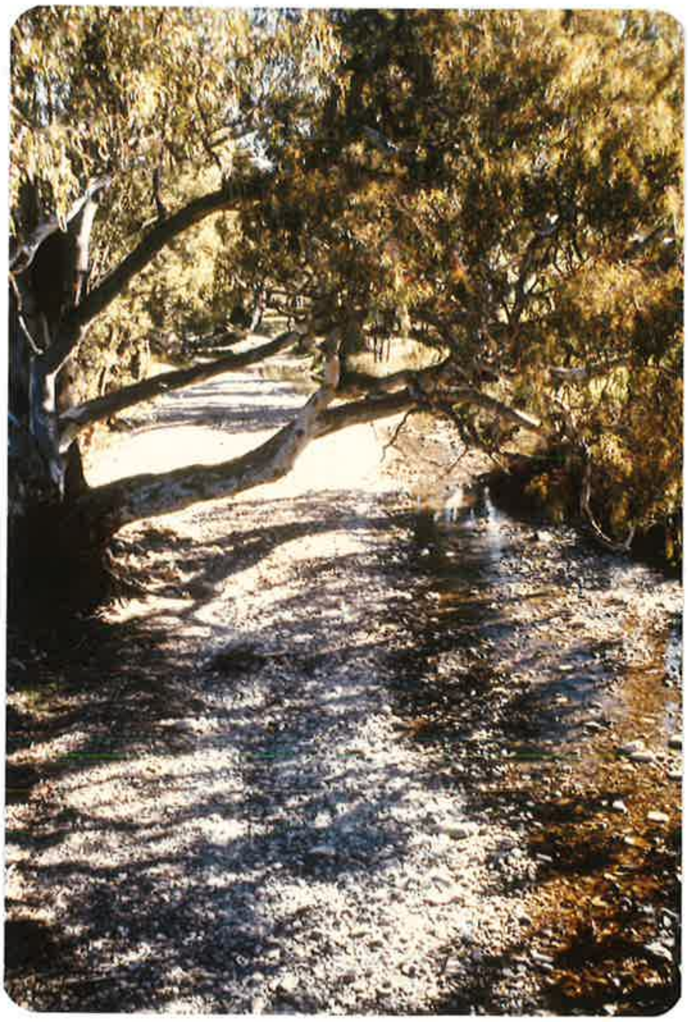

a. Melrose : Alt. 380m
● mean monthly rainfall
160
120
80
40
0
Rainfall (mm)
b. Wilmington : Alt. 320m
● mean monthly rainfall
✱ no record
160
120
80
40
0
Rainfall (mm)
J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
Months 1976-1977

Fig. III.15. The maximum and minimum monthly water and air temperatures at Spring Creek during the study period September 1976 - October 1977.

Fig. III.16. The study section of Spring Creek, South Australia, December 1976.


50
40
30
20
10
0
Temperature (T °C)
Tmax. air
No record
Tmax. water
No record
Tmin. water
Tmin. air
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977
Months 1976-1977



and the depth varies from zero in the summer months to 0.5m during the wet winter months (Fig. III.16).

A substrate analysis was performed during the summer months when the stream bed was dry. Samples from an area of $0.1m^2$ and to a depth of 5cm, from regions which were subjectively classified as depositional and erosional during the periods of flow were taken. The graphical representation of the analysis is shown in Fig. III.17. The median diameter (Md) was -4.6phi and -4.9phi and median particle size was -5phi and -5phi for the erosional and depositional samples respectively. The Q_1 and Q_3 values (Doeglas, 1968) of both samples indicate that the substrate can be classified as fine-coarse gravel.

Physical and Chemical Characteristics.

The surface discharge of Spring Creek varied greatly during the study period, being zero from January 1977 to May 1977 and exceeding an estimated 30 cumec during flash flood periods. The recorded discharges are shown in Fig. III.18 and demonstrate close correlation with rainfall. However, much of the heavy rainfall is disposed of as flood flow, with little recharging of the groundwater or the Willochra Basin aquifer (O'Driscoll, 1955).

Air temperature ranged from 4°C in October 1976 to 42°C in March 1977. The stream temperature is closely correlated with the air temperature, with an annual range of 9°C to 29°C in October 1976 and March 1977 respectively. The temperature data obtained during the study period are illustrated in Fig. III.15.

Fig. III.17. Substrate particle size distribution from depositional and erosional regions at the Spring Creek study site.

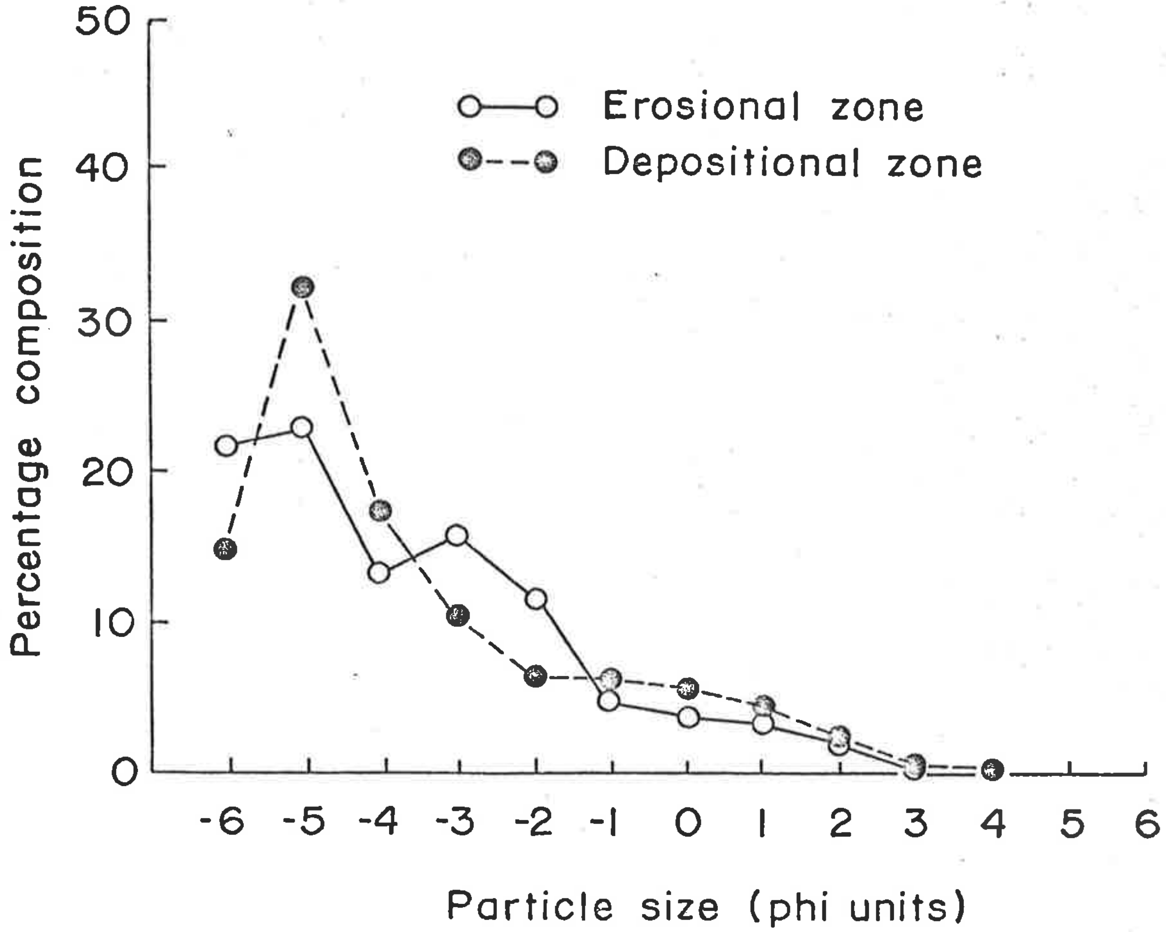
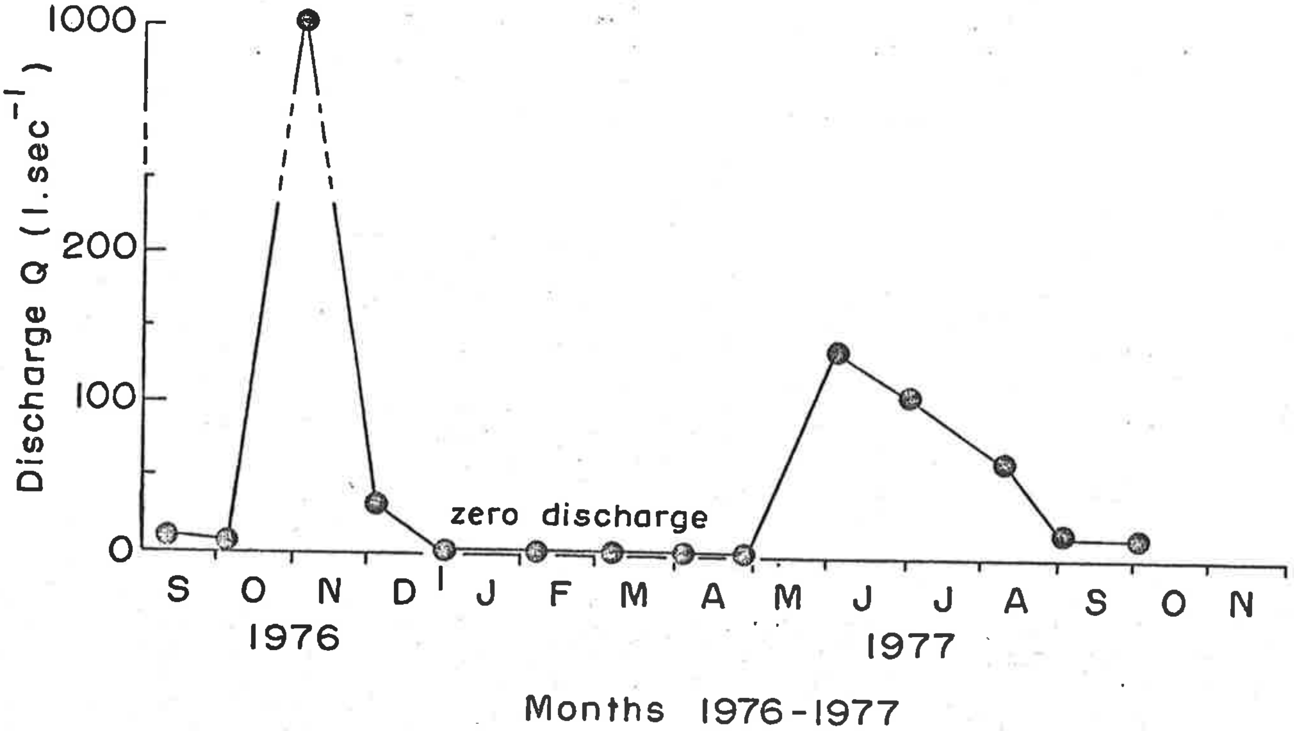
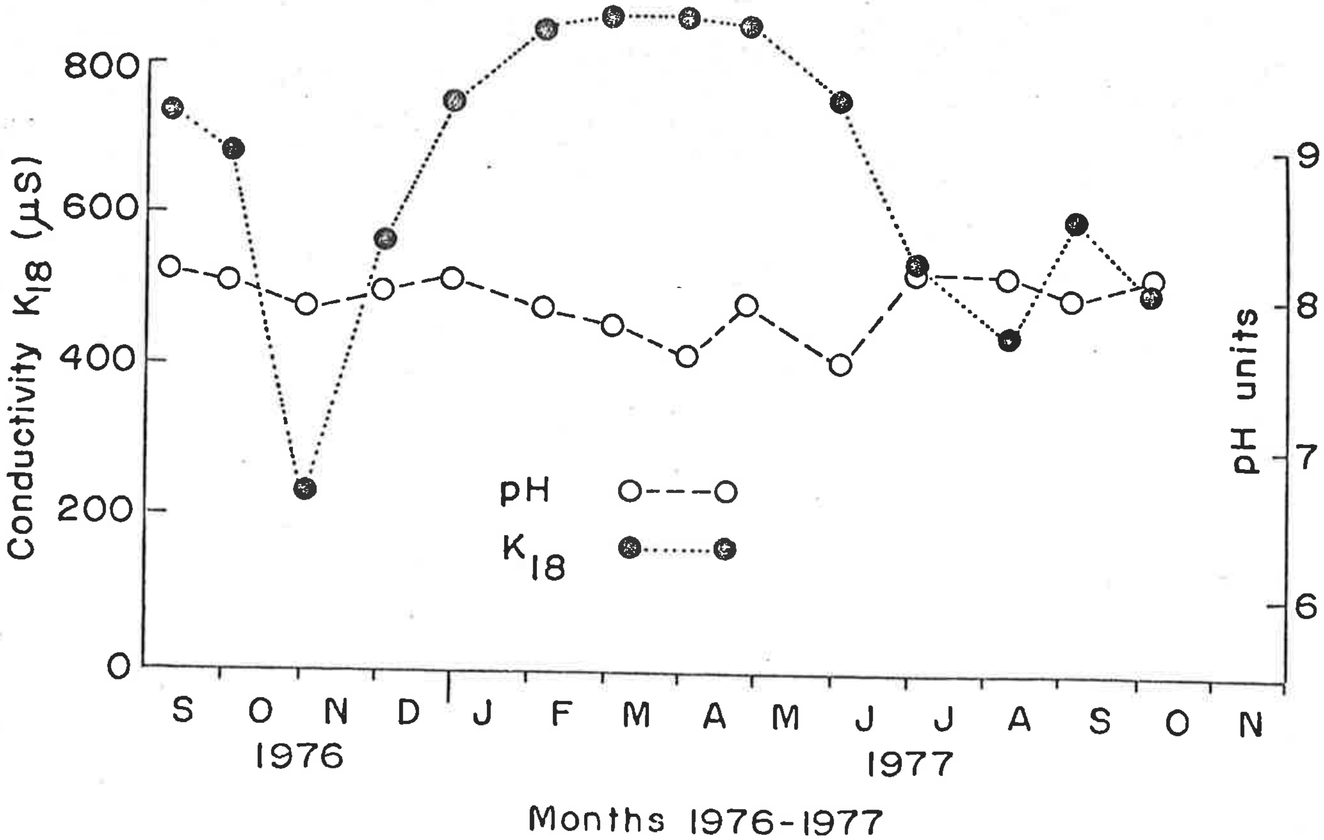

Erosional zone
Depositional zone
Percentage composition
50
40
30
20
10
0
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
Particle size (phi units)

Fig. III.18. Seasonal changes of discharge (l.sec.$^{-1}$) at Spring Creek, South Australia, during the study period September 1976 - October 1977.

Fig. III.19. Seasonal changes of pH and conductivity (K_{18}, S) at Spring Creek, South Australia, during September 1976 - October 1977.



Discharge Q (l.sec^{-1})
1000
200
100
0
zero discharge
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977
Months 1976-1977



Conductivity K_{18} (μS)
800
600
400
200
0
pH units
9
8
7
6
pH
K_{18}
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977
Months 1976-1977

The creek was always slightly alkaline with the pH ranging from 7.4 to a maximum of 8.3 attained during periods of sustained flow when the Willochra Formation Limestones contributed higher HCO_3^- levels. As flow diminished the pH decreased. The conductivity displayed a contrasting trend, being very low (K_{18} = 238μS) during flood, and becoming higher to a maximum K_{18} of 869.6μS when the stream dried to a series of isolated pools in Summer. The monthly pH and K_{18} trends are given in Fig. III.19.

The ionic dominance of Spring Creek water was $Ca^{2+} > Na^+ > Mg^{2+} > K^+$ and $HCO_3^- > Cl^- > SO_4^{2-}$. The Ca^{2+} and Na^+ dominance was periodically reversed, with Ca^{2+} dominant when there was no surface flow, and Na^+ dominant during flowing periods.

Dissolved oxygen concentrations were only low during the summer period with the lowest recorded value of 1.6ppm in a small pool isolated from the major permanent pool. No mayflies were found in this pool. During the winter period the dissolved oxygen concentrations were saturated or above.

Stream Flora.

With the exceptions of *Juncus* spp. along the river banks, there are no permanent aquatic macrophytes in the stream bed itself, but during the summer months watercress (*Nasturtium* sp.) becomes prevalent near flowing water. During periods of flow, the green filamentous algae, *Spirogyra* sp., *Mougeotia* sp. and *Zygnema* sp. can be found as short filaments. Many diatoms grow on these filaments and on the rock surfaces, these include *Cymbella, Navicula, Pinnularia, Tabellaria* and the filamentous *Melosira*. During Summer *Spirogyra*, an unattached *Eremosphaera* and a blue-green colonial alga bloom in the permanent pools. Other attached algae also increase their biomass, particularly *Mougeotia*, the rhodophyte *Batrachospermum* sp. and the blue-green filamentous *Calothrix*. Attached to the filamentous algae many diatoms; *Cymbella, Navicula, Melosira, Pinnularia* and *Synedra* were often recorded.

Mayfly Fauna.

Three species of mayfly were found in Spring Creek; *Baetis soror, Tasmanocoenis tillyardi* and *Atalonella inconspicua*. Of the 67,460 nymphs collected during the study period 44.58% were *T. tillyardi*, 37.29% were *B. soror* and 18.13% were *A. inconspicua*. These three species were also recorded upstream near Goat Rock. In October, 1975 Dr. J. E. Bishop collected specimens of *Atalophlebia australis* from the study site, but during the period of this study *A. australis* was not recorded at Spring Creek.

III.4 Results and Discussion.

III.4.1 The Effect of Mesh Size on Sieving Efficiency

A study of sieving efficiency of the coarse net, by comparison with the fine net, was undertaken. Efficiency was defined as the percentage increase in yield (numbers) of nymphs obtained by the use of 110μm mesh instead of 480μm mesh (cf. Jonasson, 1955, 1958; Barber and Kevern, 1974).

The results of this study were presented and discussed at the Third International Conference On Ephemeroptera, 1979 (Suter and Bishop, 1980), and the paper is included as Appendix 12.

III.4.2 Habitat Types.

Within the "erosional" and "depositional" zones the following stony bottom water types were sampled over the study period. The classification is similar to that presented by Allen (1951), Harrison and Elsworth (1958) and Schoonbee (1973), but has been slightly modified to suit local conditions.

1. Stationary Pools :- Non-flowing pools with depth usually less than 32cm. The substrate in these pools was usually covered with dense algal (blue green and green) growths, and the habitat is typical of the temporary streams of the Flinders Ranges during summer months.

2. Shallow Pools :- Pools less than 32cm deep and current less than $10cmS^{-1}$ and with smooth, unbroken flow.

3. Pools :- Water of depth exceeding 32cm but with current less than $10cmS^{-1}$, with unbroken flow. This habitat is similar to the category of "Pools" described by Allen, Harrison and Elsworth, and Schoonbee.

4. Flats :- Water of depth less than 48cm but with current exceeding $10cmS^{-1}$ but less than $32cmS^{-1}$. The flow in these stretches is unbroken.

5. Runs :- Water of depth exceeding 32cm and flowing at greater than 32cmS^{-1}. Flow tends to be turbulent with the water surface disturbed, but not broken.

6. Riffles :- Shallow water less than 32cm deep, with rapid current between 32cmS^{-1} and 50cmS^{-1}. Flow is turbulent and the water surface is broken.

7. Fast Riffles :- Shallow water, less than 32cm with very rapid to torrential current, exceeding 50cmS^{-1}. The water surface is always broken. In this study this latter flow category tended to be recorded during periods of high discharge in winter, or under spate conditions.

These habitat and flow characteristics are briefly summarised in Table III.4.

III.4.3 Habitat Occupation.

The occurrence of each species in each of the above habitats was examined using two methods. The number of samples taken from each habitat during the study period (N) was determined, and assuming that all species had an equal chance of being present a percentage possibility (% pos) of occurrence was calculated. From the raw occurrence data the mean number of animals in each habitat was calculated for each species. In almost all cases the variance exceeded the mean, and was not independent of the mean. Therefore the data required a log transformation to obtain comparative values of animals per habitat (Elliott, 1977). A log (x + 1)

TABLE III.4.

Summary of habitat and flow characteristics recognised in the study.

	Habitat	Depth (cm)	Velocity (cmS^{-1})	Surface Water Characteristics
1.	Stationary pool	< 32	0	smooth, unbroken
2.	Shallow pools	< 32	< 10	smooth, unbroken
3.	Pools	> 32	< 10	smooth, unbroken
4.	Flats	< 48	10 - 32	smooth, unbroken
5.	Runs	> 32	> 32	turbulent, disturbed
6.	Riffles	< 32	32 - 50	broken
7.	Fast Riffles	< 32	> 50	broken

transformation was used with data in which some zero counts were made, and a log x transformation was used in other cases. Table III.5 and III.6 summarise the results of the percentage possibility calculations, the non-transformed values, and the transformed values for each species at the two localities.

Comparing each species with only the percentage possibility occurrence, *B. soror* appears to have the more specific habitat preference at both localities, although it, and all other species occupy all habitats from stationary pools to fast riffles. *B. soror* was consistently found in habitats with flowing water, and although occasional records were made in the slower flowing and "pool" habitats, they were not consistent as in the flats, runs and riffles.

Better comparisons can be made using the transformed mean numbers per habitat, where numbers of animals occurring in each habitat are taken into account.

For *B. soror* in Spring Creek the preference for a flowing water habitat is obvious with maximum records occurring in flats, riffles and fast riffles, but in Deep Creek, the numbers are low in all habitats, with the exceptions of the pools and flats. The high value in the pools may be due to the small number (two) of samples taken from this habitat with 534 (22.12.1976) and 28 (5.5.1977) animals collected. The December 1976 sample, which exaggerates the number of animals occurring in the pool habitat, was dominated by early instar *B. soror* which hatched from eggs oviposited in November. Also, Deep Creek was filled with *Cladophora*, and the numbers of

TABLE III.5.

The occurrence of mayfly species in each habitat at Deep Creek.

N = No. of samples; % pos. = the percentage of samples in which the species was found; $\bar{x}$ = mean; S = standard deviation; S^2 = Variance.

			No./sample		Log transformed : No./sample		
Habitat	N	% pos.	$\bar{x}$	S	$\bar{x}$	S	S^2
Baetis soror							
Shallow Pools	5	20.00	9.60	21.47	2.17	5.70	32.49
Pools	2	100.00	281.00	357.80	122.28	8.04	64.64
Flats	19	89.47	248.84	328.05	64.09	8.76	76.74
Runs	5	80.00	33.00	28.59	10.24	4.42	19.50
Riffles	11	100.00	131.00	187.58	30.80	7.80	60.92
Fast Riffles	12	91.67	70.83	117.58	20.05	5.80	33.60
Atalophlebia australasica							
Shallow Pools	5	100.00	158.80	98.44	136.98	1.84	3.39
Pools	2	100.00	80.00	96.17	42.14	5.91	34.92
Flats	19	100.00	97.68	166.45	37.66	4.27	18.21
Runs	5	100.00	31.20	19.83	27.82	2.42	5.86
Riffles	11	90.91	39.55	51.59	22.02	4.16	17.30
Fast Riffles	12	91.67	17.67	15.51	11.52	3.28	10.76
Tasmanocoenis tillyardi							
Shallow Pools	5	100.00	1828.80	1880.98	1311.03	2.35	5.52
Pools	2	100.00	790.50	873.28	493.54	4.40	19.40
Flats	19	100.00	454.58	323.30	330.68	2.73	7.43
Runs	5	100.00	351.20	223.74	250.82	1.38	1.92
Riffles	11	100.00	186.18	117.81	175.56	3.12	9.75
Fast Riffles	12	100.00	179.67	131.37	109.32	4.06	16.47

TABLE III.6.

The occurrence of mayfly species in each habitat at Spring Creek. N = No. of samples; % pos. = the percentage of samples in which the species was found; $\bar{x}$ = mean; S = standard deviation; S^2 = variance.

			No./sample		Log transformed : No./sample		
Habitat	N	% pos.	$\bar{x}$	S	$\bar{x}$	S	S^2
Baetis soror							
Stationary Pools	9	44.44	2.67	5.61	1.96	2.79	7.80
Shallow Pools	14	92.86	201.71	564.21	16.99	10.87	118.08
Pools	3	66.67	58.67	65.29	18.41	13.08	171.19
Flats	10	80.00	1893.10	5563.76	66.43	21.01	441.57
Runs	1	100.00	-	-	-	-	-
Riffles	6	100.00	310.33	613.70	79.99	5.40	29.10
Fast Riffles	3	100.00	59.67	57.88	33.55	4.71	22.17
Atalonella inconspicua							
Stationary Pools	9	100.00	285.11	283.08	136.73	4.54	20.57
Shallow Pools	14	100.00	296.50	267.09	149.11	5.21	27.19
Pools	3	100.00	193.33	128.50	159.26	2.26	5.13
Flats	10	100.00	255.50	335.50	104.24	6.65	44.23
Runs	1	100.00	-	-	-	-	-
Riffles	6	100.00	98.30	65.51	78.26	2.21	4.88
Fast Riffles	3	100.00	76.67	48.60	65.28	2.07	4.29
Tasmanocoenis tillyardi							
Stationary Pools	9	100.00	647.00	652.08	364.69	3.68	13.55
Shallow Pools	14	92.86	1086.79	1402.77	307.71	10.96	120.14
Pools	3	100.00	275.67	333.08	147.18	4.28	18.29
Flats	10	90.00	623.50	987.78	100.64	14.30	204.52
Runs	1	100.00	-	-	-	-	-
Riffles	6	83.33	40.83	68.10	16.72	5.38	28.95
Fast Riffles	3	100.00	31.00	10.15	29.78	1.43	2.05

B. soror collected from each habitat sampled are all very similar, suggesting almost uniform habitat conditions (see Appendix 11). The numbers in the fast riffles are also very low, and may reflect the behaviour of *B. soror*. Nymphs of *B. soror* generally occupy the upper surfaces of the substrate, clinging and feeding on the rocks in the direct current. As the current increases this behaviour must become more precarious, resulting in the observed decrease in the numbers occupying this habitat. Since *Baetis* spp. have lost the ability to actively ventilate (Hynes, 1970a) they are dependent on the current to maintain the oxygen concentration around the gills (Ambuhl, 1959) and therefore, these aspects of the respiratory physiology and behaviour provide fairly narrow ecological requirements for *B. soror*.

Conversely, the Leptophlebiidae and Caenidae found at the two localities are capable of ventilating, and occupy all habitats with varying success. *Atalonella inconspicua* appears to occupy all habitats, except perhaps fast riffles, equally well. The behaviour of this species is also worthy of comment, as it tends to occupy the lower surface of rocks in riffles during the day, but can be seen actively feeding in the pools and flats on the surface of the substrate during the day. This, and the relatively high number of animals collected from slower flowing pools and flats suggests that *A. inconspicua* has a preference for these habitats, but is also capable of occupying the flowing riffles (and the fast riffles) although with reduced numbers present (significantly different by Students "t" test $p < .05$).

Atalophlebia australasica occupies all habitats, but there is a consistent decrease in numbers as current increases from shallow pools to fast riffles. Harker (1954) suggested that the possession of multi-furcate gills by *Atalophlebia australasica* was correlated with its habitat of "stagnant pools". The results obtained in Deep Creek show that *A. australasica* does not occupy only stagnant pools, but the numbers of animals collected were consistently higher in the slower flowing, pool habitats.

Tasmanocoenis tillyardi tends to have a similar distribution to *A. australasica*, although it dominates every habitat with the exception of the riffles and fast riffles. Although a tendency for numbers to decrease as velocity increased was evident, *T. tillyardi* was consistently found in all habitats at all localities, indicative of a broad ecological valence.

Studies of the habitats occupied by Australian mayflies are almost non-existent. The observations by Harker (1954) and Riek (1970a) are the only accounts of different species and genera occupying different habitats. Many investigations of micro-distribution of benthic organisms have been carried out, and the relationship of fauna to habitat has been a subject of study for many years. Reviews of faunal requirements and habitat relationships have been made by Macan (1961a and b), Macan (1962), Lillehammer (1965), Cummins (1966) and Hynes (1970a and b), and more recent quantitative studies, including those by Barber and Kevern (1973), Allan (1975), Ward (1975), Rabeni and Minshall (1977), Minshall and Minshall

(1977), have employed replicate sampling to examine the microdistribution of stream benthic invertebrates. Since the present study did not involve replicate sampling, but rather a standardised qualitative technique, no "micro" comparisons can be made. Although no statistical tests can be performed, broad ecological habitat characterisation, as performed by Allen (1951), Harrison and Elsworth (1958) and Schoonbee (1973), can illustrate from which habitats the majority of specimens of any species were collected. Schoonbee (1973) found that this type of comparison was useful and different species displayed different habitat tenancy preferences.

Studies on the mayflies of Deep Creek and Spring Creek, using habitat definitions similar to those of Allen, Harrison and Elsworth and Schoonbee, illustrate broad habitat utilisation by all species. When numbers of individuals per sample in each habitat were compared, it was apparent that all species had distinct habitat preferences, but *Baetis soror* and *Atalophlebia australasica* were more restricted than *Atalonella inconspicua* and *Tasmanocoenis tillyardi*. *Baetis soror* was collected in greater numbers, and consistently in slow to moderately fast flowing water. *Atalophlebia australasica* was more consistently found in the slow flowing depositional zones. The two other species, *Atalonella inconspicua* and *T. tillyardi* were consistently found in all habitats in considerable numbers but the highest densities were recorded from the stationary pools to the slow flowing flats and runs.

Hynes and Hynes (1975), suggested that the uncertain climate of Australia encouraged the development of broad ecological valence, selecting species capable of occupying numerous habitats rather than being specialists to any one niche. For most of the mayfly species examined in South Australia this appears to be true. All, except *B. soror*, appear to have a preference for slow-flowing habitats, which are dominant in South Australia, but all (except *B. soror*) are capable of occupying every habitat available for colonisation. This broad ecological valence also helps to explain the wide distribution of those species inhabiting the fresh waters of South Australia, and their success in the permanent streams of the south east, and Fleurieu Peninsula, as well as the temporary freshwater streams of the Flinders and Mt. Lofty Ranges.

III.4.4 Gut Analysis

A brief study of nymphal gut contents of the four South Australian species from Deep and Spring Creeks was carried out by examining five specimens of each species. All specimens were last or penultimate instar and were collected from the "flat" habitat in Deep Creek and a "run" habitat in Spring Creek, during December 1976. In all cases, the gut contents were consistent with those typical of scrapers and collectors (Cummins, 1973). Diatom species dominated the identifiable ingested material, with organic detritus also well represented, as is evident from the summary in Table III.7.

TABLE III.7. The relative composition of the gut contents of the mayfly species in Spring Creek (SC) and Deep Creek (DC), South Australia.

\+ present; ++ numerous; +++ abundant; ++++ dominant.

	Species of mayfly			
Food Item	*Atalonella inconspicua* (SC)	*Tasmanocoenis tillyardi* (SC)	*Baetis soror* (SC)	*Atalophlebia australasica* (DC)
Chlorophyta (green algae)				
Chlorohormidium (nr)				+
Cladophora				+
Mougeotia	++	+		
Spirogyra	+	++		
Zygnema	++	+		
Chrysophyta (yellow-green algae) Diatomaceae (Diatoms)				
Melosira	+			
Synedra	+++	++		
Tabellaria	+++	+++	+++	++++
Cocconeis				++++
Caloneis				++
Navicula	++	+		
Pinnularia	++++	++++	+	++
Gomphoneis				++
Amphora/Cymbella	++		+	
Nitzschia				++
Surirella				++
Aschelminthes				
Rotifera (Rotifers)	+			
Arthropoda				
Copepoda (Copepods)				+
Fungi (Fungal hyphae)	+			
Detritus	++	+++		++

III.4.5 Occupation of the Temporary Habitat.

In March 1977, the surface flow in Spring Creek had been zero for three months. Above the study site two large pools were still present, both shrinking as the dry period continued. Three sampling holes were dug into the stream bed in regions that had been left dry by the receding waters for one, two and three months.

Immediately downstream of the pool (dry for one month) the water table was reached 16cm below the stream bed. Numerous helodid beetle larvae were collected, and one nymph of *Atalonella inconspicua* (Head Width = 0.68mm). The second hole, in an area dry for two months, reached the water table 35cm below the stream bed; one nymph of *A. inconspicua* (Head Width = 0.52mm) and one nymph of *Tasmanocoenis tillyardi* (Head Width = 0.68mm) were recorded. The third hole reached the water table 61cm below the stream bed, and a single specimen of *A. inconspicua* (Head Width = 0.88mm) was collected. The potential living space in the substrate at this level, calculated using the technique used by Bishop (1973a), was 17.3%.

Survival of the benthic fauna in temporary streams, or permanent streams affected by a drought period, has been considered by Hynes (1958), Clifford (1966), Harrison (1966), Legier and Talin (1976), Williams and Hynes (1976a, 1977), Williams (1977) and Iversen et al (1978). Stream recolonisation mechanisms, after long periods of zero surface flow, have been categoriesed by Williams and Hynes

(1976a) into five groups: those that survive the dry period as cysts, eggs, larvae or immature stages, pupae and adults. Williams and Hynes believed the Ephmeroptera survive in the egg stage.

Williams and Hynes (1976a) examined the benthic fauna of two temporary streams in Ontario, Moser Creek and Kirkland Creek. Of these only Moser Creek had a species of mayfly present. *Paraleptophlebia ontario* was recorded in May 1972 as rare (< 10 specimens) and then this species was not recorded again until April 1973. Numbers increased in late May 1973 (11-50 specimens per sample), but information beyond this date was not presented. It was suggested that since the growth of *P. ontario* was rapid from April-May, emerging in early June, "some kind of diapausing, drought resistant eggs were laid which did not hatch until the following spring" (Williams and Hynes, 1976a). Unfortunately no direct supporting evidence, either of egg development, or from interstitial sampling was given for Moser Creek.

Hynes (1958) had previously concluded that *Siphlonurus lacustris* Eaton survived the drought in the Afon Hirnant in the egg stage, but suggested *B. rhodani* recolonized from upstream. The small nymphs he found of *S. lacustris* compared to the large *B. rhodani* specimens, led to the conclusion of different recolonization mechanisms. However, recolonization from the permanent pools and reaches above the drought affected area would have also explained the presence of *S. lacustris* nymphs. After the hyporheic studies of Coleman and Hynes (1970), Bishop (1973b), Hynes (1974b), and Williams and Hynes (1974b), a third explanation is also possible, although Hynes (1958) recorded no aquatic animals in the gravel of the Afon Hirnant stream bed. Hynes (1968) suggested that the hypoheic population in the Afon Hirnant may account for recovery after spate conditions, and a further study of this stream by Hynes, Williams and Williams (1976) showed large numbers of species present in the hyporheos including the mayflies *Baetis tenax, B. rhodani* and *Ephemerella ignita*. This alternative strategy may also account for survival after periods of drought.

Temporary stream studies by Clifford (1966) and Harrison (1966) recorded the presence of ephemeropteran species, but their survival mechanism is not clear. Clifford (1966) recorded *Heptagenia* sp. ovipositing in pools before drying was completed in spring, but recorded no nymphs in summer and autumn. He suggested they survived the summer months by "having a long hatching period", but stressed that caution was required in assigning an egg resistant stage. The mesh size used by Clifford (12 mesh/cm) was coarse, permitting little confidence in the fact that no small nymphs were recorded in the summer and autumn samples. Harrison (1966) suggested colonization occurred from three sources; resting eggs, species capable of aestivating in protected situations, and from eggs laid by flying adults from nearby permanent waters. He stated "there was no evidence that any insect eggs survived the drought." The two studies involved in categorizing and describing faunal and physical changes occurring in temporary streams (Williams and Hynes, 1976a, 1977, and Legier and Talin, 1976) both suggested two different mechanisms of recolonization by the Ephemeroptera.

Williams and Hynes considered that resistant egg stages allowed survival during the drought periods, whereas Leiger and Talin considered that species with long larval stages are those which can survive the dry stage, burrowed in the phreatic layer, when the texture of the substrate permits, by entering a dormant state" (*sic.*, translated by Furse, 1977).

Evidence for the occurrence of Ephemeroptera deep in the hyporheos has been established by several studies in permanent streams (Coleman and Hynes, 1970; Bishop, 1973b; Williams and Hynes, 1974; and Hynes, 1974b). Williams and Hynes (1976a) examined the vertical distribution of species in the dry bed of Kirkland Creek. However, mayflies were not part of the fauna so that no evidence was gained of nymphs present in the hyporheos of temporary streams. Two studies of recolonization by Williams and Hynes (1976b) and Williams (1977) in permanent and temporary streams respectively, showed the importance of recolonization from within the substrate. In permanent streams, drift, upstream migration, vertical migration and aerial recolonization, all contributed substantially, but for the Ephemeroptera, drift and upstream migration accounted for 89.3% of the taxa recorded. Vertical migration from within the substrate accounted for 7.1% of the collected mayflies. In the temporary stream (Moser Creek) Williams considered that "substrate must be the primary source" of recolonization after the dry period. The Ephemeroptera were only recorded from vertical traps (0.5% of taxa collected). The species of mayfly collected (only one specimen) was not mentioned by Williams, but it possibly was

Paraleptophlebia ontario, which was recorded in Moser Creek by the previous study of Williams and Hynes (1976a, 1977). This specimen was recorded in November, 1973 which, if *P. ontario* is inconsistent with the assumption made by Williams and Hynes (1976a) that "some kind of diapausing, drought-resistant eggs were then laid in early June which did not hatch until the following spring." The presence of a nymph in Autumn would seem to dispute this. However, if the nymph was not of *P. ontario*, but one of either *Leptophlebia* sp. or *Siphlonurus marshalli* Traver which, in the earlier study of Moser Creek (Williams and Hynes, 1976a) "were only seen as nymphs during April and May", a similar inconsistency occurs. In that paper, Williams and Hynes presumed the presence of diapausing or drought resistant eggs, but stated that all the mayflies recorded survived the summer dry period in the egg stage, without indicating that this was supposition. The presence of a mayfly nymph in the substrate in November when the stream had just recommenced flowing would seem to indicate another possible method of surviving the summer dry periods.

The observations made in Spring Creek suggest that *Atalonella inconspicua* and *Tasmanocoenis tillyardi* can survive in temporary streams in both surface pools, and in the hyporheos beneath the dry stream bed. Observations of *A. inconspicua* and *B. soror* eggs (Chapter 5) suggest that this stage cannot survive desiccation, supporting results obtained by Edmunds, Nielsen and Larsen (1956) for *Epheron album*.

The absence of *B. soror* nymphs from the hyporheos may be a result of inadequate sampling. However, the dependence of this species on flowing water may reduce its chances of entering the substrate. All collections of this species were made from localities at which there was always permanent surface water, usually with pools interconnected by shallow flowing stretches. In Spring Creek, surface flow was always present somewhere in the upper catchment during the study period. Once the stream commenced flowing in Autumn, recolonization downstream was probably by drift. *Baetis* has been shown to be severely affected by drought (Inversen et al, 1978) when numbers of *B. rhodani* were depleted after a drought in Denmark. Hynes (1958) also recorded *Ecdyonurus venosa* (F.), *Rhithrogena semicolorata* (Curtis) and *Ephemerella ignita* (Poda) eliminated from the Afon Hirnant after a drought. The utilization of the hyporheos is suggested by the recorded size distribution of each species after drought or flood conditions. Recolonization after drought and/or spate conditions is by animals of similar size and age distribution to those recorded immediately prior to the recommencement of flow, or spate (Chapter 5). Therefore, these recolonizing animals are not products of a different generation. Similar observations were made after spate conditions by Hynes (1968) and Bishop (1973b).

Observations on *T. tillyardi* and *A. inconspicua* in the hyporheos during periods of zero surface flow in Spring Creek, and the observation that eggs of *A. inconspicua* and *B. soror* did not remain viable after drying (see Chapter 5), lead to the conclusion that egg resistance is not utilized by mayflies occupying the temporary stream habitats in South Australia.

Since the majority of South Australian temporary streams, which have resident populations of mayflies, are similar to Spring Creek in possessing permanent pools along the water course, perennial ground water upwellings (rheocrenes), and coarse cobble substrate with high porosity and therefore potential living space, survival of these species is probably by one, or both of two mechanisms;

(1) by occupying surface pools in spatially isolated stretches along the water course, and/or

(2) by nymphs entering the hyporheos as the stream progressively dries.

It is stressed, however, that no direct evidence of drought resistant or drought induced diapausing mayfly eggs has been published, and the observations of *P. ontario* in Moser Creek, Ontario by Williams and Hynes (1976a, 1977) provide only circumstantial evidence suggesting their conclusion. The record of a mayfly nymph in the vertical trap in Moser Creek by Williams (1977) would seem to indicate another possibility, survival of the mayfly nymphs in the hyporheos. Evidence to date indicates that the two survival strategies used by South Australian mayflies in the temporary stream habitat are universal, with the drought resistant egg stage as a third possibility. Further research into the temporary stream habitat is obviously required, investigating recolonisation techniques, as pioneered by Williams and Hynes

(1976a, 1977) and Williams (1977), and direct observation of egg survival under laboratory "drought" conditions. Until such studies are carried out, all possible survival strategies must be considered and broad generalization avoided.

CHAPTER 4.

Life Cycles of South Australian Mayflies.

IV.1 Introduction.

In contrast with European and North American knowledge, the life histories of mayflies in Australia are almost completely unknown with casual observations and anecdotal evidence of aspects of their life cycle published in systematic publications. These observations have been concerned with adult emergence and behaviour characteristics rather than with nymphal development. This situation is similar to that which occurred in North America and Europe some 20-25 years ago. Since then numerous studies of life cycles have enabled elaborate life cycle classifications to be proposed by Hynes (1961), Macan (1965), Landa (1968) and Sowa (1975). With the exception of one publication by Harker (1950a), no experimental life cycle analysis has been published on any Australian mayfly. Duncan (1972) examined the life histories of six species in Victoria, but this work remains unpublished.

The life cycles of four species of mayfly from Deep Creek and Spring Creek in South Australia are described. Where the two localities had common species, the life history at each locality was compared in an attempt to define the environmental factors which are important in determining the life cycle of each species.

IV.2. Materials and Methods.

For the life history study the samples taken during the ecological sampling program were used. All the samples taken on each sampling date were pooled and therefore the size frequency histograms represent the size distribution of each species without habitat bias.

Since the majority of size frequency histograms were bi- or tri-modal the numerical mean and standard deviation for the total animals measured were of little value. Visual selection of each modal distribution was made, and the mean, standard deviation and range of each distribution were calculated for each sampling date. To assess the validity of this technique, the distribution parameters were calculated using the technique of Harding (1949) and Cassie (1954). The cumulative frequencies from the size frequency histograms were plotted on probability paper, and the resulting curve allowed modes to be distinguished as rapid increases in percent frequency, and points of horizontal inflection indicated gradations from one mode to another, i.e. area of overlap of two distributions. A computer program, NORMSEP, developed for fitting a series of normal curves to frequency data by Hasselblad (1966), was used to aid the determination of modes. This technique estimates the parameters of "a mixture of normal distributions" using the steepest descent frequencies, and the probability that the distributions differ is tested by χ^2. The size frequency distribution of *Tasmanocoenis tillyardi* was compared using all three techniques, and the values of the means and standard deviations are given in Table IV.1.

TABLE IV.1. Comparison of techniques for the selection of each modal distribution of size frequency data of *Tasmanocoenis tillyardi* from Deep Creek.

HW = Head width; $\bar{x}$ = Mean; S.D. = Standard deviation.

Collection Date.	Visual selection		Cumulative frequency[1]		NORMSEP[2]	
	HW$\bar{x}$	S.D.	HW$\bar{x}$	S.D.	HW$\bar{x}$	S.D.
22- 9-76	0.27	0.05	0.27	0.08	0.27	0.05
	0.72	0.15	0.70	0.13	0.72	0.16
8-10-76	0.27	0.07	0.20	0.05	0.28	0.07
	0.88	0.20	0.72	0.08	0.89	0.15
			0.96	0.06		
20-10-76	0.32	0.11	0.20	0.07	0.25	0.06
	0.90	0.17	0.70	0.18	0.78	0.24
			1.07	0.10		
10-11-76	0.34	0.04	0.31	0.02	0.40	0.22
	0.81	0.19	0.71	0.19	0.88	0.15
			0.99	0.07		
24-11-76	0.12	0.03	0.09	0.05	0.12	0.03
	0.54	0.13	0.68	0.19	0.60	0.17
	0.94	0.11	0.97	0.07	0.96	0.11
9-12-76	0.15	0.03	0.11	0.03	0.15	0.02
	0.85	0.16	0.81	0.13	0.85	0.16
22-12-76	0.17	0.06	0.14	0.05	0.18	0.05
	0.89	0.14	0.59	0.17	0.50	0.15
			0.90	0.11	0.92	0.12
6- 1-77	0.21	0.05	0.18	0.03	0.20	0.05
	0.84	0.23	0.65	0.23	0.84	0.24
			1.01	0.07		
20- 1-77	0.25	0.07	0.19	0.04	0.24	0.05
	0.64	0.14	0.35	0.02	0.39	0.01
			0.65	0.12	0.60	0.17
10- 2-77	0.23	0.07	0.22	0.07	0.21	0.04
	0.80	0.16	0.77	0.17	0.32	0.07
					0.82	0.16
10- 3-77	0.18	0.09	0.14	0.11	0.15	0.03
	0.84	0.12	0.82	0.09	0.28	0.09
					0.87	0.09
7- 4-77	0.22	0.07	0.17	0.02	0.21	0.06
	0.54	0.09	0.48	0.03	0.44	0.14
			0.86	-		
5- 5-77	0.22	0.06	0.20	0.03	0.23	0.06
	0.56	0.08	0.54	0.04	0.57	0.09
1- 6-77	0.25	0.07	0.21	0.04	0.26	0.07
	0.63	0.09	0.62	0.08	0.64	0.09
6- 7-77	0.24	0.06	0.21	0.03	0.25	0.06
	0.63	0.09	0.61	0.05	0.63	0.10
3- 8-77	0.26	0.07	0.22	0.04	0.26	0.07
	0.68	0.09	0.63	0.07	0.68	0.10
21- 8-77	0.23	0.06	0.19	0.07	0.24	0.06
	0.76	0.10	0.73	0.05	0.77	0.11
31- 8-77	0.24	0.06	0.20	0.03	0.25	0.03
	0.79	0.10	0.75	0.06	0.77	0.15
7- 9-77	0.28	0.06	0.25	0.04	0.29	0.06
	0.80	0.14	0.77	0.08	0.80	0.15
17- 9-77	0.26	0.06	0.23	0.04	0.27	0.06
	0.83	0.14	0.80	0.09	0.82	0.15
24- 9-77	0.25	0.06	0.23	0.04	0.26	0.05
	0.78	0.17	0.76	0.09	0.75	0.20
30- 9-77	0.30	0.06	0.26	0.05	0.31	0.06
	0.84	0.17	0.81	0.10	0.83	0.19
12-10-77	0.20	-	0.20	-	0.20	-
	0.47	0.06	0.76	0.23	0.43	0.02
	0.93	0.14	1.01	0.12	0.91	0.17
22-10-77	0.31	0.03	0.29	0.01	0.32	0.03
	0.86	0.20	0.82	0.11	0.86	0.20
4-11-77	-	-	0.77	0.11	0.62	0.07
	0.91	0.17	1.03	0.05	0.98	0.12

---

[1] Techniques of Harding (1949) and Cassie (1954).

[2] Technique developed by Hasselblad (1966).

All techniques gave similar results for the parameters of the polymodal distribution, but because the calculations for the cumulative frequency technique of Harding (1949) and Cassie (1954) were very time consuming, without a corresponding increase in information produced, it was not used for any other species. NORMSEP was also limited because the technique depends on a subjective decision of how many modes are present in the data to be tested (Cohen, 1966). By arbitrary selection of hypothetical modes on a set of data the effect of this decision was tested. Two methods of testing the validity of the number of modes were used, firstly the χ^2 value where possible, and secondly the upper limits of the number of iterations that the program allowed (i.e.125). By either of these techniques the number of modes visually selected required the lowest number of iterations for the parameter estimates, and the χ^2 value was the most significant. Another limit of this program for life cycle data analysis was the requirement of more than 100 specimens, preferably more than 400, per sample. Although most samples met this requirement the parameters of the few that did not were calculated using the visual selection technique. The size range and calculated mean values were plotted as a representation of seasonal growth of each species.

IV.3 Results.

Size frequency histograms for each collecting date are given for each species. These histograms include the size frequency information for each sex, and the total number of specimens used in their construction. Because the interpretation of the life cycle from a series of size frequency histograms involves assimilation of numerous sets of data, it is often difficult to determine immediately the seasonal cycle. Therefore the size ranges and calculated means of each generation were plotted against time to represent the seasonal growth curve of each species. Above each seasonal curve is included information on the presence of adults or the presence of last instar nymphs, but no adults. The presence of first instar nymphs was considered to be evidence of egg hatching.

A consistent nomenclature of generations is maintained throughout, with the first generation emerging in the sampling period referred to as generation G1; the second as G2 and subsequent emerging generations as G3, G4 etc. Generations which correspond to either G1, G2 or G3 of the previous year, are referred to as $G1'$, $G2'$ or $G3'$. For example, a generation in late 1976 is referred to as G1, and its analogous generation in 1977 is $G1'$. In this way the annual cycle was definable, and the origins of each generation were apparent.

IV.3.1 Family CAENIDAE

Tasmanocoenis tillyardi : Deep Creek.

The size frequency histograms are given in Figs. IV.1a, b. Fig. IV.3 is the seasonal growth curve which illustrates a bivoltine life cycle.

Fig. IV.1. Life cycle size frequency histograms of *Tasmanocoenis tillyardi* at Deep Creek, South Australia. a, September 22, 1976 - April 7, 1977. The number of nymphs used in the construction of each histogram is recorded below each date.

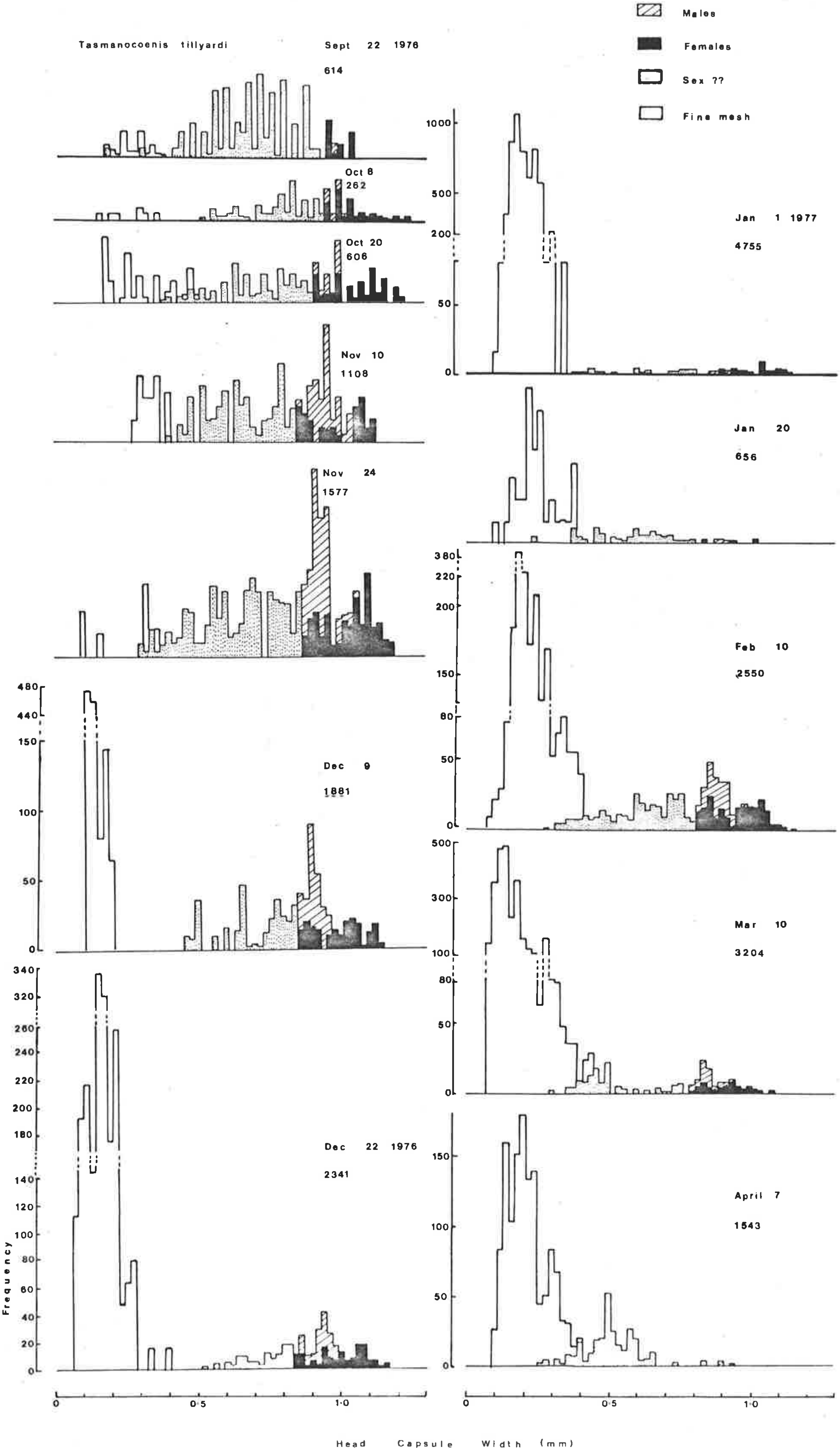
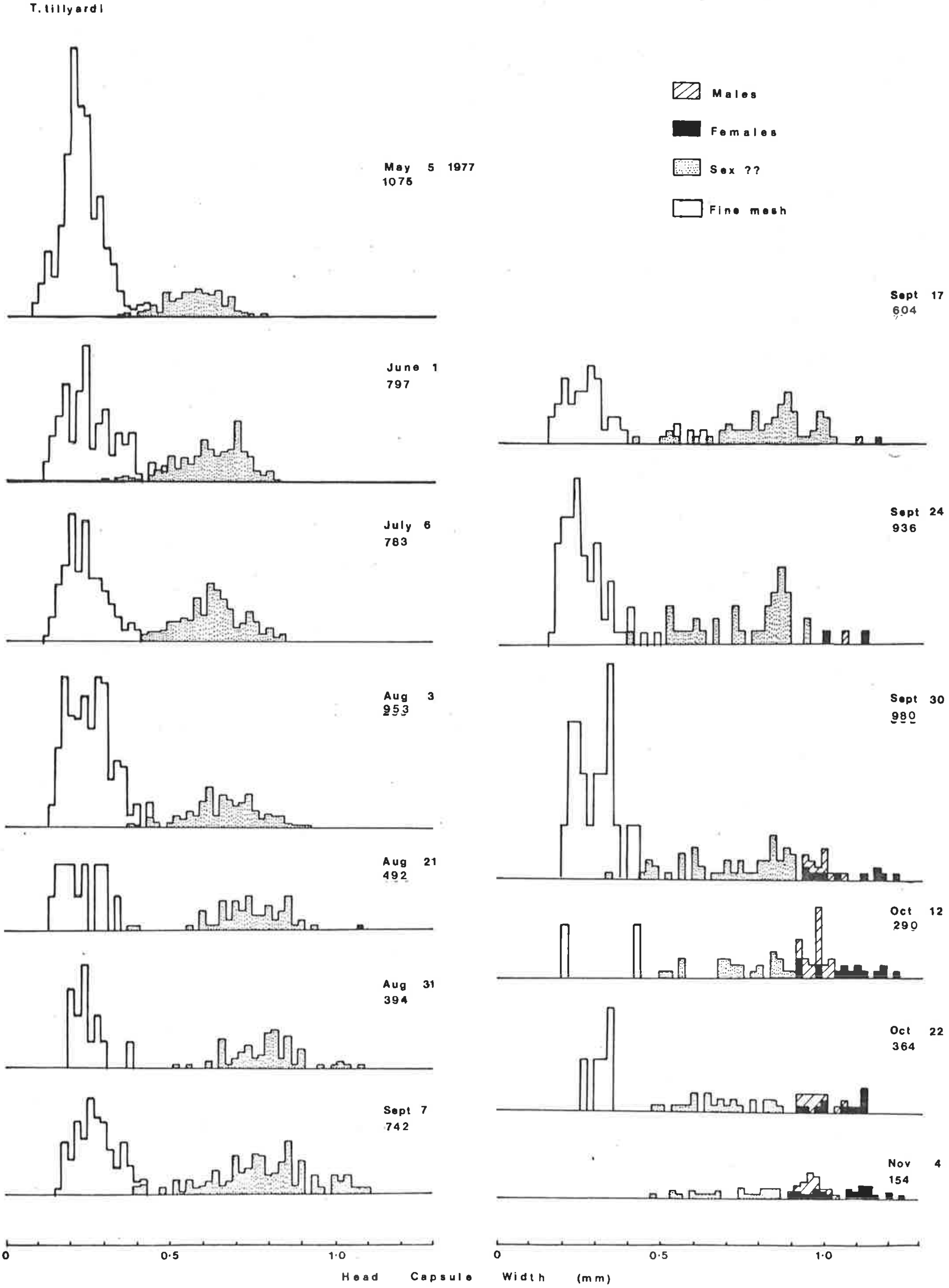

Males
Females
Sex ??
Fine mesh
Tasmanocoenis tillyardi
Sept 22 1976
614
Oct 8
262
Oct 20
606
Nov 10
1108
Nov 24
1577
480
440
150
100
50
0
Dec 9
1881
340
320
260
240
220
200
180
140
120
100
80
60
40
20
0
Frequency
Dec 22 1976
2341
1000
500
200
50
0
Jan 1 1977
4755
Jan 20
656
380
220
200
150
80
50
0
Feb 10
2550
500
300
100
80
50
0
Mar 10
3204
150
100
50
0
April 7
1543
0
0·5
1·0
0
0·5
1·0
Head Capsule Width (mm)

Fig. IV.1. cont. Life cycle size frequency histograms of *T. tillyardi* at Deep Creek. b, May 5, 1977 - November 4, 1977. The number of nymphs used in the construction of each histogram is recorded below each date.


T. tillyardi
Males
Females
Sex ??
Fine mesh
May 5 1977
1075
June 1
797
July 6
783
Aug 3
953
Aug 21
492
Aug 31
394
Sept 7
742
Sept 17
604
Sept 24
936
Sept 30
980
Oct 12
290
Oct 22
364
Nov 4
154
0
0·5
1·0
0
0·5
1·0
Head Capsule Width (mm)

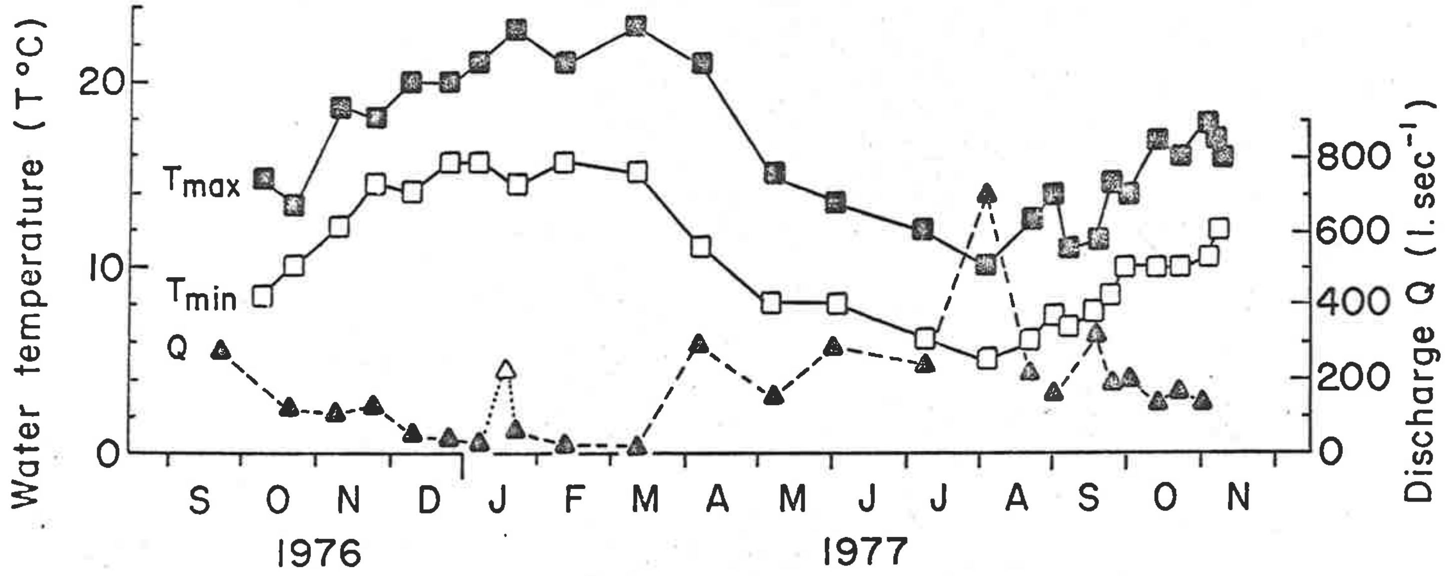
At the beginning of the sampling program in September 1976, two generations were present, one mature, nearing emergence (G1) and one of early instar nymphs (G2). Adults from G1 were first recorded in early November 1976 when spent females were found on the water surface, and males were collected in cobwebs above and beside the creek. The number of dead adults increased throughout November to early December and then declined throughout December with very few collected in early January 1977. Hatching of eggs laid by generation G1 was first recorded in November 1976 and hatching was continuous until May 1977. Although egg development of *T. tillyardi* was not studied in the laboratory, evidence from other species suggests that the length of the recruitment period was exaggerated by hatching of eggs laid by generation G2 in April-May 1977.

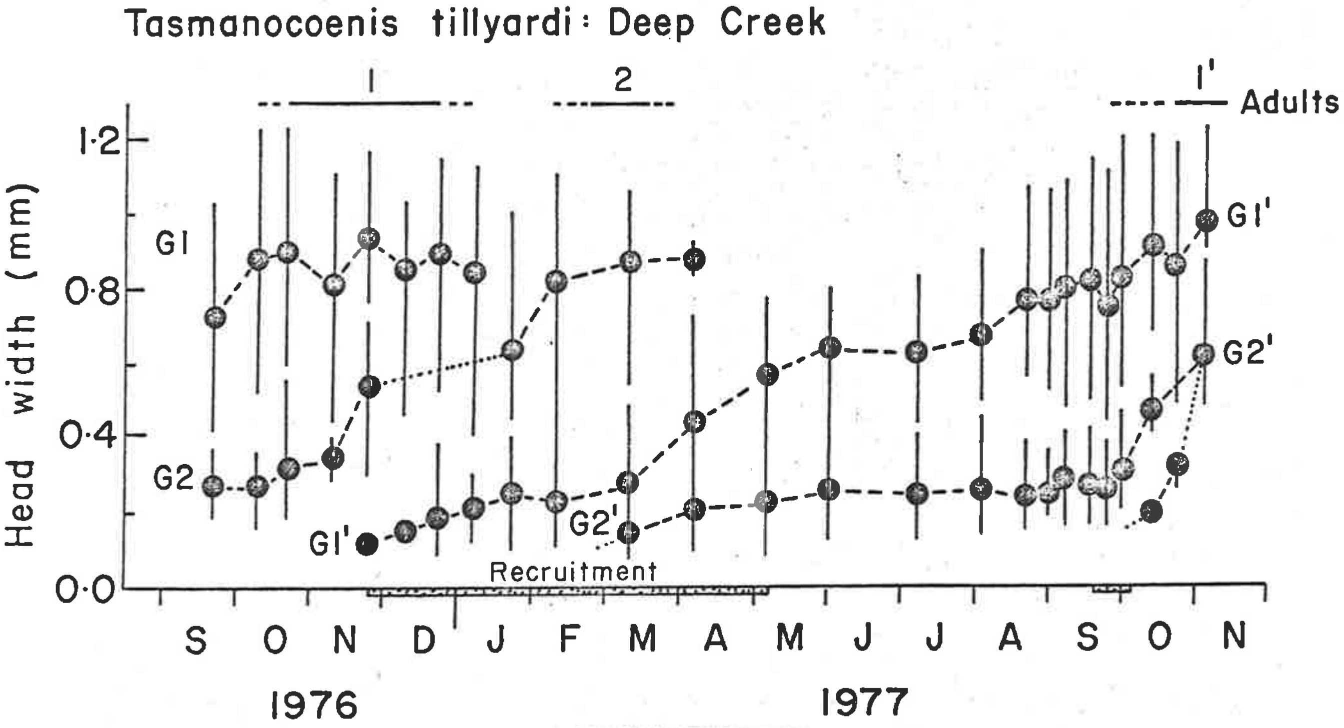
Generation G2 developed relatively rapidly throughout November 1976-January 1977, and although last instar nymphs were recorded in mid-February 1977, no adults were recorded until late February, early March. The duration of the emergence period of this generation was only half as long as that of its predecessor. The emergence of G2 completed the two generations present at the beginning of the sampling program. Both were replaced by their respective offspring forming distinct generations G1′ and G2′.

Generation G1′ was first evident in November 1976 and recruitment was continuous through the long emergence period, depressing the calculated mean size of this generation.

Fig. IV.2. Seasonal changes of water temperature (^{o}C) at Deep Creek, South Australia.

Fig. IV.3. Seasonal growth curves of *Tasmanocoenis tillyardi* at Deep Creek, South Australia from September, 1976 - November, 1977. Vertical bars indicate the size range of nymphs in each generation used to compute the mean size.


Water temperature (T °C)
20
10
0
Tmax
Tmin
Q
800
600
400
200
0
Discharge Q (l. sec^{-1})
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977


Tasmanocoenis tillyardi: Deep Creek
1
2
1'
Adults
1·2
0·8
0·4
0·0
Head width (mm)
G1
G2
G1'
G2'
G1'
G2'
Recruitment
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977

Growth rates therefore appeared slower during the summer months than in March-April 1977, when recruitment ceased. Generation G2´ was distinguishable in early March 1977, and recruitment continued until early May 1977.

Development of G1´ and G2´ was slow during the cooler months of May to August 1977, but as the water temperature began to increase in August and September, growth rate increased, and a short period of recruitment was observed in September. These early instar nymphs were indistinguishable from G2´ by early November 1977. This recruitment occurred at least one week before any last instar nymphs were collected. Laboratory egg development experiments on other species (see Chapter 5), suggested that eggs may become dormant at low temperature. Therefore, it is suggested that this hatch was probably from eggs laid by G2 adults in late Autumn, with the eggs over-wintering in a dormant state.

South Australia experienced a period of warm weather in October 1977, with high air temperatures, and consequently elevated water temperature (Fig. IV.2). During this short warm period some *T. tillyardi* from G1´ emerged; a few early in October, with numbers increasing daily. With the return of cooler weather, and lower water temperatures, in November 1977 (after the sampling program had ceased) emergence halted, even though last instar nymphs were still present. No further emergence took place until early December when temperatures again began to rise, thus completing the emergence of G1´. By this time both G1´ and G2´ attained similar sizes to generations

G1 and G2 of October 1976, suggesting the above is an annual cycle.

The life cycle of *T. tillyardi* in Deep Creek can be summarised as bivoltine with emergence occurring in Spring-early Summer, and a second emergence period in later Summer-early Autumn. Both generations were present throughout the winter months, but the earlier emerging generation had its origin from eggs oviposited by the Spring-Summer generation the previous year. The Summer-Autumn generation had its origin in the Summer-Autumn hatching of eggs oviposited by its analogous generation of the previous year. Therefore both generations occur as nymphs throughout the Winter months, and require some 12-13 months to complete their development.

Nymphal Stage :

Nymphs of *T. tillyardi* are difficult to sex, except in the last instar when the development of genitalia in males, and eggs in females can be observed through the nymphal skin. The sternum of females is much broader than males, but was not always easy to measure. The most successful technique in determining the sex of penultimate and last instar nymphs was the relationship of head width to mesothoracic wing sheath length. Nymphs with a head width greater than 0.90mm and wing sheath length exceeding 1.50mm were all females, and conversely, with head widths greater than 0.90mm and wing sheath length less than 1.45mm were male.

The sex ratio of last instar nymphs varied from month to month, with males usually more numerous than females. On ten of the seventeen sampling dates the sex ratio was statistically different from unity at $p < 0.05$ using χ^2 (Table IV.2). Of these significant comparisons only three reversed the normal male dominance. Over the annual cycle 2,488 last instar nymphs were collected and the ratio of males to females was 1.00 : 0.65. Assuming an equal sex ratio a χ^2 comparison was highly significant ($p < 0.001$), indicating the sex ratio was significantly different from a 1 : 1 ratio.

The dominance of male over female numbers is possibly due to the reproductive strategy of *T. tillyardi*. This species emerges in the evening (see below) and mating swarms occur at night, and extend into the early dawn. Collections from these swarms indicate that they are dominated by males, with very few females recorded. It is assumed that the females fly into this swarm, and the high number of males virtually guarantees successful mating of each female. The dawn swarms were almost entirely male, being the residual animals necessary to ensure successful mating. This large percentage of residual males may account for the 1.00 : 0.65 sex ratio observed in the nymphal collection.

The size of the last instar nymphs of both males and females tends to decrease as the emergence season progresses. The early Spring-Summer emerging generation appears to be larger than the late Summer-Autumn generation. The size changes of the last instar are given in Table IV.3. Similar changes have been

TABLE IV.2.

Numbers of male and female last instar nymphs of *Tasmanocoenis tillyardi* from Deep Creek, South Australia, on dates when the sex ratios deviated significantly from unity as tested by χ^2.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Date	No. of Males (oo)	No. of Females (♀♀)	χ^2	Dominance
8-10-76	18	32	3.92**	♀
20-10-76	58	90	6.92***	♀
10-11-76	344	83	159.16***	o
24-11-76	350	248	17.40***	o
9-12-76	198	160	4.03**	o
22-12-76	112	80	5.33**	o
6- 1-77	9	23	6.13**	♀
10- 3-77	52	2	46.30***	o
30- 9-77	44	24	5.88**	o
12-10-77	88	44	14.67***	o
Annual Total	1508	980	56.03***	o

TABLE IV.3.

Mean Head Widths of last instar nymphs of *Tasmanocoenis tillyardi* from Deep Creek, South Australia, illustrating the decrease in size throughout the emergence period.

Date	Generation	Mean Head Width Males (mm)	n	Mean Head Width Females (mm)	n
8-10-76	G1	0.98	18	1.09	32
20-10-76	G1	0.98	58	1.13	90
10-11-76	G1	0.95	344	1.08	83
24-11-76	G1	0.94	350	1.09	248
9-12-76	G1	0.91	198	1.04	160
22-12-76	G1	0.92	112	1.07	80
6- 1-77	G1	0.93	9	1.07	23
20- 1-77	G2	0.90	5	-	-
10- 2-77	G2	0.89	132	1.02	112
10- 3-77	G2	0.86	52	-	-
30- 9-77	G1′	0.99	44	1.15	24
12-10-77	G1′	0.97	88	1.12	44
22-10-77	G1′	0.97	48	1.12	36
4-11-77	G1′	0.96	44	1.13	34

observed by many authors with species which develop over Winter larger than those of summer generations, (Harker, 1952; Pleskot, 1958; Macan, 1957b; Minshall, 1967; Coleman and Hynes, 1970; Corkum, 1978; Cianciara, 1979). It is not clear if this size change is due to a change of the number of instars, or the duration of these. Minshall (1967) suggested that temperature was not the best explanation of size changes in *Epeorus pleuralis* (Banks) and postulated that decreased competition in areas with smaller populations may be a better explanation. Cianciara (1979) illustrated the effect of two food cultures on growth of *Cloeon dipterum* (L.). She noted differences in moult number and development duration, but the "final larval size was the same on each food ....". Since both generations, and all animals within each generation of *T. tillyardi* required 12-13 months to complete their life cycle it is unlikely that food was so different, but the stage at which each generation over-wintered differed. Generation G1/G1' were larger than G2 over the winter period, and were also larger at the time of emergence. This temperature difference at different stages may have some effects on the physiology of development. Cianciara (1979) noted two larval stages in which the relationship of metabolic rate and body weight were significantly different. If such development differences occur in nymphs of *T. tillyardi*, the stage at which an individual over-winters may be important in determining its size at emergence. Corkum (1978) suggested that high water temperature "probably forced the emergence of the smallest nymphs". This also could explain the decrease in size at maturity of *T. tillyardi* as the emergence season progressed.

Subimago Stage :

Emergence did not commence until dusk when direct sunlight was no longer on the stream. At Deep Creek the study section was in a gorge, and the hillside shading created an effective twilight approximately two hours before sunset. Emergence continued after dark, for as long as the air temperature exceeded 12-14°C. Subimagos were collected at a blue actinic fluorescent light trap for three to four hours after sunset. Although no emergence was observed prior to dawn, swams of adults were observed until the sun actually illuminated the gorge. Emergence therefore probably occurred all night as long as the air temperature remained high enough, and wind was absent.

The length of the subimago stage was variable, depending on humidity and air temperature. On one evening in November 1977, when the air temperature was 24°C, water temperature 18.5°C and humidity near 20% (as recorded by the Bureau of Meteorology for Adelaide City); subimagos of *T. tillyardi* were moulting within 30 seconds of emerging. Many emerged directly onto the water surface and immediately moulted to imagos and took flight.

Adult Stage :

Adult *T. tillyardi* had very short life spans; those that emerged in the evening were dead before dawn. In the laboratory the maximum observed life span was 4½ hours. Under natural conditions longevity may be different, but it is unlikely that the life span is much longer than observed in the laboratory.

Only dawn swarms could be clearly observed and, as mentioned above, collections from these were almost all males, with only an occasional female being collected. Swarming ceased once the sun directly illuminated the creek. On cloudy mornings swarming did not continue long after dawn, suggesting that a change in light intensity, rather than absolute intensity influenced the flight period.

Oviposition was never observed, but bodies of numerous dead females, with ruptured abdomens could be found on the water surface each morning during the emergence period.

Eggs :

The hatching of eggs, as recorded by the presence of first instar nymphs (head width = 0.10mm) occurred throughout the summer months from November 1976 to May 1977. Although experimental development of *T. tillyardi* eggs was not carried out in the laboratory, observation of development of eggs of other species (Chapter 5) illustrated the dependence of development time to incubation temperature. Because temperatures were lower in April-May than observed in December-January the duration of incubation was probably longer in the Autumn than in the Summer. Some of the eggs oviposited in late March 1977 apparently did not hatch after the temperature fell below a mean of between 10-12°C. These eggs hatched in late September 1977 once the mean water temperature began to rise and exceeded 10-12°C. This is consistent with the hatching results obtained for *Atalonella inconspicua* and *Atalophlebia australis* (see

Chapter 5) and therefore a similar mechanism of egg development for *T. tillyardi* is postulated.

T. tillyardi : Spring Creek.

The life cycle in Spring Creek differs from that in Deep Creek in that there are more generations per year, three, rather than two as in Deep Creek. The size frequency histograms Fig. IV.4 and growth curves Fig. IV.5 demonstrate that the period of each generation is shorter than in Deep Creek, ranging between eight and twelve months.

At the beginning of the sampling program in September 1976, two generations were apparent, one already emerging (G1) and a second (G2) consisting of much smaller nymphs. By early October 1976, generation G1 had almost completed emergence. Early instar nymphs were also collected in October suggesting that eggs laid by G1 were hatching. This recruitment was the beginning of the third generation G3. As observed in Deep Creek, the recruitment period was very long, with first instar nymphs recorded from October 1976 to February 1977. The length of the recruitment period was exaggerated by the hatching of eggs laid by generation G2 in November-December 1976.

Generation G2 developed rapidly during September-October 1976, and although no adults were collected on the sampling date in October, last instar nymphs were abundant. Very few last instar nymphs were collected in November-December 1976, which suggests that a large emergence occurred during October, between the sampling dates. Eggs oviposited by this generation commenced hatching in November 1976 and continued until January 1977, initiating generation G1′.

Fig. IV.4. Size frequency histograms of *Tasmanocoenis tillyardi* at Spring Creek, South Australia for the period September 11, 1976 - April 2, 1977. The number of nymphs used to construct each histogram is recorded below each date.

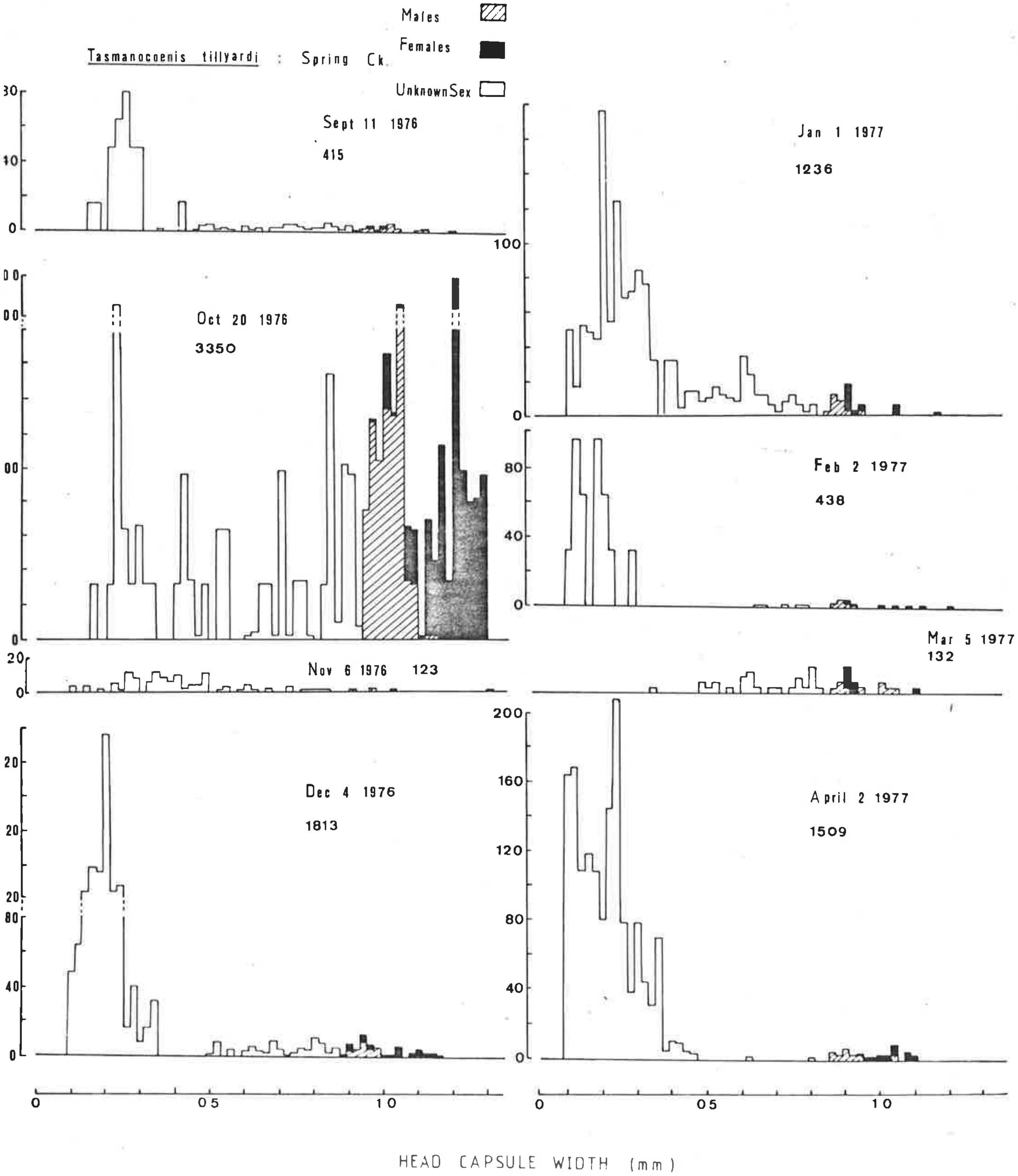
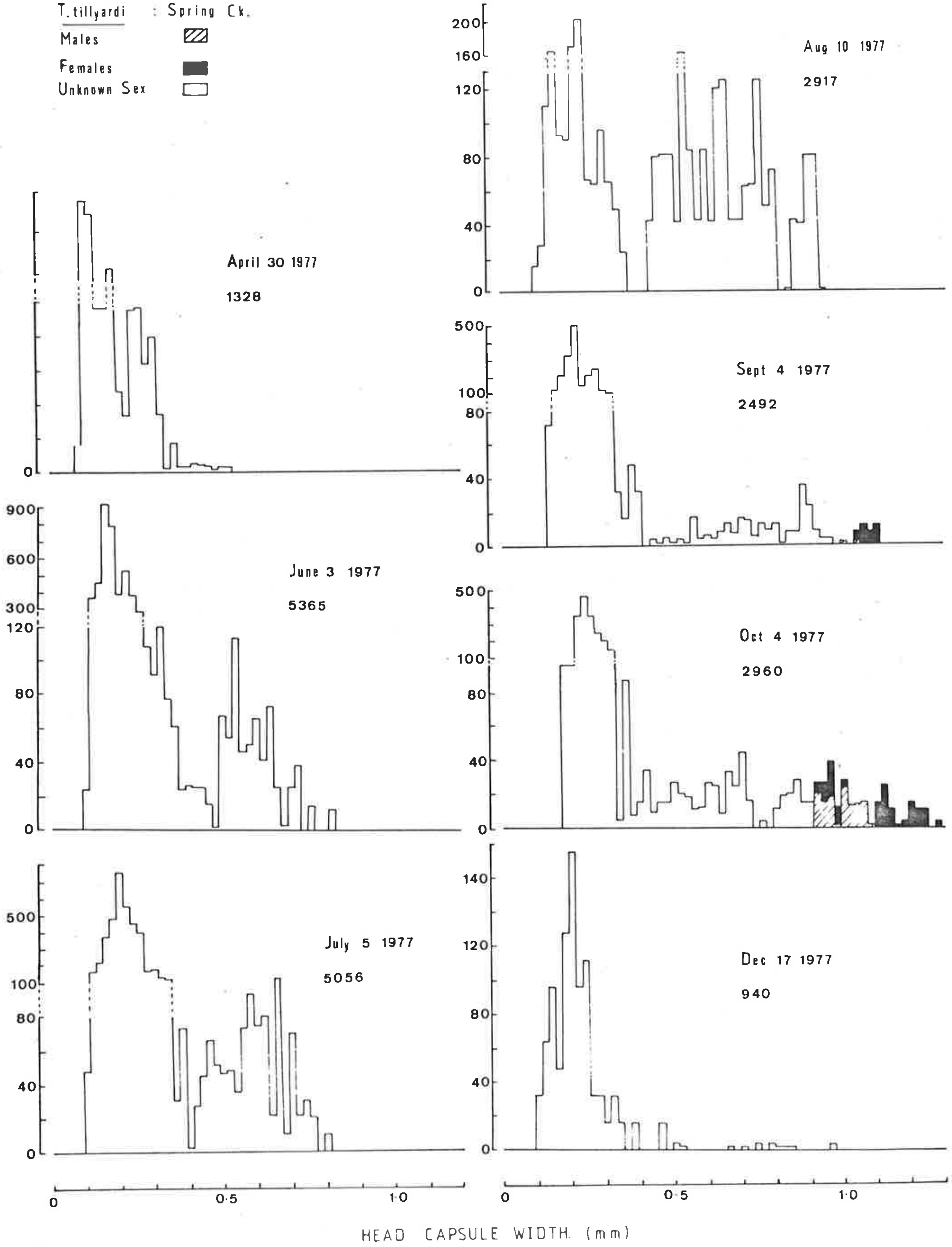

Tasmanocoenis tillyardi : Spring Ck
Males ▨
Females ■
Unknown Sex ☐
Sept 11 1976
415
Oct 20 1976
3350
Nov 6 1976 123
Dec 4 1976
1813
Jan 1 1977
1236
Feb 2 1977
438
Mar 5 1977
132
April 2 1977
1509
30
10
0
00
00
00
0
20
0
20
20
20
80
40
0
100
0
80
40
0
200
160
120
80
40
0
0
0.5
1.0
0
0.5
1.0
HEAD CAPSULE WIDTH (mm)

Fig. IV.4. cont. Size frequency histograms of *T. tillyardi* at Spring Creek, for the period April 30, 1977 - December 17, 1977. The number of nymphs used to construct each histogram is recorded below each date.


T. tillyardi : Spring Ck.
Males ▨
Females ■
Unknown Sex ☐
April 30 1977
1328
June 3 1977
5365
July 5 1977
5056
Aug 10 1977
2917
Sept 4 1977
2492
Oct 4 1977
2960
Dec 17 1977
940
0
40
80
100
120
140
160
200
300
500
600
900
0
0·5
1·0
HEAD CAPSULE WIDTH (mm)

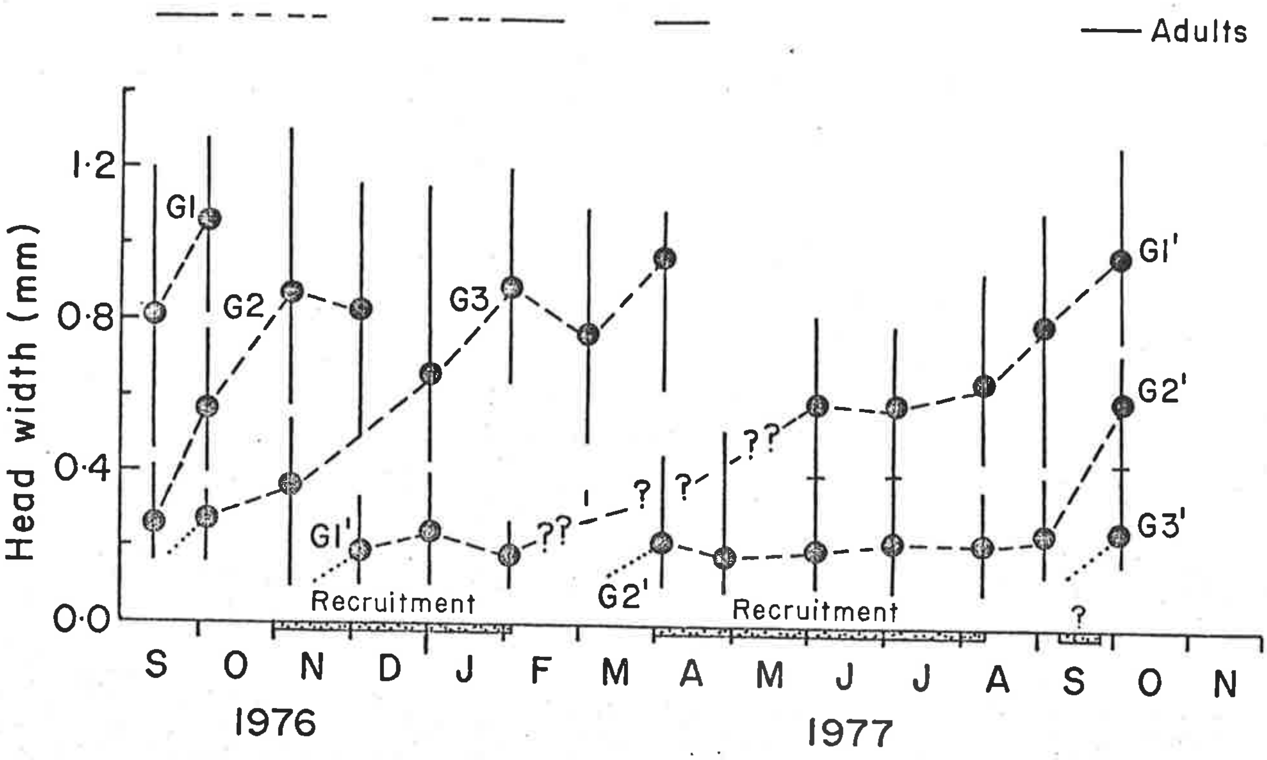
Generation G3, recruited from the offspring of G1, grew rapidly during Summer and commenced emergence in February 1977. Emergence was not continuous, but occurred in two parts, the later period in March-April 1977. Eggs laid by G3 hatched in March-April, and recruitment continued throughout Autumn and Winter until August 1977. This long period of recruitment, influenced by decreasing water temperatures (Fig. IV.6) and increasing incubation times, depressed the average size of the resultant generation G2′ throughout these months. Even so, two generations were apparent throughout the Winter, G1′ and G2′.

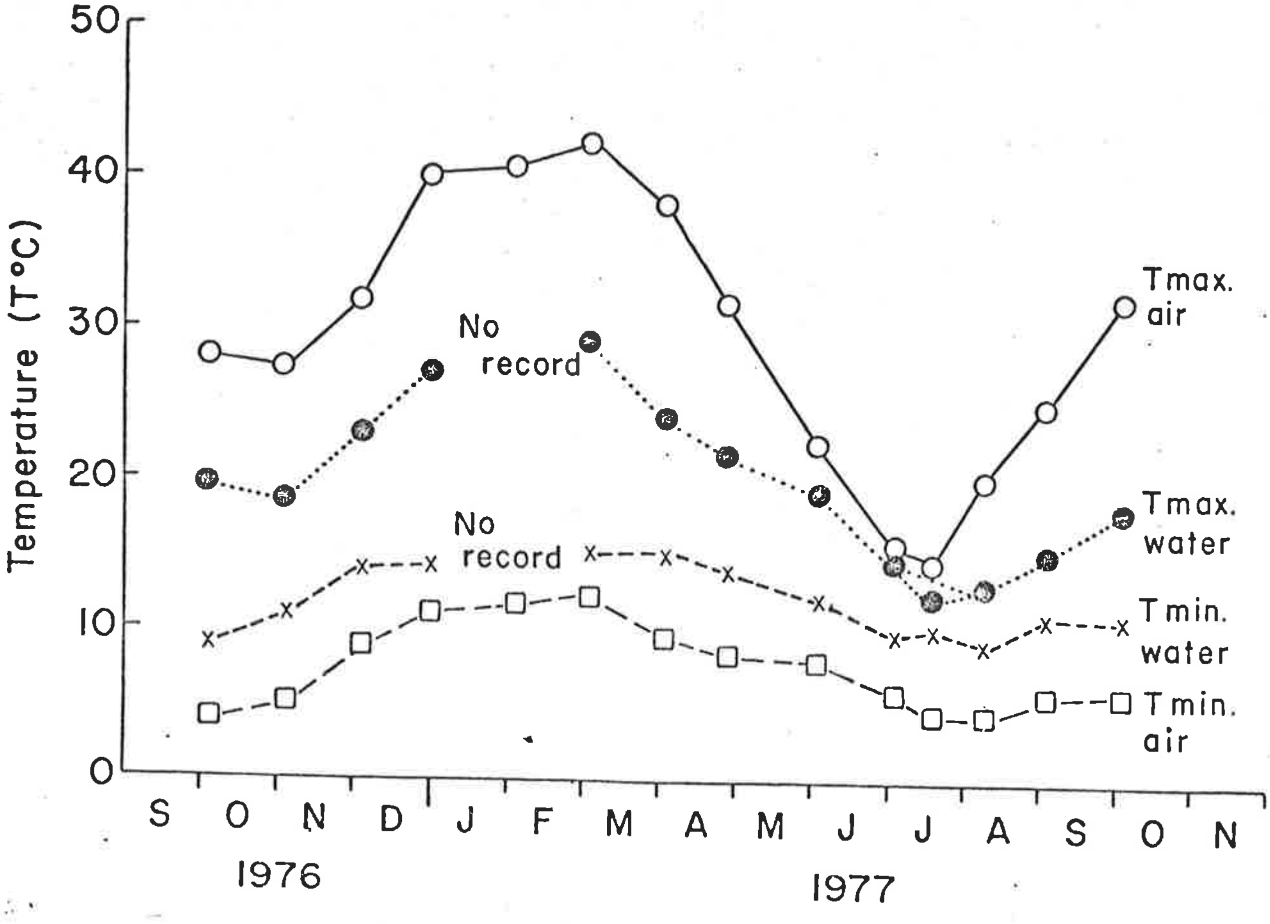
During February-May 1977 G1′ was not evident in the fine samples, creating some uncertainty in life cycle interpretation during this period. However, the presence of early instars in November-February, and their absence until April, when two modes were apparent, suggests that G1′ was ineffectively sampled during the ensuing period. Considering that the sampling technique was capable of collecting first instar nymphs, their absence may reflect the movement of the smaller sized nymphs into hyporheos during the period of zero surface flow. This would also explain why only newly hatched nymphs and mature nymphs approaching emergence size were recorded in these samples. Once hatched, the smaller nymphs may have entered the hyporheos to escape the high summer temperatures; sometimes exceeding 28°C in the pools, as recorded in February-March 1977 (Fig.IV.6). In the subterranean waters during this period the temperature did not exceed 22.5°C at 61cm, and consequently growth rates may be depressed. This slower development would allow the animals to remain in the hyporheos until the available living

Fig. IV.5. Seasonal growth curves of *Tasmanocoenis tillyardi* at Spring Creek, South Australia. Vertical bars indicate the size range of nymphs of each generation.

Fig. IV.6. Seasonal changes of water and air temperatures (°C) at Spring Creek, South Australia.

Tasmanocoenis tillyardi: Spring Creek





space became limiting, when they would have to return to the surface waters. The presence of nymphs of *T. tillyardi* (Head Width = 0.68mm) in water 35-40cm below the dry stream bed supports this suggestion, but further examination of the hyporheos is certainly required.

In June 1977, once the stream had recommenced flowing, the animals returned to the surface habitats, migrating vertically with the rising water table and therefore the two distinct generations were evident. The origins of these two generations (G1′ and G2′) were from eggs laid in December-January (oviposited by G2′ females) and in February-April (oviposited by G3 females) respectively. Both developed slowly during the cooler months, with recruitment to G2′ continuous for four to five months from April to August. As temperature increased in August and early September, the growth rate also increased, with G1′ emerging in August-September 1977. Eggs oviposited by G1′ hatched in late September and were recorded in the early October sample; beginning generation G3′.

Sampling ceased in October 1977, but in the 12-13 month sampling period an annual cycle was completed with generations G1 and G1′ emerging in September (1976, 1977 respectively), and G2′ and G3′ at similar size in October 1976. Generation G2 (G2′) emerged in November-December (1976, and probably 1977) and G3 (G3′) emerged in February-April (1977, and probably 1978). The duration of each generation differed with the winter generations G1 (G1′) and G2 (G2′) requiring some 10-12 months and the summer generation G3 requiring only eight months to complete its development.

The major difference between subimago and adult observations in Deep Creek and Spring Creek were the flight times during the year. In Spring Creek four emergence periods were observed over the sampling period compared with three in Deep Creek.

Nymphal Stage :

Nymphs were sexed as described previously for Deep Creek, and sex ratio and size changes with time of last instar nymphs were recorded.

The sex ratio of last instar nymphs in Spring Creek differed significantly ($p < 0.05$) from a 1 : 1 ratio for three months of the year, September and October 1976 and March 1977 (Table IV.4). In only the October sample, females were more abundant than males, but their numbers were so great that they dominate the annual comparison χ^2 value that suggest females were more abundant than males. Of the 1,988 last instar nymphs collected, 1,810 were collected in the October sample. Including the October sample the annual ratio of males to females was 0.89 : 1.00, with 937 males and 1,051 females. The χ^2 value for this is significantly different from the 1 : 1 ratio ($p < 0.02$). Of the 1,051 last instar females collected, 1,000 were collected in October. For the same date 810 males were collected. The difference in this sample is is inconsistent with all others in which males dominate, (as in Deep Creek). The sex ratio without the October sample was 1.00 : 0.54, similar to the ratio observed in Deep Creek.

TABLE IV.4. Numbers of last instar nymphs of *Tasmanocoenis tillyardi* from Spring Creek, South Australia, on dates when the sex ratio differed significantly from unity as tested by χ^2.
* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Date	No. of Males (♂♂)	No. of Females (♀♀)	χ^2	Dominance
4- 9-76	16	3	8.89*	♂
2-10-76	810	1000	19.95***	♀
5- 3-77	24	3	16.33***	♂

TABLE IV.5. Size changes of last instar nymphs of *Tasmanocoenis tillyardi* from Spring Creek, illustrating the tendency of nymphal size to decrease in each emergence period.

Date	Generation	Mean Head Width Males (mm)	n	Mean Head Width Females (mm)	n
11- 9-76	G1	0.99	16	1.14	3
2-10-76	G1	1.01	810	1.20	100
6-11-76	G1	0.99	2	1.30*	1*
4-12-76	G2	0.95	23	1.08	19
1- 1-77	G2	0.89	12	1.07	8
5- 3-77	G3	0.96	24	1.10	3
2- 4-77	G3	0.91	18	1.05	17
4- 9-77	G1′	0.92	32	1.07	40
4-10-77	G1′	1.02	80	1.17	97

* only one measurement.

The fact that only three samples were significantly different from a 1 : 1 sex ratio would suggest that they reflect a bias of the collection time for matures, especially in October 1976. In Deep Creek there appeared to be a high percentage of residual males, and observations of mating swarms at Spring Creek would suggest that this is also the case for the streams of the Flinders Ranges. It is possible that the October sample was taken after a large, precocious male swarm, thus resulting in the collection of more female nymphs the next day.

The average head width of last instar nymphs followed similar trends to those observed in Deep Creek (Table IV.5), but the details of the trends are not as clear in this data, probably because the less regular sampling in Spring Creek reduced the effective monitoring of size change. However, the observations made in Deep Creek appear to apply also in Spring Creek, with the over-wintering generations larger at maturity than the summer generation.

Eggs :

The hatching of eggs in Spring Creek was almost continuous, with only six samples not containing first instar nymphs of *T. tillyardi*. The periods of egg hatching over the sampling period were October 1976 to February 1977, April 1977 to August 1977 and November-December 1977. The record of no hatching in March 1977 was an artifact resulting from the loss of the fine net sample. It is likely that hatching was therefore continuous from October 1976 to August 1977. The other period of no hatching, between late August 1977 and October 1977, was during the period of lowest water temperature (July to November) (Fig. IV.6). However, it followed a long period of emergence, and therefore it is unlikely to be the result of an absence of eggs, but rather a quiescence of development at the lower temperatures, as suggested for the Deep Creek population. As soon as water temperatures began to rise, recruitment recommenced.

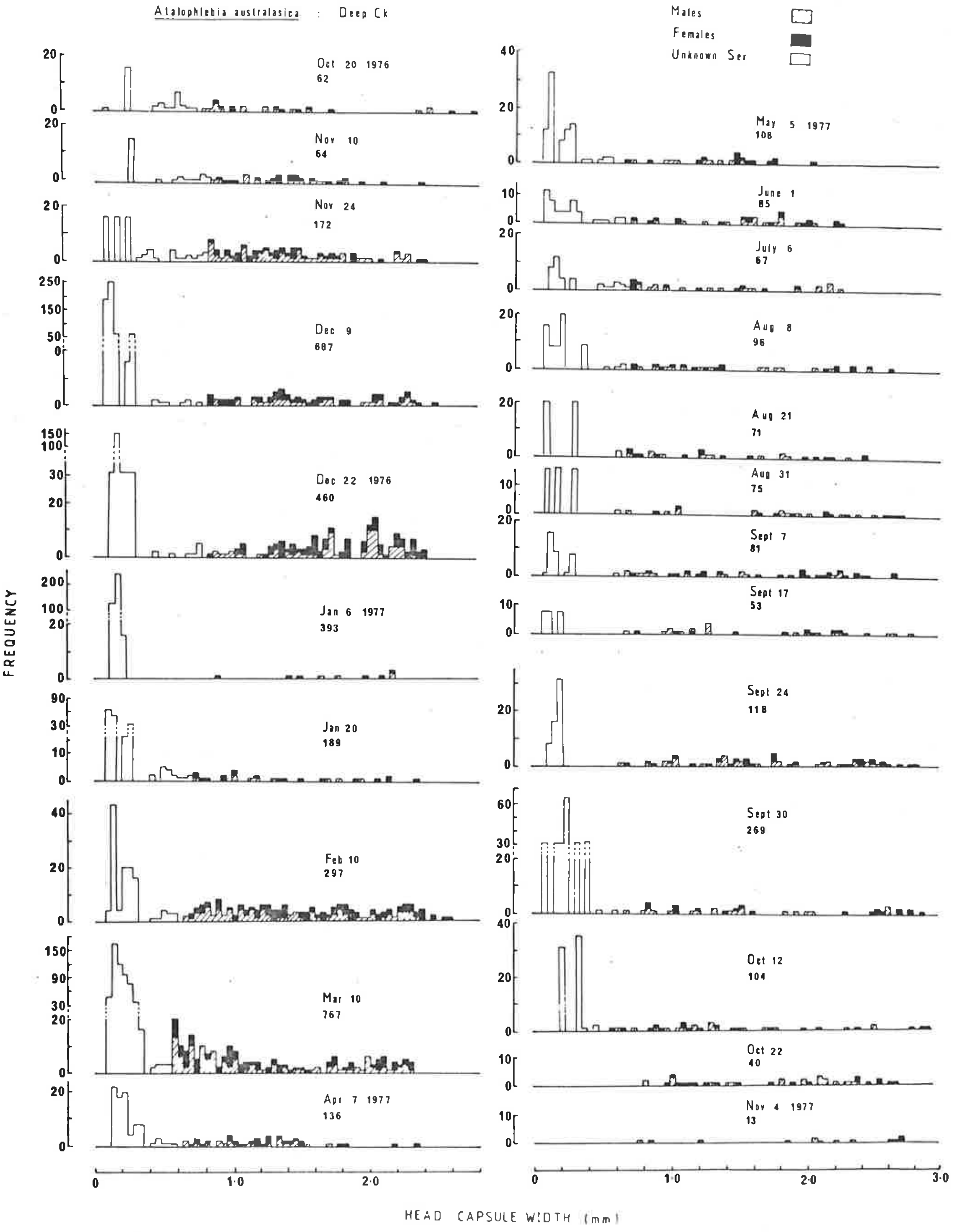
IV.3.2 Family LEPTOPHLEBIIDAE.

Atalophlebia australasica

A. australasica was the only leptophlebic represented in consistent enough numbers in Deep Creek to allow assessment of its life history. *Atalonella inconspicua* was irregularly recorded in the study area, but the numbers were very low, suggesting their presence was only as casual immigrants from upstream populations, rather than permanent residents.

Fiv. IV.7 illustrates the size frequency histograms for *Atalophlebia australasica*, and Fig. IV.8 shows the seasonal growth curves as determined from the size frequency data. These curves and the emergence periods are consistent with a multi-voltine life cycle with three generations per year.

Fig. IV.7. Size frequency histograms of *Atalophlebia australasica* at Deep Creek, South Australia. The number of nymphs used to construct each histogram is recorded below each date.


Atalophlebia australasica : Deep Ck
Males
Females
Unknown Sex
Oct 20 1976
62
Nov 10
64
Nov 24
172
Dec 9
687
Dec 22 1976
460
Jan 6 1977
393
Jan 20
189
Feb 10
297
Mar 10
767
Apr 7 1977
136
May 5 1977
108
June 1
85
July 6
67
Aug 8
96
Aug 21
71
Aug 31
75
Sept 7
81
Sept 17
53
Sept 24
118
Sept 30
269
Oct 12
104
Oct 22
40
Nov 4 1977
13
FREQUENCY
0
1·0
2·0
3·0
HEAD CAPSULE WIDTH (mm)

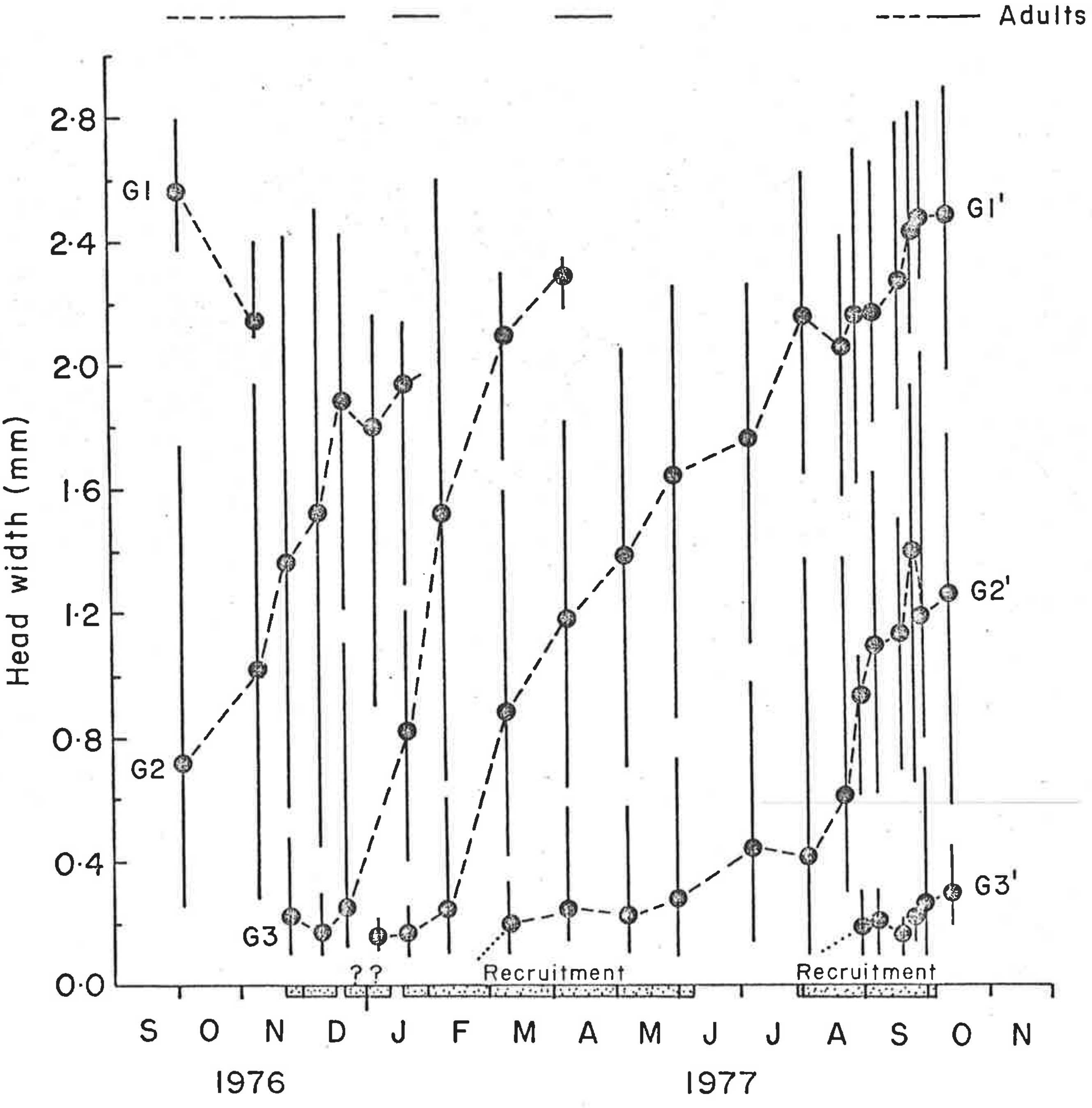
In October 1976, when sampling of the population of *A. australasica* began, two generations were present, G1 of near mature nymphs and G2 of early instar nymphs. Adults from G1 were first recorded in November 1976 and emergence continued into mid-December 1976. Hatching of eggs laid by G1 was first recorded in late November 1976 and, although no first instar nymphs were collected in late December 1976-early January 1977, it is likely that recruitment was continuous throughout this time. The offspring of G1 constituted generation G3 and part of G1′ (see below).

Generation G2 developed rapidly during November and December 1976, and adults were recorded in mid-January 1977. Eggs laid early in this emergence period probably hatched during February, but were indistinguishable from offspring of late emerging G1 (emerging in December 1976) using either NORMSEP or visual selection techniques. They were therefore regarded as part of G1′. Eggs laid by late emerging G2 adults hatched in March and April 1977 to initiate generation G2′.

As mentioned, the offspring of G1 formed a distinct generation, G3, which developed rapidly during the summer months, November 1976 to April 1977, and began emerging in early April. Adults from this generation were recorded until early May 1977. Eggs oviposited by G3 began hatching in early June. The resultant offspring were indistinguishable from the offspring of G2 and later size frequency analysis showed that generation G2′ constituted some offspring of both G2 and G3.

Fig. IV.8. Seasonal growth curves of *Atalophlebia australasica* at Deep Creek, South Australia. Vertical bars indicate the size range of nymphs in each generation.

Atalophlebia australasica : Deep Creek



Development during the winter months was slow in both generations G1′ and G2′. By late August 1977, last instar nymphs were recorded, but no adults were collected until early October 1977, when the water temperature began to increase. This period of recruitment probably resulted from the hatching of eggs, oviposited in May, which had lain quiescent for two months while the water temperature was low.

At the end of the sampling program all generations observed during the study had completed their full cycle. The three generations recorded in September and October 1977 were almost certainly analogous to the three generations present at the beginning of the sampling program in 1976, i.e. G1, G2, G3. Generation G3′ appeared earlier than G3 in the previous year, but with the hatching of eggs from G1′ due in early November the two groups would have been combined, resulting in a slightly depressed mean size of G3′. The precocious hatching in late August was probably initiated by hatching of eggs oviposited in late Autumn. An explanation is that as the water temperature fell a quiscence occurred similar to that observed in *A. australis* Chapter 5). If these eggs were successful in completing their development, and hatched in Autumn before the water cooled to below the quiescent initiating temperature, then G3′ would not have begun until after the emergence of G1′, as occurred in November 1976. Reference to Adelaide air temperatures prior to the beginning of sampling (Fig. III.5), shows that the autumn period in 1976 was cooler than in 1977. This may account for the late start of generation G3.

The life cycle of *A. australasica* is therefore multivoltine, with three distinct generations emerging in Spring, Summer and Autumn. Of the three generations, two develop over the winter months, requiring some 10-12 months (G1 and G2) while G3 completes its development during the warm summer months, requiring only 7 months.

Nymphal Stage :

The sex of nymphs was easily determined early in their development at stage IIc or IId as defined by Clifford (1970a). At this and subsequent growth stages, the medial eye development of the male nymphs was apparent.

The sex ratio of *A. australsica*, as calculated from the 1,385 male and female nymphs collected during the 14 month study, was close to 1 : 1, with only two sampling dates having significantly more females than males as tested by χ^2,

				χ^2	significance
i.e.	7. 9.1976	35	55	4.44	$p < 0.05$
	9.12.1976	18	58	21.05	$p < 0.001$

Over the annual cycle, the ratio of males to females was 1.00 : 1.11 which was significantly different from a 1 : 1 ratio ($p < 0.05$). The two dates above, bias the ratio towards female dominance, whereas all other samples are consistent with a 1 : 1 ratio. It is therefore suggested that *A. australasica* has a sex ratio near 1 : 1.

The size change of last instar nymphs throughout the annual cycle followed similar trends to those observed in

T. tillyardi, with precocious emergers larger than those collected later in the emergence period. Also, nymphs that developed over the winter months were larger than those which completed their life cycle in the summer months (Table IV.6). In all cases the females were much larger than the males. The head width range of last instar females was 2.28-2.90mm, compared with 2.12-2.60mm for the males. Cianciara (1979) noted that female nymphs of *Cloeon dipterum* passed through a greater number of moults, and that they were larger at maturity than males. This phenomenon could explain the consistent size difference in *A. australasica*.

Subimago Stage :

Subimagos were observed to emerge in the afternoon, but the presence of many subimagos in sheltered culverts and beneath bridges in the early morning suggests that many may emerge during the evening or night. None was attracted to the ultra-violet light trap.

The nymph rises to the water surface of slow flowing pools or flats where the subimago emerges, using the cast skin as a raft. The newly emerged subimago then flies to a stable surface to dry. The duration of the subimago stage was not determined, but specimens in emergence containers at 20°C in the laboratory remained as subimagos for between 12 and 36 hours before the final moult. Once the subimago skin ruptured along the thorax, moulting was completed in less than three minutes.

TABLE IV.6.

Size changes of last instar nymphs of *Atalophlebia australasica* from Deep Creek, South Australia, illustrating the tendency of nymphal size to decrease in each emergence period.

Date	Generation	Mean Head Width Males (mm)	n	Mean Head Width Females (mm)	n
20-10-76	G1	2.45	3	2.72	2
10-11-76	G1	2.40*	1	-	
24-11-76	G1	2.28	7	2.42	2
9-12-76	G1	2.32	5	2.35	7
22-12-76	G1	2.25	13	2.33	17
10- 2-77	G2	2.28	12	2.47	8
10- 3-77	G2	2.22	9	2.30	5
31- 8-77	G1′	2.46	2	2.66	4
7- 9-77	G1′	-	-	2.68*	1
17- 9-77	G1′	2.48*	1	2.71	3
24- 9-77	G1′	2.54	2	2.70	6
30- 9-77	G1′	2.60	3	2.66	10
12-10-77	G1′	2.45	3	2.87	3
22-10-77	G1′	2.39	4	2.61	4
4-11-77	G1′	2.30	2	2.57	4

* only one record.

Imago Stage :

The life span of the imago of *A. australasica* is unknown, but laboratory observations suggest that it is relatively long, being measured in days rather than hours. Reared imagos survived for two to three days, but under natural (non-confined) conditions survival time may be different.

Mating "swarms" were observed during the day when the air was still. Swarms of 3-20 males "patrolled" the smooth flowing reaches of the stream, flying up and down the length of these reaches, about 1m above the water surface. These swarms dispersed rapidly with the first evidence of a breeze, and the males alighted in sheltered vegetation or rocks. During the "patrols" males approached and touched each other, but disengaged rapidly, repeating these approaches until they contacted a female, at which time mating might occur.

The length of time after copulation before oviposition, is unknown. Females were observed to fly close to the smooth water surface, dipping their abdomen into the water, releasing many individual eggs. No oviposition was observed in regions of broken or rapidly flowing water.

Eggs :

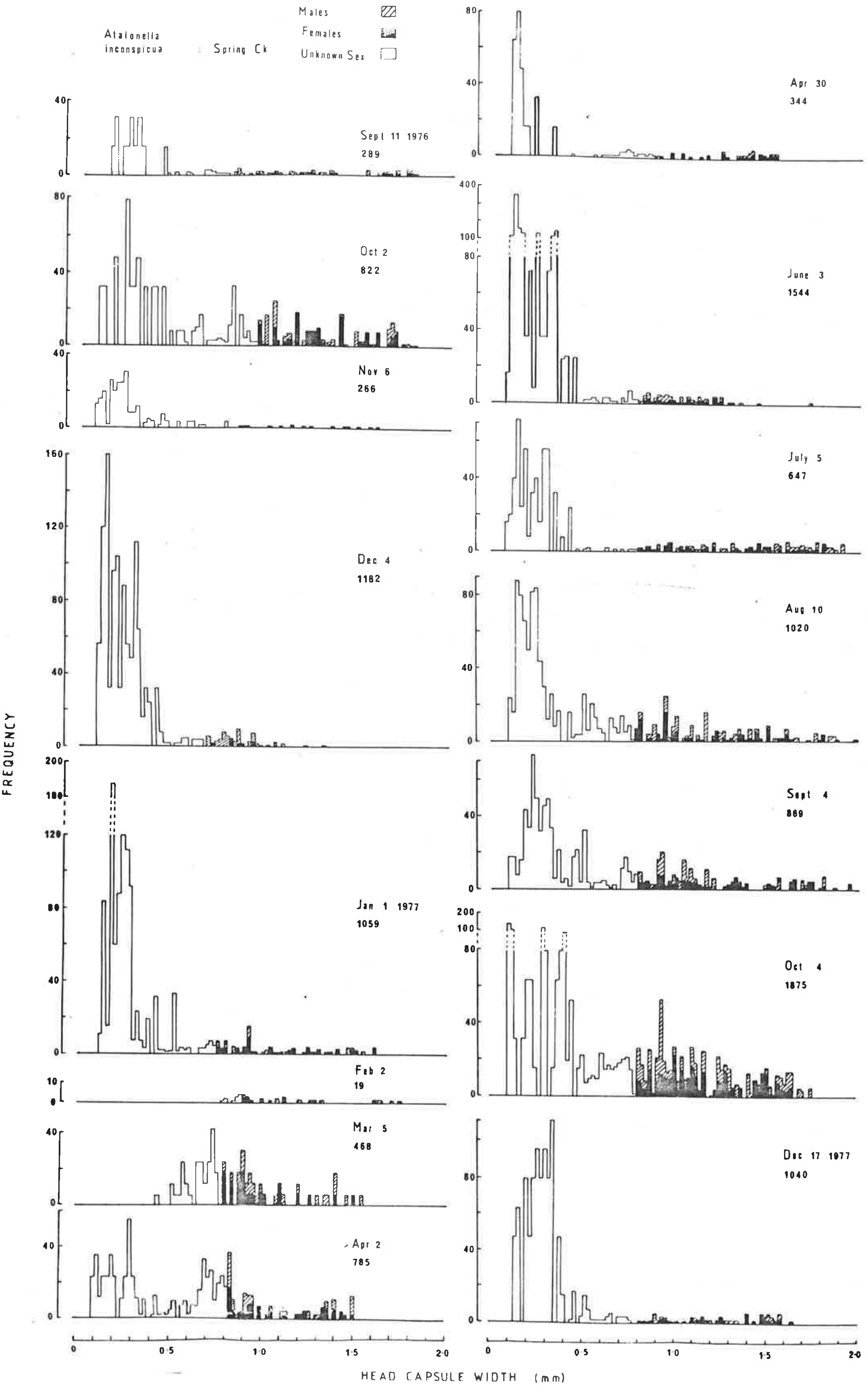
The presence in collections of first instar nymphs (Head Width = 0.10mm) was considered indicative of egg hatching. During the study period there were five periods of recruitment, from November-December 1976; January-February 1977; March-April 1977; April-May 1977 and August-September 1977. Each period of hatching followed a period of emergence with the exception of the August-September 1977 hatch. As mentioned above, this may be explained by a temperature enforced quiescence of eggs laid in late Autumn. Eggs laid earlier in the emergence period (April 1977) developed in water of higher temperature (15°C) and were observed to hatch in May, but the eggs oviposited later in May when the water temperature approached 10-12°C probably over-wintered in a quiescent state until the water temperature began to rise above 10-12°C. *A. australasica* therefore appears to have a similar egg development mechanism to *A. australis*, with a temperature induced quiescence (Chapter 5).

Atalonella inconspicua : Spring Creek.

A. inconspicua was the only leptophlebiid recorded in Spring Creek during the study period. Fig. IV.9 illustrates the size range frequency histograms recorded during twelve months of sampling. The seasonal growth curves are given in Fig. IV.10, and show three generations per year, with emergence and recruitment occurring over at least nine months of the year.

In September 1976, three generations were represented, one, emerging (G1) was represented by last and penultimate instar nymphs. The second generation (G2) consisted of specimens with head widths ranging from 0.43-1.40mm ($\bar{x}$ = 0.93). The third generation (G3) consisted of early instar nymphs with head widths less than 0.40mm. By November 1976, G1 had completed its emergence. Hatching of eggs, oviposited by G1, began in October 1976 and continued until December 1976

Fig. IV.9. Size frequency histograms of *Atalonella inconspicua* at Spring Creek, South Australia. The number of nymphs used to construct each histogram is recorded below each date.


Atalonella inconspicua
Spring Ck
Males ▨
Females ▩
Unknown Sex ☐
Sept 11 1976
289
Oct 2
822
Nov 6
266
Dec 4
1182
Jan 1 1977
1059
Feb 2
19
Mar 5
468
Apr 2
785
Apr 30
344
June 3
1544
July 5
647
Aug 10
1020
Sept 4
889
Oct 4
1875
Dec 17 1977
1040
FREQUENCY
HEAD CAPSULE WIDTH (mm)
0
0·5
1·0
1·5
2·0
0
40
80
120
160
200
400
100
10

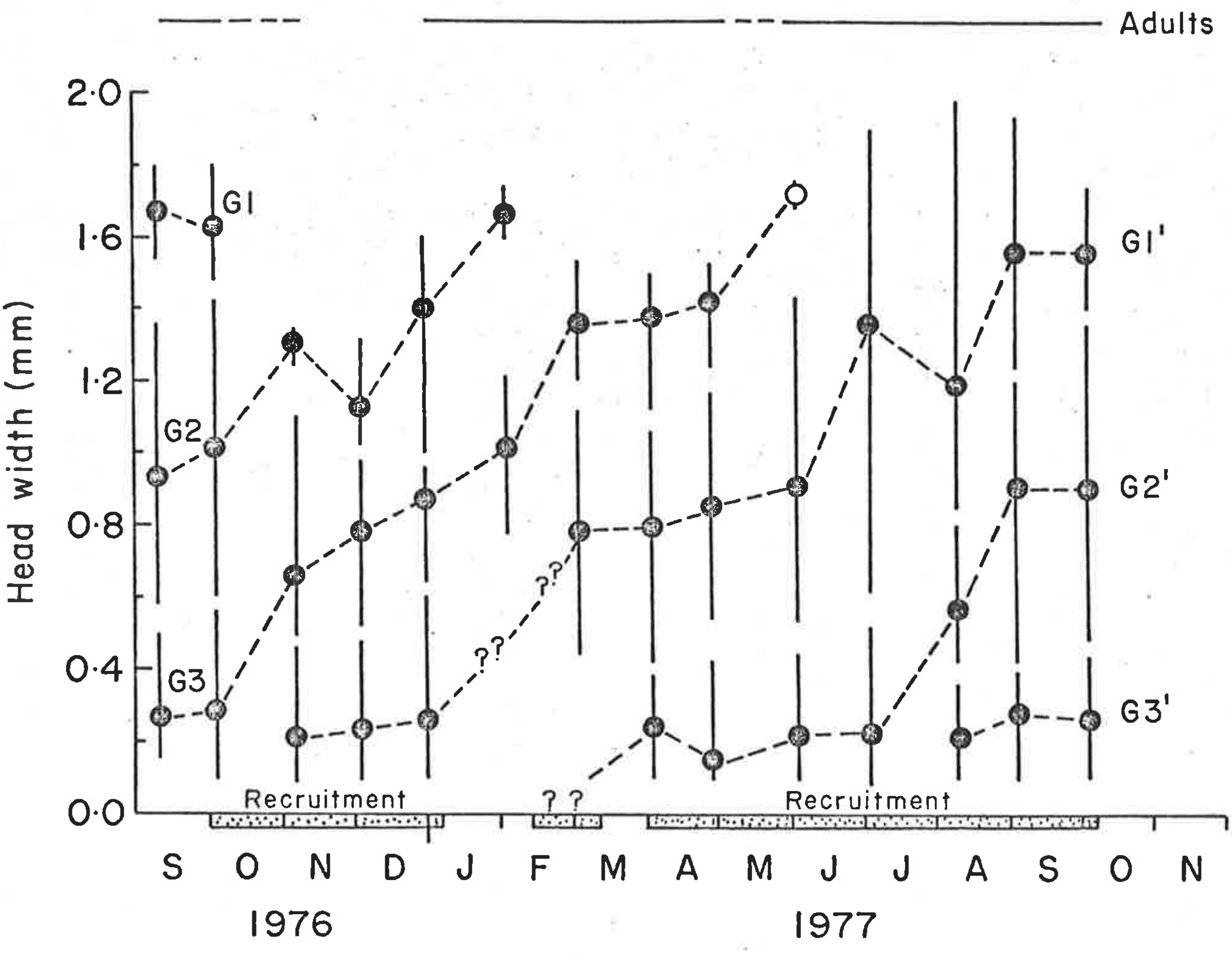
giving rise to G1′.

Generation G2 adults were recorded in January 1977 and emergence continued into April-May 1977, by which time adults from G3 were also emerging. Offspring of G2 were recorded in April 1977, but, since the March fine mesh sample was misplaced, earlier evidence of hatching was not available. The incubation period of *A. inconspicua* eggs, at temperatures experienced in Spring Creek during February-March 1977 (average of 21°C), would be relatively short, approximately 14-20 days (see Chapter 5). Therefore eggs laid by G2 females probably commenced hatching in February 1977. Clearly the "kick" samples from the available pools in February were inadequate to sample the early instars of the *A. inconspicua* population during periods of zero surface flow. However, the recorded offspring of G2 in April-May 1977 gave rise to generation G2′.

By May 1977 G3 began to emerge, but the offspring of these early emerging adults were initially indistinguishable from the offspring of G2′. However, by July, a third generation was apparent, being the offspring of late emerging adults of G3. These hatchings initiated generation G3′.

Generation G1′ emerged continuously from June to October 1977. Eggs laid by this generation probably hatched from July-September 1977 and were therefore initially confused with early instars of G3′.

Fig. IV.10. Seasonal growth curves of *Atalonella inconspicua* at Spring Creek, South Australia. Vertical bars indicate the size range of nymphs in each generation.



Atalonella inconspicua : Spring Creek

At the end of the twelve month sampling period in October 1977 three generations were present, G1′, G2′, G3′, all of which had a mean size similar to that reached by G1, G2, G3 in October 1976. Therefore a complete cycle was duplicated over the twelve month period with the three generations G1, G2 and G3 in 1976 analogous to G1′, G2′ and G3′ of 1977. All generations required 10-12 months to complete their development.

Nymphal Stage :

The sex of *A. inconspicua* nymphs was easily determined once they had reached the IIc or IId development stage as defined by Clifford (1970a). At this and subsequent growth stages the medial eye development of the male nymphs was apparent.

The sex ratio of the nymphs collected varied throughout the year, with six samples having ratios significantly different from 1 : 1 ($p < 0.05$) as tested by χ^2. There was no consistent pattern of male or female dominance with both males and females dominating three samples. The significant samples are given in Table IV.7. Over the annual cycle in which 1,160 males and 1,206 females were collected the χ^2 test was not significant. This suggests that *A. inconspicua* has a 1 : 1 sex ratio, and that the six significant values (Table IV.7) were artifacts of point sampling and their effects were obscured when the annual cycle was considered.

TABLE IV.7.

Numbers of nymphs of *Atalonella inconspicua* from Spring Creek, South Australia, on dates when the sex ratio differed significantly from unity as tested by χ^2.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Date	No. of Males (♂♂)	No. of Females (♀♀)	χ^2	Dominance
2-10-76	150	88	16.15***	♂
4-12-76	18	52	16.51***	♀
5- 3-77	24	44	5.88*	♀
30- 4-77	13	4	4.76*	♂
5- 7-77	53	83	6.62*	♀
4- 9-77	65	92	4.64*	♀

Last instar nymphs of *A. inconspicua* which developed over the winter months were larger at the time of emergence than generations which had the majority of development during the summer months. Also within any one generation a steady decrease occurred in the mean size of the last instar nymphs over the duration of the emergence period (Table IV.8). In all cases, the average size of last instar female nymphs was equal or larger than their male counterparts (Table IV.8). The size ranges of head widths of last instar female and male nymphs were 1.40-1.98mm and 1.34-1.80mm respectively. The consistent size difference may be explained as suggested for *Atalophlebia australasica* by the females having at least one more moult than males.

Subimago Stage :

Subimagos were observed emerging from exposed rocks during the morning and afternoon. Once the nymph had climbed to the air-water surface, the subimago emerged onto the dry upper surface where it either remained, or flew to other dry rocks on the stream bank. On hot, sunny days the subimagos could be found in the shade between rocks or beneath the Spring Creek highway bridge, avoiding the direct heat of the sun.

The duration of the subimago stage is unknown. The presence of numerous imagos and few subimagos early in the morning, suggests that the final moult to imago occurs during the night, and therefore the subimago stage is probably less than 24 hours.

TABLE IV.8.

Size changes of last instar nymphs of *Atalonella inconspicua* from Spring Creek, South Australia, illustrating the tendency of nymphal size to decrease in each emergence period.

Date	Generation	Mean Head Width Males (mm)	n	Mean Head Width Females (mm)	n
11- 9-76	G1	1.68	4	1.72	10
2-10-76	G1	1.62	39	1.69	23
6-11-76	G1	1.60*	1	-	-
1- 1-77	G2	1.49	10	1.52	10
2- 2-77	G2	1.60*	1	1.68	4
5- 3-77	G3	1.45	12	1.50	12
2- 4-77	G3	1.38	22	1.46	23
30- 4-77	G3	1.45	12	1.45	7
5- 7-77	G1′	1.75	7	1.82	23
10- 8-77	G1′	1.79	6	1.82	14
4- 9-77	G1′	1.68	20	1.83	15
4-10-77	G1′	1.56	28	1.68	26

* only one record.

Imago Stage :

The mating swarms of *A. inconspicua* were usually large, with 50-100 imagos, flying between two and four metres above ground level. Males were observed to fly vertically for about a metre, beating of wings then ceased, and the imago dropped slowly to near its original position, at which point it flew vertically again, repeating the rapid active rise and slow passive fall of its mating flight. Many swarms were observed over pools and above the dry cobbles of the stream bed. One curious behaviour of the imagos was to swarm over a white sweep net held above the ground. If the net was moved along the creek bed the swarm tended to follow, maintaining its position above the net. Swarms were also observed over the roof of a stationary car. It is likely that the swarms orientate to bright reflecting surfaces such as pools, white cobble beds, and consequently the white net and reflective metal surfaces.

Mating was observed in these swarms, and lasted less than 10 seconds. The time interval between mating and oviposition is unknown. Females were observed to fly over the smooth surface of pools where they dipped their abdomens into the water, releasing many individual eggs which sank to the bottom at a rate of about 1mm sec^{-1}. No eggs were oviposited in broken or moderately flowing water.

Eggs :

First instar nymphs (Head Width = 0.10mm) were recorded during two main periods, from October-December 1976 and from April (February-March?)-October 1977, with only January-March

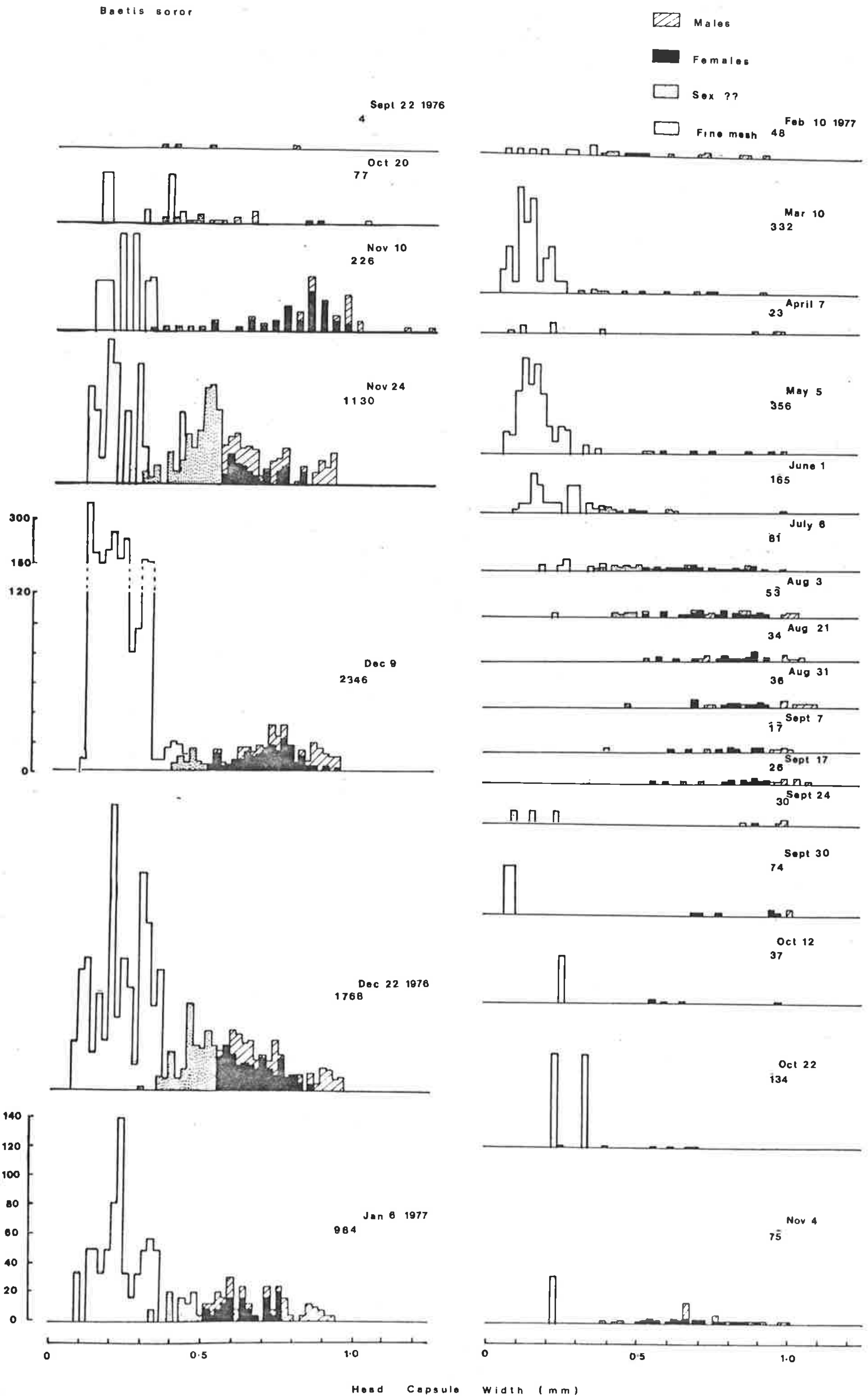
1977 without direct evidence of egg hatching. This apparent period of no recruitment resulted from the absence of adults during November-December 1976, and, as discussed above, the loss of the March fine net sample. Otherwise, whenever there were adults present, there appeared to be continuous recruitment, even throughout the winter months. The water temperature during the winter months and the evidence of egg development of *A. inconspicua* may explain this continuous recruitment (see Chapter 5). The minimum water temperature recorded was 9°C in August 1977, but fluctuated between 9-13°C and probably never fell below 10-12°C long enough to halt development.

IV.3.3 Family BAETIDAE.

Baetis soror : Deep Creek.

Field data of *B. soror* from Deep Creek are illustrated as size frequency histograms in Fig. IV.11. Fig. IV.12 illustrates the seasonal growth curves, showing evidence of three generations during the study period. The number of nymphs collected after January 6, 1977 is dramatically lower than for the previous months. Over January 2, 3 and 4, a spate scoured the stream bed removing the *Cladophora* bed, and clearly affected the population of *B. soror*. At no time during the study did numbers of *B. soror* recover to their previous levels, suggesting that the effect of the spate was at least semi-permanent.

Fig. IV.11. Size frequency histograms of *Baetis soror* at Deep Creek, South Australia. The number of nymphs used to construct each histogram is recorded below each date.


Baetis soror
Males
Females
Sex ??
Fine mesh
Sept 22 1976
4
Oct 20
77
Nov 10
226
Nov 24
1130
300
150
120
0
Dec 9
2346
Dec 22 1976
1768
140
120
100
80
60
40
20
0
Jan 6 1977
984
0
0·5
1·0
Feb 10 1977
48
Mar 10
332
April 7
23
May 5
356
June 1
165
July 6
81
Aug 3
53
Aug 21
34
Aug 31
36
Sept 7
17
Sept 17
26
Sept 24
30
Sept 30
74
Oct 12
37
Oct 22
134
Nov 4
75
0
0·5
1·0
Head Capsule Width (mm)

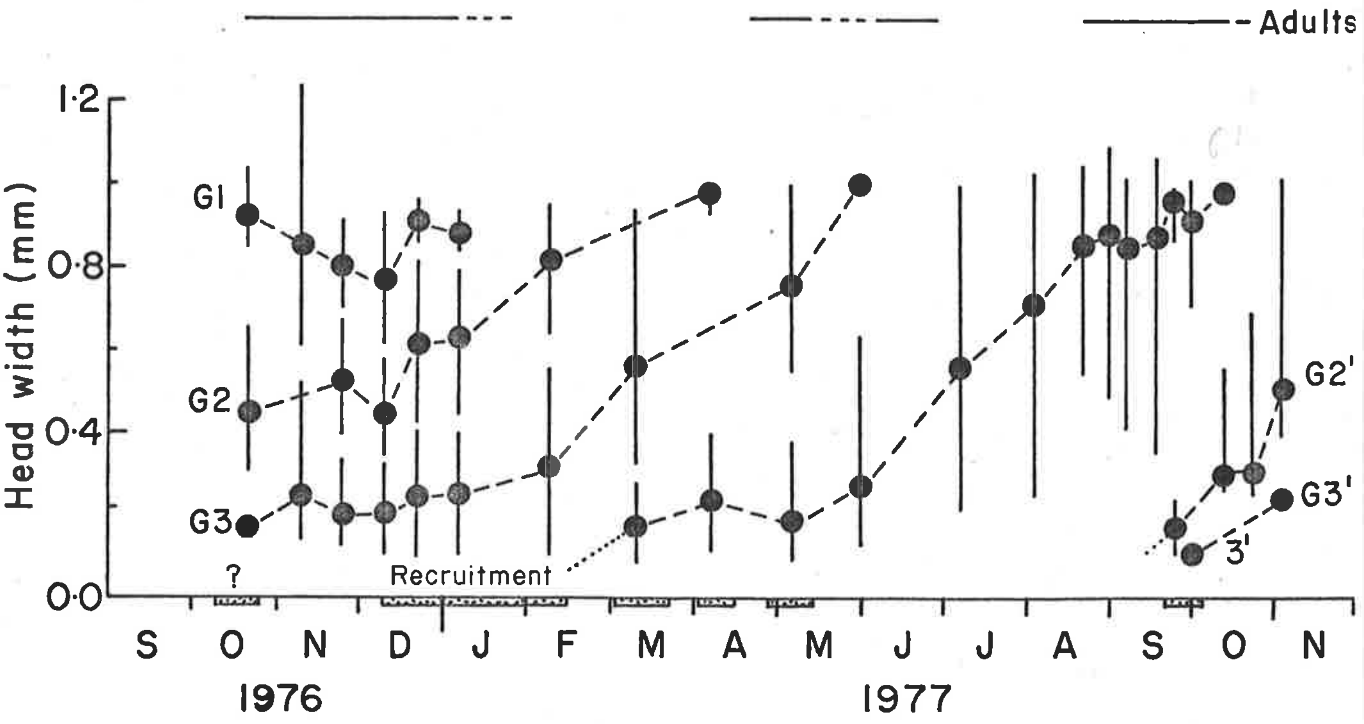
The first sample in September 1976 was from near a ford on Deep Creek, 1km above the study area. A previous survey had determined that population numbers of *B. soror* were high in this area. Prior to the September sample a substantial flood occurred displacing the population of *B. soror* downstream to the stretch of water above the River Torrens confluence. From October 1976 to the end of the study this stretch of water became the permanent sampling locality for all species.

The field data for October 1976 suggested the presence of three generations, one emerging with nymphs approaching last instar (G1); a second generation with head widths between 0.30mm and 0.66mm (G2) and a third generation of early instar animals of head widths less than 0.20mm (G3).

Generation G1 began to emerge in October 1976 but continued over an extended period to January 1977. Generation G2 developed rapidly over this period and began to emerge in late April-early May 1977. The growth curve discontinuity of G3 during December and January was caused by recruitment from early hatchings from eggs laid by G1 females. Not until March 1977 could offspring of G1 be distinguished from G3 and therefore were included in the calculation of G3 mean size classes. Generation G1′, therefore began in February-March 1977. Recruitment from eggs of G2, oviposited in April and May 1977 caused the depression of the mean size of G1′, and from June to August 1977 the two hatches appeared as the one generation G1′. Therefore G1′ was the sole generation developing throughout the winter period. Last instars were collected and emergence began in late August 1977 continuing

Fig. IV.12. Seasonal growth curves of *Baetis soror* at Deep Creek, South Australia. Vertical bars indicate the size range of nymphs in each generation.

Baetis soror : Deep Creek



through until the end of the study in November 1977.

Although first instar nymphs were missed in the August-early September 1977 samples, evidence of a new generation (G2′) in the form of instar 3+ nymphs was apparent. These, perhaps recruited from eggs laid by G3 females in May to June, developed slowly in the low temperatures of Winter. Laboratory experiments showed that no quiescence or diapause occurred in eggs of *B. soror* (see Chapter 5), and at the winter temperatures experienced (greater than 5°C) development was continuous although very slow. Recruitment was observed in late September-early October 1977, from eggs laid by the early emerging adults of G1′ beginning generation G3′ and completing the annual cycle of three generations.

In summary, generation G1 gave rise to G3 and part of G1′; G2 gave rise to the rest of G1′ and G2′ originated from G3.

The duration of each generation from earliest hatching to last emergence, as extrapolated from the annual cycle, is as follows, G1 (G1′) eleven months (February-January); G2 (G2′) eight months (September-May) and G3 (G3′) eight months (November-June). The generations which developed during warmer months of Spring, Summer and Autumn, (G2 and G3) had similar development periods of eight months, while G1 which had the majority of development during the Winter, took about three months longer to complete its life cycle.

Nymphal Stage :

As in the Leptophlebiidae, sex of *B. soror* nymphs could be determined very early in the generation as medial eye development appeared in males in all stages after stage IId as defined by Clifford (1970a).

Over the entire sampling period sex ratio was not significantly different from 1 : 1, but on five occasions collections differed significantly from this ratio ($p < 0.05$). On December 9, and December 22, 1976 two generations, G1 and G2, were considered separately, and both significantly deviated from the expected 1 : 1 ratio. Of the seven significant comparisons, three showed a female bias, and four a male bias (Table IV.9).

The size of the last instar nymphs of *B. soror* also showed a tendency to decrease throughout the emergence period, and generations G1 and G1′, both of which developed over the winter months, were generally larger than their spring-autumn counterparts, G2 and G3 (Table IV.10). In Table IV.10 it is clear that the mean head width of the last instar female nymphs was smaller than the males. This contrasts with observations made of *T. tillyardi*, *Atalophlebia australasica* and *Atalonella inconspicua*. Although it was postulated that females of the latter species had an extra instar, it appears that the consistent head width difference in *B. soror* is due to the development of the turbinate eyes of the males, greatly increasing the last instar head width. The size range of male and female nymphs, in terms of head width, was 0.84-1.24mm and 0.80-1.08mm respectively.

TABLE IV.9.

Number of nymphs of *Baetis soror* from Deep Creek, South Australia on dates when the sex ratio differed significantly from unity as tested by χ^2.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Date	Generation	No. of Males (♂♂)	No. of Females (♀♀)	χ^2	Dominance
24-11-76	G1	102	37	30.40***	♂
9-12-76	G1	56	7	31.50***	♂
9-12-76	G2	69	213	26.41***	♀
22-12-76	G1	61	4	49.98***	♂
22-12-76	G2	142	190	6.94**	♀
6- 1-77	G1′	76	30	19.96***	♂
6- 7-77	G1′	6	17	5.26*	♀

TABLE IV.10.

Size changes of last instar nymphs of *Baetis soror* from Deep Creek, South Australia, illustrating the tendency of nymphal size to decrease in each emergence period.

Date	Generation	Mean Head Width Males (mm)	n	Mean Head Width Females (mm)	n
20-10-76	G1	1.04*	1	0.86	2
10-11-76	G1	0.99	18	0.87	26
24-11-76	G1	0.90	57	0.82	8
9-12-76	G1	0.89	52	0.84	16
22-12-76	G1	0.92	53	0.82	20
6- 1-77	G1	0.88	48	0.74	8
10- 2-77	G2	0.91	3	-	-
10- 3-77	G2	0.94*	1	-	-
7- 4-77	G2	0.97	3	-	-
5- 5-77	G3	1.00	1	0.96*	1
1- 6-77	G3	1.00	1	-	-
3- 8-77	G1′	1.02	5	0.92	4
21- 8-77	G1′	1.02	8	0.91	8
31- 8-77	G1′	1.04	11	0.91	11
7- 9-77	G1′	0.99	5	0.91	4
17- 9-77	G1′	1.03	3	1.08*	1
24- 9-77	G1′	1.00	4	-	-
30- 9-77	G1′	1.01	4	0.97	3
4-11-77	G1′	1.01	2	-	-

* only one record.

Subimago Stage :

Subimagos were observed flying from the stream surface from mid-day to early evening, but actual emergence was not observed. Subimagos were found in the overhanging vegetation. The duration of the subimago stage is unknown.

Imago Stage :

Large swarms of males were observed during mid-day and afternoon, but the latter swarms were more obvious because the rays of the setting sun were reflected from the swarming adults. These mating swarms occurred above water, or over the riparian vegetation. Mating was never observed.

Females oviposited by successive dipping of the abdomen into the water in pool areas above the riffles or in areas of broken water. A stream of very sticky eggs was released at each submergence, these sank slowly and adhered to any substrate surface.

Eggs :

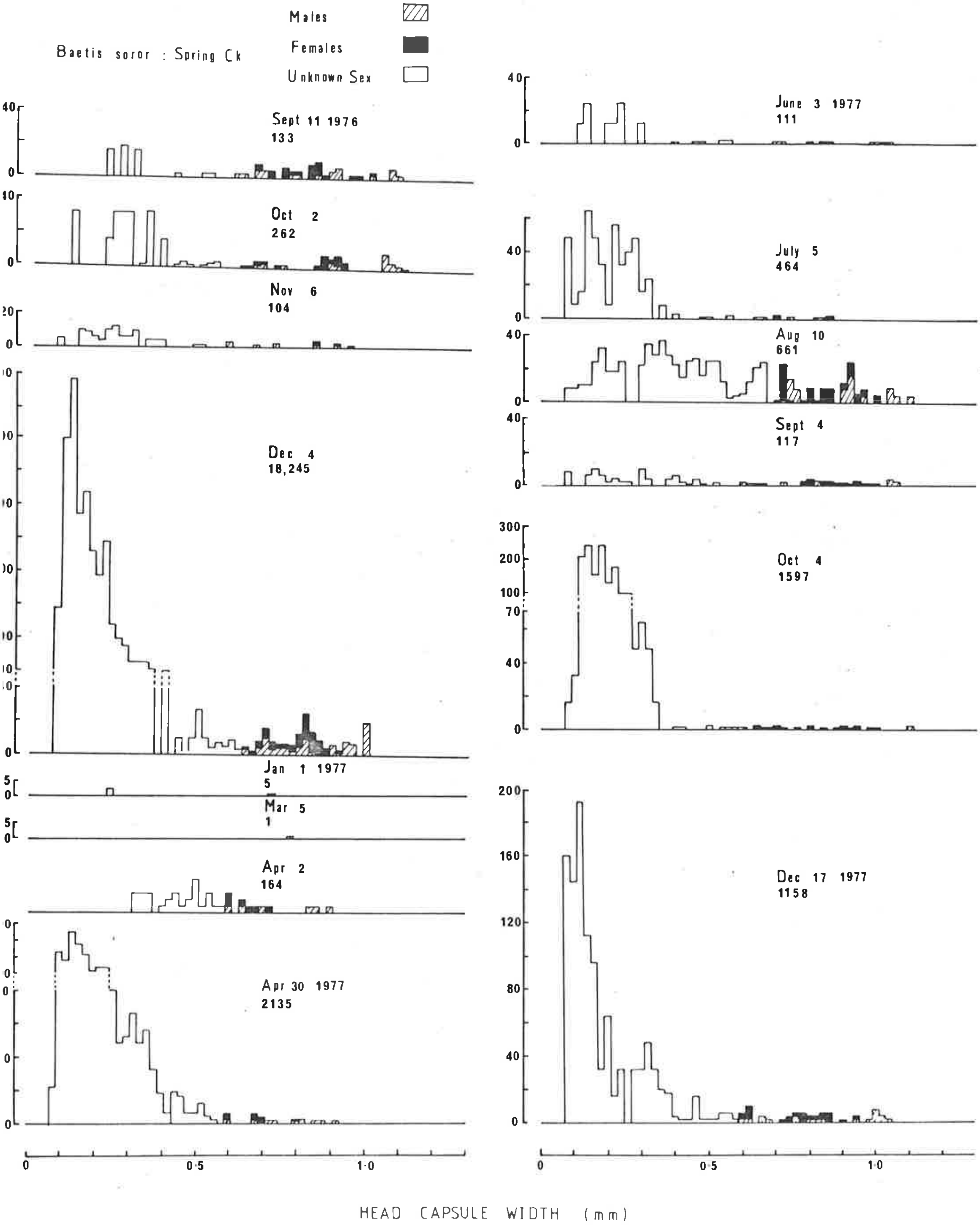
First instar nymphs, with head widths of 0.08mm were recorded in October 1976, from November 1976 to May 1977 and in September and October 1977. All hatches were preceded by a period of emergence, and as demonstrated artificially in the laboratory, no dormancy occurred. At all temperatures experienced at Deep Creek development was continuous.

Baetis soror : Spring Creek.

The life history of *B. soror* in Spring Creek was similar to that described for this species in Deep Creek, but included an extra generation. Fig. IV.13 shows the size frequency histograms, and Fig. IV.14 illustrates the annual growth curves as interpreted from these histograms and field observations. From both graphs the period January to March 1977 was apparently inadequately sampled for this species; the reason for this being absence of flowing water in the sampling area. In April this also was the case, but about one kilometre upstream of the sampling site permanent running water was found. A sample from this area collected *B. soror*, and allowed interpretation of the life cycle.

The first sampling date in September 1976 showed the presence of two generations, G1 and G2. Generation G1 consisted of last instar nymphs and nymphs nearing maturity. Adults were also present. This generation completed its emergence period in early November. Generation G2, of smaller nymphs, developed steadily until emergence began in December 1976. The eggs laid by G1 commenced hatching in October 1976 and recruitment continued until early December 1976, initiating generation G3. The protracted emergence period of G1 explains the long period of egg hatch, and the resultant depression of the average size of G3 in December 1976. Although development of G3 was not followed because of the inadequacies of sampling, it is likely that this generation developed parallel to G2 and emerged in February-March 1977. This suggestion is supported by the presence of first instar nymphs in April-May 1977. This hatch

Fig. IV.13. Size frequency histograms of *Baetis soror* at Spring Creek, South Australia. The number of nymphs used to construct each histogram is recorded below each date.


Baetis soror : Spring Ck
Males
Females
Unknown Sex
Sept 11 1976
133
Oct 2
262
Nov 6
104
Dec 4
18,245
Jan 1 1977
5
Mar 5
1
Apr 2
164
Apr 30 1977
2135
June 3 1977
111
July 5
464
Aug 10
661
Sept 4
117
Oct 4
1597
Dec 17 1977
1158
40
0
20
5
300
200
100
70
160
120
80
0.5
1.0
HEAD CAPSULE WIDTH (mm)

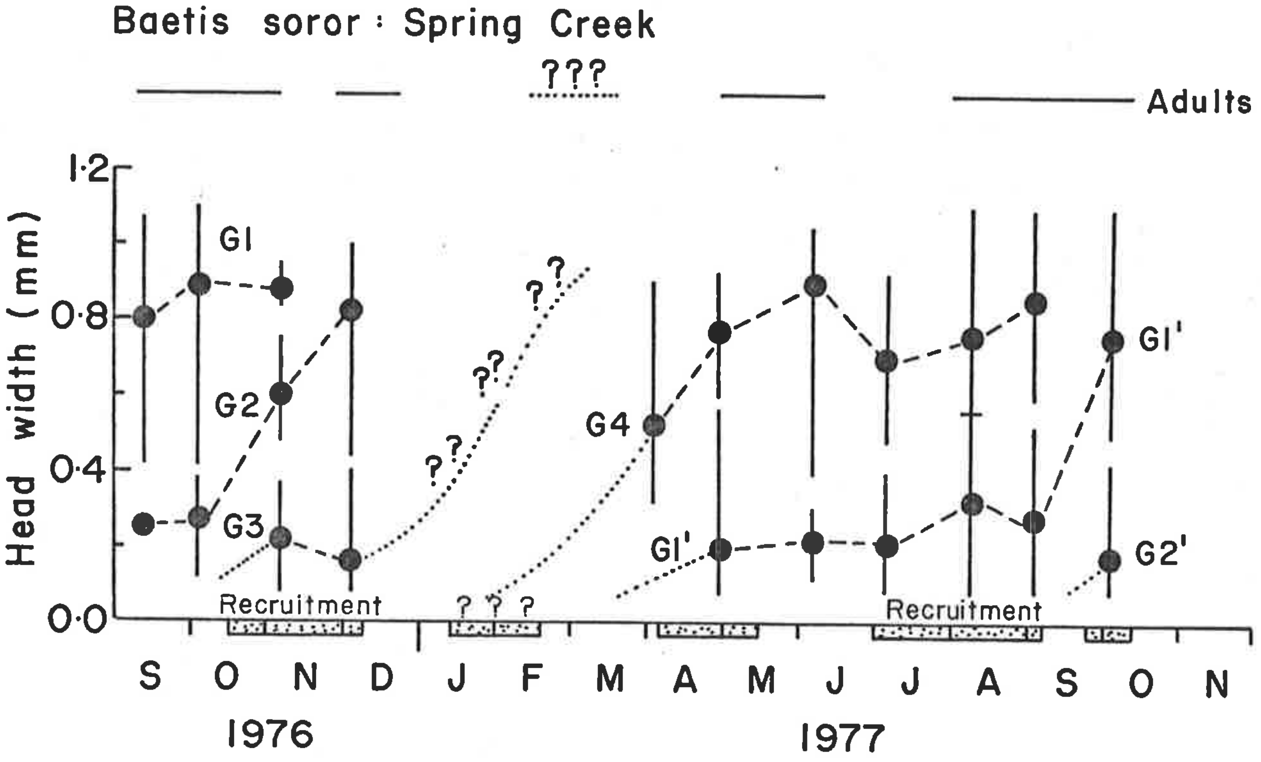
occurred four months after the emergence of G2 during a period of high water temperature, and associated rapid egg development (Chapter 5). Therefore it is unlikely that the eggs hatching in April-May originated from G2, but an intermediate generation, G3. Similarly the eggs oviposited by G2 females probably hatched in January-February 1977 initiating generation G4 which was approaching maturity in April 1977.

Emergence of G4 began in May 1977, and ended in September 1977. This long emergence period was characterised by two peaks, the first in May-June, and the second in early August. This may suggest two generations, or alternatively a period of air and water temperatures too low for emergence to occur, thus dividing the normal emergence period in two. Analysis of the temperature conditions between June and August suggested that the latter is a likely explanation.

The G1´ generation began in April-May 1977 from eggs laid by G3, developed slowly during the Winter and then, as water temperatures began to rise in August, increased its rate of development to emerge in September 1977. During the slow development period June-August 1977 there was continuous recruitment to G1´, as eggs from the early emergence of G4 started to hatch. This recruitment depressed the average size of G1´ through the winter months and therefore exaggerated the spring growth rate.

A period of egg hatching occurred in late September and initiated generation G2´. These eggs were from the second period of emergence of G4 . With the imminent emergence of

Fig. IV.14. Seasonal growth curves of *Baetis soror* at Spring Creek, South Australia. Vertical bars indicate the size range of nymphs in each generation.



Baetis soror : Spring Creek

G1′, and the presence of G2′ in late September 1977, the annual cycle of *B. soror* at Spring Creek was virtually completed, although no adults from G1′ had been collected. The duration of each generation, as calculated from the seasonal growth curves, were G1 (G1′) five-six months; G2(G2′) four-five months; G3 five months and G4 seven-eight months. The winter generations, G1 and G4, both required longer development periods than the summer generations G2 and G3.

Nymphal Stage :

Throughout the sampling period the sex ratio of *B. soror* nymphs did not significantly depart from the expected 1 : 1 ratio as tested by χ^2.

As observed in Deep Creek, the last instar nymphs tended to decrease in size as the emergence period progressed, and the summer generations were smaller than their winter counterparts (Table IV.11). Last instar females also were consistently smaller than the males. The size range of last instar males and females, in terms of head width, was 0.80-1.10mm and 0.80-1.00mm respectively.

Subimago and Imago Stages :

Observations of subimago and imago stages at Spring Creek were similar to those made at Deep Creek, with only the time of the emergence periods differing.

TABLE IV.11.

Size changes of last instar nymphs of *Baetis soror* from Spring Creek, South Australia.

Date	Generation	Mean Head Width Males (mm)	n	Mean Head Width Females (mm)	n
11- 9-76	G1	1.05	10	0.97	6
2-10-76	G1	1.05	17	0.88	22
6-11-76	G1	0.90*	1	0.88	4
4-12-76	G2	0.96	45	0.84	49
3- 6-77	G4	1.00	4	0.88	2
10- 8-77	G4	1.06	17	0.94	26
4- 9-77	G1′	1.05	11	0.93	6
4-10-77	G1′	1.10	2	0.94	7

* only one record.

IV.4. Discussion :

IV.4.1 Comparison of Life Cycles Between the Deep Creek and Spring Creek Populations.

Direct comparisons can be made only with those species common to each locality, namely *T. tillyardi* and *B. soror*. The most obvious dofference between the two populations of both *T. tillyardi* and *B. soror* was the increase in the number of generations in Spring Creek. *T. tillyardi* had two generations per year in Deep Creek, and increased to three generations in Spring Creek; *B. soror* increased from three to four generations. The much higher air and water temperatures at Spring Creek may explain this. In Spring Creek, the mean monthly water temperature fell below 12°C for only July and August 1977 (Fig. IV.6). In contrast, in Deep Creek the mean water temperature was below 12°C in October 1976, and from May to September 1977 (Fig. IV.2). During Summer, temperatures were higher in Spring Creek with mean monthly water temperatures exceeding 18°C from December 1976 until April 1977. In Deep Creek 18°C was only exceeded from January to March 1977. Although the differences between the two localities does not seem that great for the Summer temperatures, in Deep Creek the mean water temperature never exceeded 20°C, whereas at Spring Creek 20°C was exceeded from January to March 1977. This higher temperature regime (by 3-4°C), allowed more rapid development throughout the year, especially during Summer, and therefore one more generation could complete its cycle within the year.

A further physical difference between the two localities was the flow regime. The stationary pools in Spring Creek exacerbated the higher temperatures when compared with the flowing Deep Creek. Algal and detrital build up in both localities was high, with *Cladophora* and diatom species dominating in Deep Creek in contrast to *Spirogyra,* colonial blue greens and diatoms dominant in Spring Creek. Food supply therefore was unlikely to be limiting in either locality during the summer months.

Analogous alteration of life cycle has been known since 1935 when Ide showed that a species could have different life cycles in different areas of the same stream. Ulfstrand (1968) noted locality differences in the life cycle of *Hexagenia* spp., and Macan (1970) stressed that a definite life cycle in any locality may differ at another locality if environmental conditions are different. More recently Flowers and Hilsenhoff (1978) recorded alteration of the number of generations in *Stenonema tripunctatum* (Banks), *Stenacron interpunctatum* (Say) and *Heptagenia hebe* McDunnough. In each species the life cycle was univoltine in cooler streams, and bivoltine in warmer streams. Newell and Minshall (1978) showed that the life cycle of *Tricorythodes minutus* Traver varied from a multivoltine cycle in one section of a stream (warm) to bivoltine in another cooler section of the same stream. Clifford (1970a) recorded a univoltine cycle in Alberta for *T. minutus*. Newell and Minshall (1978) considered that "the life cycle of *T. minutus* is unquestionably influenced by water temperature". With the observations made on *Tasmanocoenis tillyardi* and *Baetis soror* the influence of temperature in South Australia is also apparent. It is likely that a univoltine cycle may be possible at more southern localities e.g. in Northern Tasmania, for *T. tillyardi*.

IV.4.2 Life Cycle Classification and South Australian Mayflies.

The numerous life cycles utilised by ephemeropteran species have resulted in the production of classification systems (e.g. Macan, 1965; Landa, 1968; Sowa, 1975). Hynes (1961, 1970a) developed an annual classification based on non-, slow-, and fast- seasonal patterns. Both Hynes and Landa systems have received a wide acceptance with the latter scheme being commonly adopted for the Ephemeroptera.

Landa's (1968) classification was constructed using evidence from European mayfly life histories, and no attempt was made to include any other Order of the stream fauna. The classification was based primarily on the number of life cycles per year.

Group A : Univoltine species.

Group A1: "Winter species"; species in which the eggs hatch "about one month after oviposition" and the nymphs develop through the Autumn and Winter and emerge in Spring and/or Summer.

Group A2 : "Summer species; eggs oviposited in Autumn, enter and remain in diapause until Spring-Summer. The nymphs develop rapidly during the summer months and emerge in Summer.

Group A3 : Nymphs develop in Autumn and then cease growing in Winter, entering a diapause, until late Spring or Summer, after which they develop rapidly, emerging in late Summer.

Group B : Bivoltine species.

Group B1 : Eggs hatch in Autumn, develop over the winter period, emerge in the Spring and commence ovipositing. Eggs hatch soon after being laid and a further generation is completed during the summer months, to oviposit in Autumn.

Group B2 : Two generations in rapid succession in the summer months, with the winter cycle similar to that in A2.

Group B3 : Similar to B1, but with two summer generations effectively producing three generations per year.

Group B4 : A proportion of eggs hatch in Autumn, and give rise to one generation, and the remaining eggs over-winter before hatching in Spring. These newly hatched nymphs develop rapidly often parallel to the autumn hatchlings, and two emergence periods occur in Summer.

Group C : Semivoltine with one generation in two or more years.

Group C1 : Two year development.

Group C2 : Three year development.

Group D : Development cycle to year cycle relationship variable.

Group D1 : Three generations in two years.

Group D2 : Two generations in three years.

Landa's classification was accepted by Clifford, Robertson and Zelt (1973), Sukop (1973) and Sowa (1975), but the latter author redefined the life cycles of the Carpathian mayflies into three groups, the semivoltine, univoltine and polyvoltine cycles, each of which was subdivided. Sowa included ovoviviparous species in the latter group, species which were ineffectively accounted for by Landa's classification. Flowers and Hilsenhoff (1978) also modified Landa's scheme to include the uni- and bivoltine species recorded in Wisconsin. They observed, however, that life cycle classification may be valuable for many species, but certain species will fall into more than one category depending on environmental conditions. Landa (1968) in fact made a similar proviso in recognising that species need not be confined to any one of his groupings, and that they may alter position due to temperature changes at different latitudes and altitudes.

In all the classifications mentioned above only the Landa and Sowa schemes mention polyvoltine species, and in each case this refers to a three generation per year cycle. In South Australia all species studied, except *T. tillyardi* in Deep Creek, had polyvoltine life histories with at least three generations per year. *Baetis soror* in Spring Creek was the only species which exceeded this with four generations annually. On close examination, only the life cycle of *B. soror* in Deep Creek was covered by any of the classifications; resembling a B3 cycle in Landa's scheme.

Tasmanocoenis tillyardi in Deep Creek is bivoltine, but is distinct from the four group B life cycles defined by Landa. Both generations developed over the winter months, with one emerging in Spring and the other in Autumn. Eggs laid by each of these generations led to the two successive generations of the following year. Suter and Bishop (1980 : Appendix 12) showed how mesh size of collecting nets could lead to erroneous classification of the life cycle of this species. With only a coarse net (480µm) sampler, *T. tillyardi* appears to have a bivoltine life cycle with one winter generation and one summer generation, similar to a B1 cycle in Landa's scheme. With both fine (110µm) and coarse nets (480µm) Suter and Bishop suggested a modification of Landa's scheme was necessary; a B5 cycle of two "winter" generations per year. In Spring Creek the annual cycle of *T. tillyardi* had three generations per year, with one generation completing development in the summer period, and two generations developing over the winter months, one emerging in Spring, and the other in Summer. Both the polyvoltine classifications, Landa (1968) and Sowa (1975) account for one winter and two summer generations, but not the reverse.

The life cycle of *Atalonella inconspicua* in Spring Creek resembles that of *T. tillyardi* at this locality, with one summer generation and two winter generations. This cycle is also unlikely to be consistent throughout the geographical range of *A. inconspicua*. Casual observations in the cooler streams of the southern Fleurieu Peninsula showed that no adults emerged except during the Spring-early Autumn months (September-March). This suggested a decrease in the number of generations in cooler localities, similar to that recorded for *T. tillyardi*.

In Deep Creek the other leptophlebid studied, *Atalophlebia australasica*, also exhibited a polyvoltine life cycle with one summer and two winter generations. The flexibility of life cycle of this species throughout its geographical range is unknown, but in cooler regions the number of cycles may decrease.

As mentioned, the only species with a life cycle which could be categorised using Landa's scheme was *B. soror* in Deep Creek. This species had a two summer, one winter generation cycle, similar to a B3 cycle proposed by Landa. However, in Spring Creek this species bred almost continuously with possibly four generations, three developing in the summer months and one over Winter. A cycle of four generations per year has not previously been observed or classified.

Clearly the South Australian mayfly fauna do not conform with the classifications established for the Ephemeroptera in the Northern Hemisphere. Hynes and Hynes (1975) were unable to include many Australian stonefly species to the "fast" or "slow" life history categories devised for the aquatic insects of the Northern Hemisphere. The South Australian mayflies have a high number of cycles per year, but this may only reflect the warm-temperate environmental conditions under which development takes place. Although each species examined was somewhat opportunistic, there appeared to be definite seasonal cycles, since, in each case, at the end of the sampling period each generation completed an annual cycle with similar sized animals as those collected twelve months earlier. The cycles appear well synchronised with water temperature as the environmental cue. The emergence period of each winter generation was long and not confined to a short definitive period. Minshall (1967) suggested that a long emergence period was a response of species living in a mild climate, and Boerger and Clifford (1975) demonstrated the trend of increased emergence periods in warm temperate climates. However, the requirement for accurate control of emergence time, concentrated over a short period, as occurs in many species in the Northern Hemisphere (e.g. Macan, 1975b; Leonard and Leonard, 1962; Ulfstrand, 1968; Coleman and Hynes, 1970; Harper and Magnin, 1971; Thibault, 1971a; Clifford, Robertson and Zelt, 1973; Boerger and Clifford, 1975) may be unnecessary because of the long, protracted, warm summer conditions and the broad niche occupation of each species. The wide range of habitat type utilised may result in greater numbers of developing nymphs being present throughout the emergence period than in the Northern Hemisphere where distinct niches are occupied by different species. In South Australia, the species' number is reduced, but the number of mayflies occuring in streams is probably comparable to any other locality. Given a similar number of niches but fewer species, the problem of synchrony of emergence is somewhat reduced and overcome by high density and relatively long emergence periods. Newell and Minshall (1978) observed similar emergence strategies in *Tricorythodes minutus* noting "the problem of synchronization of emergence is overcome by high densities of nymphs emerging simultaneously over much of the year".

The flexibility of life cycle, as observed here and in various other studies, e.g. Ide (1935); Pleskot (1958, 1960); Petra (1961); Ulfstrand (1968); Macan (1970); Thibault (1970a, b); Flowers and Hilsenhoff (1978); Newell and Minshall (1978), has been suggested as an important requirement for a widely distributed species (Zahar, 1951; Newell and Minshall, 1978). *T. tillyardi* fits into this category. The flexibility of its life cycle has enabled *T. tillyardi* to occupy streams and lake habitats from cool temperate northern Tasmania (Tillyard, 1935) to tropical localities in northern Queensland and northern Western Australia (Chapter 6). The distribution of *B. soror*, although inadequately known because of the limited taxonomic studies on the Baetidae in Australia, also appears relatively wide.

With the life cycles of only four species determined it would be premature and speculative to develop a life cycle classification based on the South Australian material, particularly as the great flexibility of the species in their life cycle expression tends to question the value of classification schemes. The influence of environmental conditions, latitude and altitude, is such that any one species may have different life cycles in two successive years. A classification scheme tends to erect a rigid framework, a rigidity which clearly is not justified. The value of any life cycle classification scheme is therefore questionable, especially if it does not provide for a number of variable categories. However, since such schemes have been erected to simplify comparisons of life cycles of different species it is important to note that they are inadequate, in their present form, to categorise the South Australian mayflies, and probably the Australian mayfly fauna as a whole. Hynes and Hynes (1975) also found that Northern Hemisphere classifications were inadequate for the Australian stonefly fauna. They suggested that the flexibility of life cycles of the Australian Plecoptera was a response by the fauna to the Australian climate (famed for its savage droughts and general uncertainty". Hynes and Hynes also considered that this flexibility of life cycle had "probably reduced the total number of niches available on the continent". It is unlikely that the real number of niches has been reduced but perhaps flexibility of life cycle and broad ecological tolerance have enabled each species to occupy a range of the available niches, which in the Northern Hemisphere would be occupied by many species; one per niche. This strategy appears to have been adopted by the South Australian mayflies, and may apply in the wider context of other components of the Australian freshwater fauna. This would require many more observations before the life cycle strategy of the Australian freshwater fauna can be understood.

CHAPTER 5.

Post Oviposition Development of Eggs

V.1 Introduction.

During the study of life cycles of some South Australian mayflies the seasonal occurrence of first instar nymphs suggested at least two distinct egg development relationships. First instar nymphs of *Atalophlebia australasica* and *Tasmanocoenis tillyardi* were never recorded during the cool winter months but were found in early Spring, before any emergence of adults had taken place. In contrast, first instar nymphs of *Baetis soror* were recorded in the winter months, and an emergence period preceded each recruitment period.

The differences observed in the presence of the first instar nymphs of *A. australasica* and *T. tillyardi* could be accounted for by two alternatives :

1) that the nymphs may have lived for several months without growing, but were inadequately collected; or

2) they remained as eggs, unhatched, over the winter months.

The sampling technique effectively collected first instar nymphs during the Spring, Summer, and Autumn, and for *B. soror*, first instar nymphs were recorded throughout the year, suggesting that the absence of observations was not an artifact of the sampling technique, unless the early instars of

T. tillyardi and *A. australasica* entered the hyporheos immediately after hatching, (in which case they would not have been collected), remaining there until Spring.

Illies in 1959 observed *Baetis* eggs remaining unhatched over Winter and Elliott (1972), Benech (1972) and Elliott (1978) have since shown close correlation between egg development time and water temperature in *Baetis rhodani* Pictet and *Ephemerella ignita* (Poda). Similar temperature dependence was observed in eggs of *Hexagenia rigida* McDunnough, by Friesen, Flannagan, and Lawrence (1979) and in *Baetis alpinus* (Pict.) by Humpesch (1979). Bohle (1972) concluded that an obligatory diapause occurred in the tenth stage of the embryo of *Ephemerella ignita*, below 13.3°C, but Elliott (1978) found no evidence of this. A further study by Tsui and Peters (1974) on *Tortopus incertus* (Traver) indicated that hatching in this species did not occur at low temperatures, and development was blocked at 13.65°C. Flannagan (1979) suggested that eggs of *Hexagenia limbata* and *H. rigida* may overwinter and not hatch until the following Summer, and Friesen *et.al* (1979) working with eggs of *H. rigida* found the lower threshold of hatching to be between 8°C and 12°C. Eggs stored at 8°C hatched after the incubation temperature was stepwise elevated, although percentage success was reduced.

Delayed hatching and/or migration into the hyporheos could lead to errors in the interpretation of life histories, growth rates, and production estimates. Therefore a series of egg development experiments at constant temperature, as suggested by Andrewartha and Birch (1954), were designed to determine if the observed phenomena could be explained by delayed hatching.

Other environmental parameters, other than temperature, were also considered in the developmental experiments. Elliott (1978) suggested that the differences between his developmental data and those presented by Bohle (1972) for *Ephemerella ignita* might be explained by photo-period differences. In the present study eggs at different temperatures were allowed to develop in total darkness and in normal summer photo-period of long day : short night (16 hours : 8 hours). Williams (1968) noted that mayflies have never been recorded in any Australian lakes that were even slightly saline. Because saline waters dominate the athalassic water bodies of South Australia the effect of salinity on egg development was also tested. Eggs were also tested for resistance to drying.

V.2 Materials and Methods.

Eggs artificially inseminated with crushed male reproductive tissue (Pescador and Peters, 1974), failed to fertilize any of the eggs stripped from female imagos reared in the laboratory, therefore eggs which had been fertilized naturally had to be obtained. All species examined, *Baetis soror, Atalonella fuscula, A. inconspicua* and *Atalophlebia australis* oviposited by dipping the abdomen in slow flowing reaches of streams or in stationary pools or lakes. The eggs, once liberated, sank individually towards the bottom, and therefore no convenient egg mass could be collected from the substrate (c.f. *Baetis* *rhodani* Elliott, 1972, and Benech, 1972). Females in the process of ovipositing were collected and allowed to continue laying into a clear plastic vial of stream water. This technique of collection was not reliable, but it was the only successful method available. The vials of collected eggs were maintained at or near stream temperature and were immediately returned to the laboratory.

A series of 5cm diameter plastic petri dishes containing stream water 4-5mm deep were prepared and approximately 100 eggs were transferred to each dish. The petri dishes were then placed under different experimental conditions.

(i) In constant temperature cabinets at 24°C, 22 or 20°C, 19 or 18°C, 14°C, 12.5°C and 11°C. A further series of 9°C, 5°C and 4°C were added for *Atalonella fuscula* and *Baetis soror*.

(ii) Under dark conditions at 24°C, 20°C and 18 or 19°C constant temperature.

(iii) In saline waters prepared from natural saline streams, diluted with fresh stream water to salinities of 3.75, 4.6, 5.1, 5.8, 7.7, and 8.9 parts per thousand, maintained at 19°C.

In all experiments at temperatures below 24°C the temperature variation was ± 1°C, but at 24°C the range was ± 2°C.

Experiments (i) and (ii) were performed for all species, but (iii) was performed only on eggs of *Atalonella fuscula* because more eggs of this species were collected. In all experiments replicates of 2-3 petri were used.

The petri dishes were examined daily and development recorded. After eyes became apparent, the dishes were examined every three to four hours, and when hatching commenced the nymphs were counted and removed from the petri dish using a fine pipette. The volume of water in all experimental dishes was maintained every 3-4 days, or as required. When hatching ceased, the petri dishes were maintained and examined daily for a further 21 days, and the number of undeveloped eggs and dead embryos then counted.

V.3 Results.

The incubation period, percentage egg hatch and duration of eclosion for each species are shown in Table V.1. Two incubation periods were determined; a minimum time, taken as the number of days from oviposition to the initial egg hatch, determined by regular observation, and a mean time, as the number of days from oviposition to the day on which 50% of the eggs ultimately hatching successfully had hatched. Both values were used in the calculation of subsequent regressions. The mean value is probably more relevant to the population especially if used as a predictive tool as it overcomes the extreme cases of early and late hatchings that occur under normal circumstances, but comparisons between the minimum and mean values were considered valuable.

In the following discussion each species is considered individually, but the data presentation is consistent throughout, and is therefore discussed separately.

TABLE V.1. Incubation temperature, number of eggs, minimum incubation period (until first egg hatched), mean incubation period (50%), total duration of hatching and hatching success for eggs of four South Australian mayflies.

Species	Temperature (°C)	No. of Eggs	Minimum incubation period (d)	Mean incubation period (d)	Total duration of hatch (d)	Hatch success (%)
Atalophlebia australis	24	25	9.0	12.5	3.5	56.0
	19	68	13.0	14.7	1.7	79.4
	12	25	?	?	?	?
	15*	25	8*	?	-	16.0
Atalonella inconspicua	24	53	10.0	10.3	1.8	79.3
	22	262	13.0	14.1	3.8	82.8
	20	24	15.0	17.2	4.3	83.3
	20	50	15.0	16.8	5.8	82.0
	18	115	16.3	17.0	4.6	87.0
	18	29	18.2	19.7	5.9	69.0
	15	63	-	-	-	-
	12	26	-	-	-	-
	11	23	-	-	-	-
Atalonella fuscula	24	74	13.9	14.3	5.0	93.2
	19	65	17.9	20.0	5.0	76.9
	19	86	17.9	20.3	5.0	72.1
	14	55	30.9	35.5	5.0	52.7
	14	118	30.9	36.9	7.0	52.5
	12.5	54	34.9	36.0	5.1	88.9
	12.5	68	35.2	36.2	4.1	92.7
	12.5	90	35.9	37.5	4.7	67.8
	9	82	71.9	73.0	14.0	69.5
	9	85	71.9	73.2	7.7	72.9
	9	93	72.0	74.4	6.0	55.9
	4	111	-	-	-	-
	4	78	-	-	-	-
	4	63	-	-	-	-
Baetis soror	24	86	7.8	8.4	3.0	87.2
	19	20	10.9	11.6	4.0	90.0
	19	10	10.9	11.9	2.0	50.0
	14	12	21.9	22.5	2.0	91.7
	14	12	21.9	22.5	2.0	66.7
	12.5	24	26.0	26.7	1.9	87.5
	12.5	22	26.0	27.7	1.9	68.2
	9	50	62.1	-	18.8	34.0
	4	16	-	-	-	-

---

* Eggs incubated at 12°C for 120 days were transferred to 15°C. Hatching occurred after eight days at the new temperature.

The number of eggs that hatched and the total hatching success was variable with temperature, and therefore counts of newly hatched nymphs were expressed as cumulative percentages of the total number of eggs that hatched at each temperature. These data were plotted against time and the resulting sigmoid curves allowed determination of the mean incubation period for each temperature. The relationship between the incubation period and water temperature was linear on a logarithmic scale, and is given by the regression equation

$$\log Y = \log a - b \log T$$

or $$Y = a T^{-b}$$

where Y = incubation period (days) and T = temperature (°C) and a = a constant.

The relationship between the rate of development (V) (V = the reciprocal of the duration of the hatching) and temperature is also given by a linear equation

$$V = bT + a$$

When this is the case, the regression line may be extrapolated to determine the temperature at which $V = 0$, where theoretically no development occurs, i.e. the "threshold temperature" (Andrewartha and Birch, 1954). Andrewartha and Birch (1954) and Elliott (1978) both emphasized that this threshold temperature may not be a biological threshold, as development may continue below this temperature.

If the regression lines represent the relationship between hatching time and temperature the number of degree days required by the eggs to hatch can be calculated using the equation

$$D = d\ (T - t)$$

where D = total number of days required for hatching,

d = days after oviposition, T = incubation temperature and

t = threhold temperature.

Atalophlebia australis

Part of the total egg compliment from one *A. australis* female imago was obtained and eggs were allowed to develop at 24°C, 19°C and 12°C.

Eggs hatched at the higher temperatures, none at 12°C. The duration of hatch curves for *A. australis* are shown in Fig. V.1a. With only two values determined, no regressions were calculated and consequently a threshold value could not be determined.

After four months at 12°C the eggs were transfered to 15°C, where hatching commenced within eight days, and continued for three days. A reduced rate of hatching success was observed, with only 24% of the eggs hatching at the elevated temperature. The requirement of only eight elapsed days to hatch at 15°C compared with ten days at 25°C and 13 days at 19°C suggests that much of the embryonic development had occurred at 12°C. The three ocelli of the developing nymph could be clearly seen in the egg after 18 days, but no further development was apparent at 12°C. On dissection of some eggs, the embryos were found to have differentiated cephalic, thoracic and abdominal regions, and the thoracic appendages were distinguishable. Wigglesworth (1972) defined this type of arrested development i.e. "controlled directly by external conditions and brought to an end when the temperature or water relations are favourable again", as quiescence, and eggs which "undergo an arrest of development which may persist even though environmental conditions are favourable" as diapause. These definitions have been accepted throughout the study.

Eggs of *A. australis* are considered to enter a period of quiescence when water temperatures fall below a temperature between 12°C and 15°C. More accurate determination of the quiescent initiating temperature was not possible as no further fertilised eggs of this species were obtained.

Unfortunately no eggs of *A. australasica* were obtained for comparison.

Atalonella inconspicua

A greater number of experimental temperatures ranging from 11°C to 24°C were included for eggs of *A. inconspicua*, but once again no hatching occurred at the lower temperatures.

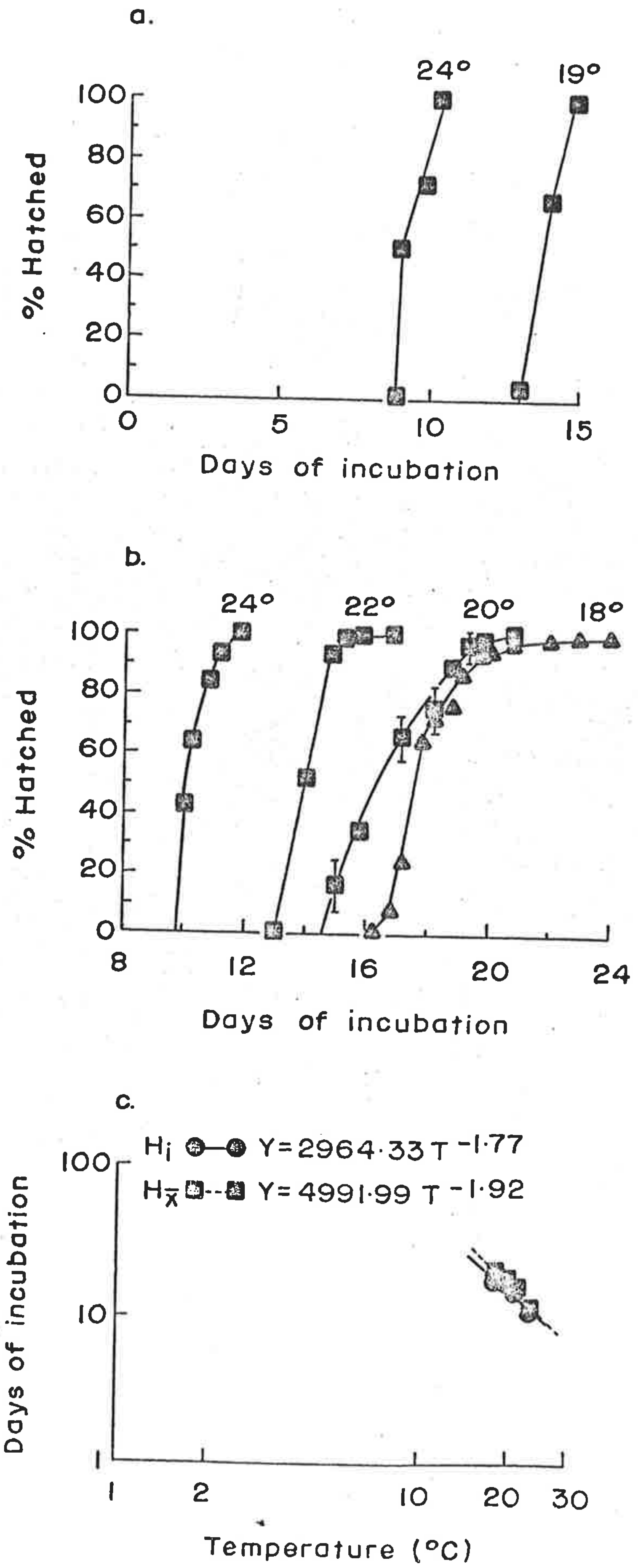
The duration of hatch curves, from which the mean incubation period was determined, are shown in Fig. V.1b. The length of the minimum incubation period varied between 10.0d. and 18.2d and was linearly related to water temperature on a logarithmic plot (Fig. V.1c). The regression constants are tabulated in Table V.2.

Fig. V.1. Egg development of *Atalophlebia australis* (a) and *Atalonella inconspicua* (b, c).

a, duration of incubation of eggs of *Atalophlebia australis* at 19 and 24°C.

b, duration of incubation of eggs of *Atalonella inconspicua* at 18, 20, 22 and 24°C.

c, relationship between the time required for hatching (days of incubation) and water temperature (°C) for initial hatch (Hi) and mean hatch ($H\bar{x}$).


a.
24°
19°
100
80
60
40
20
0
% Hatched
0
5
10
15
Days of incubation
b.
24°
22°
20°
18°
100
80
60
40
20
0
% Hatched
8
12
16
20
24
Days of incubation
c.
H_i ●—● $Y = 2964{\cdot}33\,T^{-1{\cdot}77}$
$H_{\bar{x}}$ ■--■ $Y = 4991{\cdot}99\,T^{-1{\cdot}92}$
100
10
1
Days of incubation
1
2
10
20
30
Temperature (°C)

The duration of the initial and mean incubation periods were correlated with temperature and a linear relationship was found when the rate of development (V) was plotted against temperature (T). The values of these regrssions for the minimum and mean incubation periods are given in Table V.3.

An iterative process was used to calculate the value of the threshold temperature from the regression equation. The threshold temperatures of the minimum and mean incubation period were 9.34°C and 10.63°C respectively. The values of the mean number of degree-days, with 95% confidence limits are 155 (145-165) degree - days above 9.34°C (± 0.0018°C) for the first hatching and 148 (136-158) degree-days above 10.63°C (± 0.0026°C) for 50% hatch. Clearly this cannot be a realistic situation with the mean number of hatchings occurring before the initial hatch. However, the values are really only applicable for development above 15°C. The threshold temperatures calculated above bear little resemblance to the observed hatching data obtained, because no hatching occurred below 15°C. The eggs were observed to stop developing at a similar stage to that observed for *Atalophlebia australis* and a similar development mechanism is suggested for both these species.

Eggs maintained at 20°C and 18°C, and in total darkness, hatched at the same time as those in the normal summer photoperiod, suggesting that light and/or photoperiod were of minor importance in determining the incubation period of *Atalonella inconspicua*.

TABLE V.2. The relationship between length of incubation period (Y) and incubation temperature (T) for initial (H_1) and mean egg hatch ($H_{\bar{x}}$), where $Y = aT^{-b}$.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Species		a	b	r^2	95% confidence limits of b	Probability.
Atalonella inconspicua	H_1	2964.33	1.77	0.93	0.47	**
	$H_{\bar{x}}$	4991.99	1.92	0.89	0.67	**
Atalonella fuscula	H_1	3136.66	1.75	0.99	0.14	**
	$H_{\bar{x}}$	2835.92	1.69	0.99	0.12	**
Baetis soror	H_1	5904.09	2.12	0.99	0.20	***
	$H_{\bar{x}}$	5485.61	2.08	0.99	0.24	***

TABLE V.3. The relationship between rate of development (V) and temperature (T) for initial (H_1) and mean egg hatch ($H_{\bar{x}}$), where $V = bT + a$.

* $p \leqslant 0.05$; ** $p \leqslant 0.01$; *** $p \leqslant 0.001$.

Species		b	a	r^2	95% confidence limits of b	Probability.
Atalonella inconspicua	H_1	0.0065	-0.061	0.93	±0.0018	**
	$H_{\bar{x}}$	0.0069	-0.073	0.88	±0.0026	**
Atalonella fuscula	H_1	0.0040	-0.022	0.99	±0.0002	**
	$H_{\bar{x}}$	0.0037	-0.020	0.99	±0.0002	**
Baetis soror	H_1	0.0078	-0.059	0.99	±0.0006	***
	$H_{\bar{x}}$	0.0072	-0.052	0.99	±0.0005	***

Atalonella fuscula.

In contrast to the previous species, eggs of *A. fuscula* were observed to develop and hatch at temperatures from 9°C to 24°C. Eggs at 5°C did not hatch.

The duration of hatch curves are shown in Fig. V.2a. The minimum incubation period varied from 13.9d to 72.0d depending on the water temperature. The relationship of incubation time to temperature was linear on logarithmic plot (Figs. V.2b, c) and the regressions for the minimum and mean incubation periods were highly significant (Table V.2).

The relationship of rate of development (V) and temperature was linear, and the regressions for both initial and mean hatch were also highly significant (Table V.3).

Using an iterative process with each regression the threshold temperature for *A. fuscula* was determined, being 5.40°C (± 0.0002°C) and 5.38°C (±0.0002°C) for the initial and mean hatch respectively. The values of the mean number of degree-days with 95% confidence limits were 255 (245-265) degree-days above 5.40°C for the initial hatch, and 267 (257-277) degree-days above 5.38°C for 50% hatch.

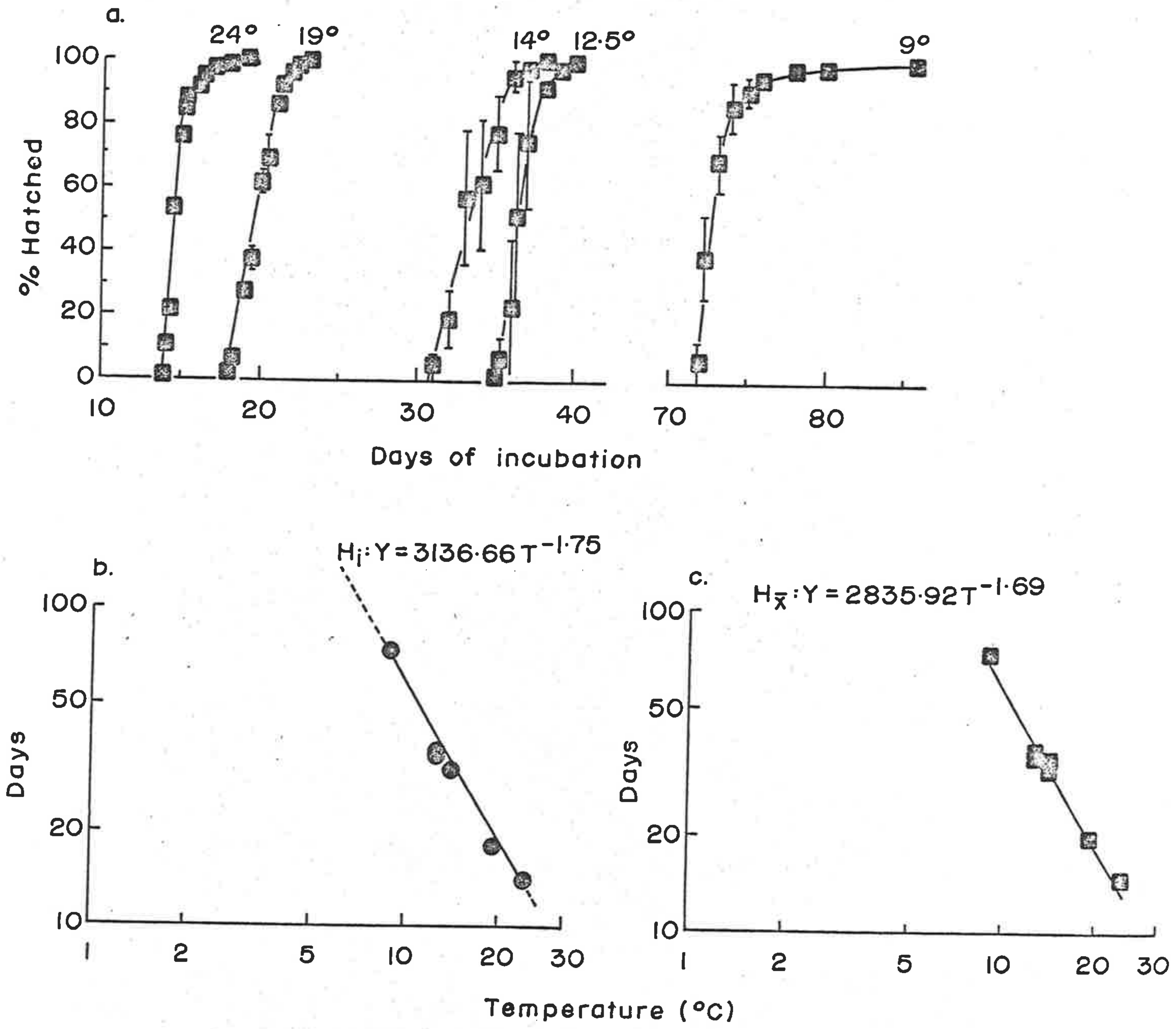
The calculated degree-day values at each temperature were very similar for each of the initial and mean incubation periods of the eggs of *A. fuscula*, and therefore they may be useful in predicting the hatching times of field populations. The adequacy of these values was not tested for the type of fluctuating temperature regime experienced in streams. However, a

Fig. V.2. Egg development of *Atalonella fuscula*.

a, duration of incubation of eggs at 9, 12.5, 14, 19 and 24°C.

b, relationship between the time required for hatching (days of incubation) and water temperature (°C) for initial hatch (Hi).

c, relationship between the time required for hatching (days of incubation) and water temperature (°C) for mean hatch ($H\bar{x}$).


a.
24°
19°
14°
12·5°
9°
100
80
60
40
20
0
% Hatched
10
20
30
40
70
80
Days of incubation
b.
$H_i : Y = 3136{\cdot}66\,T^{-1{\cdot}75}$
100
50
20
10
Days
1
2
5
10
20
30
c.
$H_{\bar{x}} : Y = 2835{\cdot}92\,T^{-1{\cdot}69}$
100
50
20
10
Days
1
2
5
10
20
30
Temperature (°C)

different mechanism of development to that observed in *Atalophlebia australis* and *Atalonella inconspicua* is indicated.

The extrapolated threshold value of approximately 5.4°C was not a biological zero temperature because development did occur in eggs maintained at 5°C. The ocelli of the developing nymphs were visible after five months at the experimental temperature, but no hatching was observed. The calculated threshold temperature may therefore be close to the minimum hatching temperature rather than the temperature of zero development. Eggs were initially placed in a 6°C constant temperature room, but a misadventure occurred and all the eggs were frozen. On thawing, and raising the incubation temperature gradually to 18°C, no hatching occurred, suggesting that eggs may not survive being frozen. It is noted that freezing is not a likely natural stress on eggs of this species in South Australia.

Eggs maintained at 24°C and 19°C and in total darkness hatched at the same time as those in the normal summer photoperiod, suggesting that light and/or photoperiod were not important in the determination of the incubation period of *A. fuscula*.

The effect of salinity on hatching of eggs of *A. fuscula* was also tested. One hundred and twenty eggs were placed in natural saline water diluted to K_{18} values between 3.19 and 7.51 mS. Twenty eggs were placed in each of six experimental concentrations and were incubated at 19°C. The results of this experiment are shown in Table V.4.

No eggs hatched at the higher salinities, and there appeared to be a decrease in the hatching success with increasing salinity. However the numbers were small and because of paucity of egg material no replicates could be performed. Therefore definite conclusions about hatch success cannot be drawn.

Drying of *A. fuscula* eggs was also performed at 24°C to determine if eggs were capable of surviving in temporary streams in resistant egg stages. Williams (1968) suggested mayflies were able to survive in the temporary stream habitat because their eggs diapause, and Williams and Hynes (1976a, 1977) postulated the presence of resistant eggs. Two batches of 48 and 60 eggs were allowed to dry at 24°C. Drying was gradual, and took eight days, a process similar to drying pools in temporary stream beds. Some eggs were observed to collapse, but many maintained their shape. After 28d at 24°C the dry eggs were re-wetted with fresh water (K_{18} = 311μS) and subsequently observed daily for a further 28 days. No eggs hatched, and no development took place. It was concluded that eggs of *A. fuscula* were unable to survive periods of drying.

Baetis soror.

The eggs of *B. soror* also hatched at temperatures between 9°C and 24°C, with minimum incubation periods ranging from 7.8d to 62.1d respectively. At 5°C no hatching occurred.

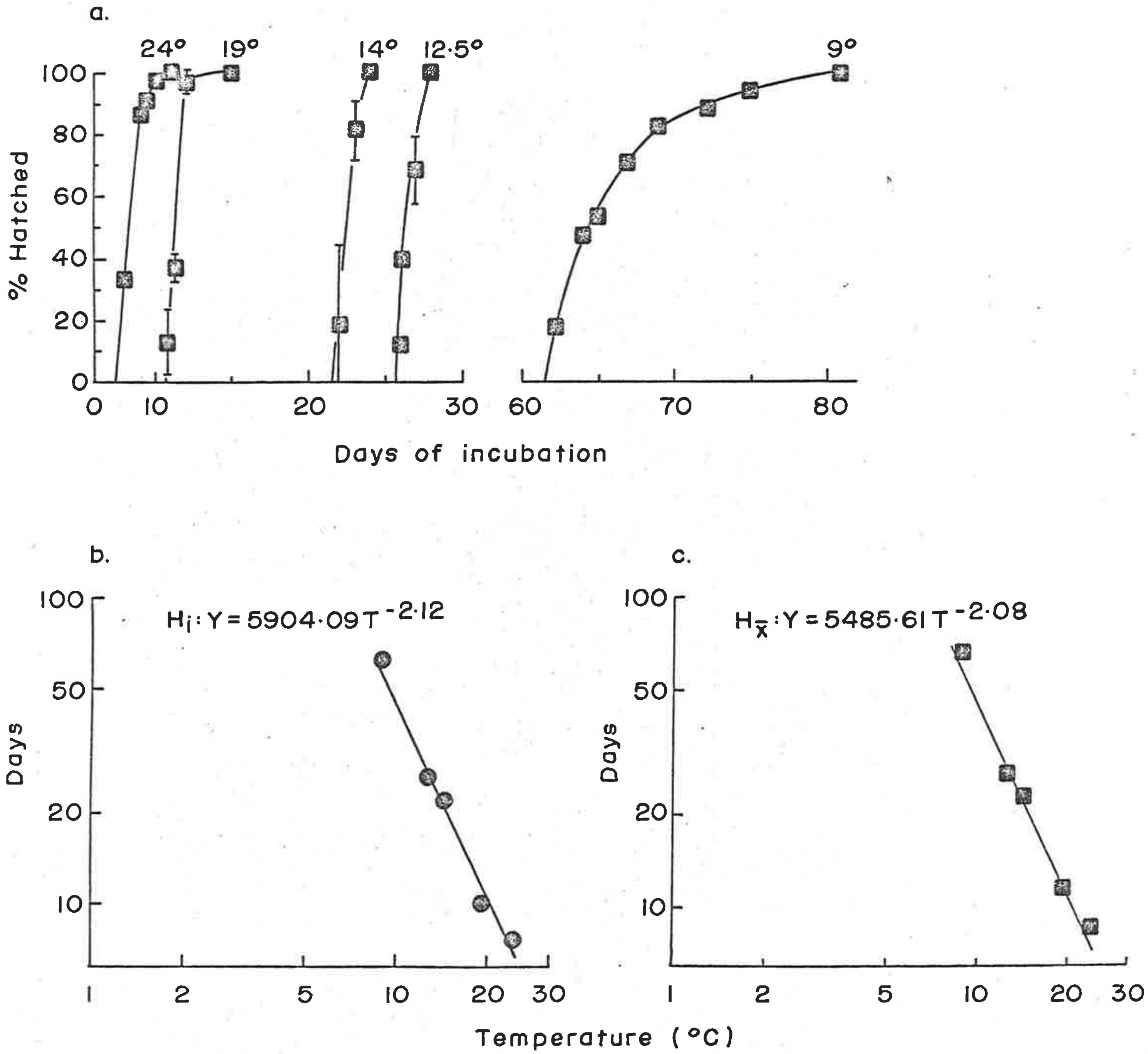
The curves for duration of egg hatch are shown in Fig.V.3a. The relationship between incubation period and temperature was linear on logarithmic plot, (Figs.V.3b, c) and the regressions for the minimum and mean incubation periods are given in Table V.2.

Fig. V.3. Egg development of *Baetis soror*.

a, duration of incubation of eggs at 9, 12.5, 14, 19 and 24°C.

b, relationship between the time required for hatching (days of incubation) and water temperature (°C) for initial hatch (Hi).

c, relationship between the time required for hatching (days of incubation) and water temperature (°C) for mean hatch ($H\bar{x}$).


a.
24°
19°
14°
12·5°
9°
% Hatched
100
80
60
40
20
0
0
10
20
30
60
70
80
Days of incubation
b.
$H_i : Y = 5904{\cdot}09T^{-2{\cdot}12}$
Days
100
50
20
10
1
2
5
10
20
30
c.
$H_{\bar{x}} : Y = 5485{\cdot}61T^{-2{\cdot}08}$
Days
100
50
20
10
1
2
5
10
20
30
Temperature (°C)

The linear regressions of development rate versus temperature were both highly significant and regression values are given in Table V.3.

The threshold temperatures were calculated using an iterative process and were 7.55°C (± 0.0006°C) and 7.25°C (± 0.0005°C) for the initial and mean hatched respectively. Using these values the number of degree-days required for initial and mean hatching with 95% confidence limits were calculated, 126 (118-134) degree-days above 7.55°C and 137 (129-145) degree-days above 7.25°C respectively.

As for *Atalonella fuscula*, the calculated number of degree-days required for egg development and hatching shows good correspondence for all the experimental water temperatures used. This agreement with the concept of thermal summation and degree-days may enable prediction of egg hatches from field observation of adult emergence periods, if mating and oviposition occur immediately.

Development was not tested under fluctuating temperature regimes, and therefore the applicability of the above data to field conditions is still unknown. An attempt was made, however, to assess these mean hatching data by using the observed field emergence times and calculating the date at which the first instar nymphs should have been collected. The date at which collections of adults were first made was taken as the zero time for each emergence period and it was assumed that eggs were oviposited on that date. Mean temperatures were obtained by taking the average of maximum and minimum temperatures recorded between collecting dates. The area under the temperature curve was used to calculate the number of degree-days experienced between collecting dates, and therefore estimates of the earliest date at which hatching should occur were obtained. Although this technique is crude, close correspondence with the predicted and observed dates was obtained.

For eggs laid on 8 October 1976, initial and mean hatching should have occurred by 10 November 1976. Similarly, for eggs laid on 6 January 1977 hatching should have occurred by 20 January 1977; for eggs laid 1 June 1977 hatching should have been evident by 31 August 1977 and for eggs laid on 21 August 1977 hatching should have been evident by 12 October 1977. From the derived life cycle graphs of *B. soror* (Chapter 4) there is some agreement to these calculated dates, if the presence of second or third instar nymphs is considered evidence of hatching. The 31 August 1977 sample did not include early instar nymphs, and in fact they were not recorded until 24 September 1977. This suggests that development under fluctuating stream temperatures may not be as simple a relationship as indicated under constant conditions. Alternatively early instar *B. soror* may enter hyporheos during cooler, high discharge periods. Twenty-six eggs of *B. soror* were allowed to dry as described for *A. fuscula*, at 24°C. The results were similar to those observed for *A. fuscula*, with no eggs hatching after drying and no microscopic evidence of any development. Thus *B. soror* would appear unable to survive in temporary streams as dry, resistant eggs.

V.4 Discussion

Detailed studies of egg development of mayflies have been performed by Bohle (1969), Elliott (1972) and Benech (1972) on *Baetis rhodani* Pictet; Bohle (1972) and Elliott (1978) on *Ephemerella ignita* (Poda), Friesen *et al* (1979) on *Hexagenia rigida* McDunnough and Humpesch (1979) on *B. alpinus* (Pictet). In *B. rhodani* the incubation periods were shown to be correlated with incubation temperature; all three studies (Bohle, Elliott and Benech) found similar results. Elliott (1972) concluded that the agreement between his and Bohle's (1969) results suggested that "the regression equations calculated from the results of all experiments are applicable to a population of *Baetis rhodani*, and both the start and length of the hatching period can be estimated for all water temperatures between 3°C and 22°C." The results obtained by Benech (1972) strongly supported this conclusion. Humpesch (1979) recorded that embryonic development of *B. alpinus* was dependent on water temperature and was continuous, without any delay in hatching, between 4±0.5°C and 15±0.5°C.

Similar continuous development over a range of temperatures was observed for *B. soror* and *Atalonella fuscula*, but the threshold temperatures for these two Australian species were higher than for *B. rhodani* and *B. alpinus*; 5.4 (5.38)°C and 7.55 (7.25)°C respectively. Incubation periods above these threshold temperatures were linearly related to temperature when plotted logarithmically, while rates of development were directly related to temperature. Flattum (1963) and Friesen et al. (1979) recorded no hatching of *H. rigida* eggs at 8°C and it was suggested that this was near the threshold temperature. Above 8°C egg hatching of *H. rigida* was directly related to temperature. Brittain (1977) recorded similar temperature dependence for egg hatching in the stonefly *Taeniopteryx nebulosa* (L).

Elliott (1978) recorded comparable linear relationships with *Ephemerella ignita* at temperatures between 5.9°C and 14.2°C. At higher temperatures, above 15°C, he found the incubation periods lengthened, being linearly related to temperature, in direct contrast to the hyperbolic relationship at lower temperatures. These results differ from those obtained by Bohle (1972) in which an obligatory diapause at temperatures below 13.3°C was indicated. The hatching times determined by Bohle therefore differed greatly from those recorded in Elliott's study. Elliott suggested that differences between the two studies could be explained by different development mechanisms occurring within a single species, with some populations entering an obligatory diapause, and others not. He also suggested that photoperiod differences may have accounted for the different results.

A third development mechanism for ephemeropteran eggs was suggested by Tsui and Peters (1974) from eggs of *Tortopus incertus* (Travers); a non obligatory temperature controlled quiescence or dormancy. This pattern of development was evident for *Atalophlebia australis* and *Atalonella inconspicua*. The observed enforced quiescence in these species supports the conclusion that the first instar nymphs collected during the life history studyin early Spring, before a period of emergence, came from eggs which were oviposited during the previous Autumn and remained quiescent until temperatures increased, allowing development to be completed. Because eggs incubated in dark conditions hatched at similar times to those incubated under normal light regimes, photoperiod changes are of little importance in determining the incubation period. Bohle (1972) assumed no photoperiodic effect, and Brittain (1977) with *Taniopteryx* found similar results to those obtained in the present study.

The three types of egg development,

(i) the direct relationship between temperature and incubation period (Bohle, 1969; Elliott, 1972; Elliott, 1978 in part; Benech, 1972; Brittain, 1977; Flattum, 1963; Friesen *et al*, 1979; Humpesch, 1979; and the present study);

(ii) development with an obligatory diapause (Bohle, 1969); and

(iii) a direct relationship between temperature and incubation period with a temperature enforced quiescence (Tsui and Peters, 1974; and the present study);

allow different mechanisms of regulation of life cycle in the egg stage. The direct relationship is the least effective of the three. The obligate diapause and developmental quiescence strategies of egg development allow the animal to persist in the egg stage during periods of unfavourable environmental conditions (i.e. low stream temperatures, high stream flow, low algal biomass, reduced organic detrital material) and synchronises hatching when the conditions become favourable. This facilitates re-colonisation during conditions conducive to survival of the nymph. Hatching from the obligate diapause stage is a more complex mechanism than from simple quiescence, requiring very specific conditions to break the diapause. This strategy therefore synchronises the hatching of eggs more precisely than the quiescent mechanism.

In South Australia both direct development and quiescent development occurred, but an obligatory diapause was not observed. Danileoskii (translated by Johnston and Waloff, 1965) suggested that diapause was usually associated with species occupying severe climates, especially cold climates, conditions foreign to the South Australian environment. The two *Atalonella* species, *A. inconspicua* and *A. fuscula,* exhibited both forms of development, with quiescence occurring in *A. inconspicua* at temperatures between 15°C and 18°C. *Atalophlebia australis* also had a quiescence at temperatures below 15°C.

The technique of measuring rates of development under constant conditions in the laboratory inevitably imposes reservations on any extrapolation back to field conditions. Sweeney and Schnack (1977) and Sweeney (1978) considered the development of eggs of the corixid *Sigara alternata* (Say) and the mayfly *Isonychia bicolor* (Walker) in a fluctuating experimental regime. In both studies development rate was positively correlated with "increased magnitude of the diel temperature pulse" and for *Sigara* they found that the relationship between "degree-hours and temperature does not support the rule of 'sum of degree-hours'". They concluded that "thermal summation" should be abandoned because "the relationship between developmental rate and temperature is not linear". With *Isonychia,* Sweeney (1978) suggested that "fluctuating regimes are best characterised for egg hatching by a thermal value lying between average and maximum diel temperature and more closely aligned with the latter."

In both the above studies no constant temperature experiments were performed, so the development types of *Sigara* and *Isonychia* were not determined. The conclusions drawn for *Sigara* by Sweeney and Schnack (1977) may be valid if the development of *Sigara* eggs was continuous over the range of the diel fluctuations, but if not, and a quiescence occurred at lower temperatures, then the fluctuating regimes may be introducing a considerable error in the degree-hours calculated. Sweeney and Schnack observed an inverse relationship between development time and accumulated degree-hours with thermal increments above 15°C. This suggests that development may be retarded at temperatures below 15°C and introduces error into their degree-hour calculation.

Because of the problems inherent in either technique of recording egg development, where possible both should be used. The rates at constant temperature should be determined first and once these have been established, studies in fluctuating temperature regimes would be useful to determine their validity in the field situation.

Hynes and Hynes (1975) working with eggs of Australian stoneflies used an alternative method, involving temperature conditions ranging from 10°C in Winter to 16°C in Summer. Their temperature conditions were adjusted fortnightly to allow a "smooth seasonal transition". Many species hatched at all temperatures, suggesting a direct relationship between temperature and incubation period, while other species remained dormant for long periods without change. It appears that the Plecoptera, like the mayflies, have different egg development mechanisms determining life cycle regulation. Hynes and Hynes stressed that no attempts were made to discover the seasonal control of the incubation period, but suggested that this would be an interesting field of study.

In the present study day length or light appeared to be of minor importance in regulation of the life cycle, with water temperature explaining the duration of incubation for all species.

Also considered was the effect of drying. Williams (1968) discussed the existence of mayflies in temporary streams in Australia, and stated that the eggs of these had a diapause. Williams and Hynes (1977) claimed that the Ephemeroptera survived in temporary stream habitats with resistant eggs, but presented no direct evidence to support this. Since temporary streams dominate the lotic habitats in South Australia, the mechanism or survival during the summer months is of prime importance. Edmunds, Nielsen and Larsen (1956) noted that desiccated eggs of *Ephoron album* (Say) from a temporary canal system did not remain viable, and concluded that early instars of *Epheron* appearing in the canal after flooding could not be explained by a hatching of dried eggs. Non-viability of dried eggs of *B. soror* and *A. fuscula* was observed in this study. Unfortunately eggs of all South Australian species could not be collected to allow a complete assessment of the effects of desiccation. However, resistant eggs of the Ephemeroptera still remain to be recorded, and available evidence suggests that survival in temporary habitats is not by resistant eggs, but by alternative mechanisms.

V.5 Summary

The egg development of ephemeropteran eggs can be explained by three mechanisms, all related to the water temperature experienced during incubation.

1) Direct development, in which the incubation period is related to water temperature above a threshold temperature, or a temperature at which no development or hatching occurs. This type of development has been recorded in *Baetis rhodani* (Bohle, 1969; Elliott, 1972; and Benech, 1972), *B. alpinus* (Humpesch, 1979), *Hexagenia rigida* (Friesen *et al*, 1979), *Ephemerella ignita* (Elliott, 1978) and in *Atalonella fuscula* and *Baetis soror* from South Australia. Brittain (1977) recorded this mechanism in the Plecoptera, and the observations of Hynes and Hynes (1975) from Australian Plecoptera are also consistent with this development type.

2) Development includes an obligatory diapause which persists until conditions required to break the diapause are experienced, as recorded by Bohle (1972) in *Ephemerella ignita*. No evidence of an obligatory diapause was recorded in the South Australian species.

3) Direct development above a certain temperature, below which a quiescence or dormancy is maintained until temperatures are increased above the quiescent inducing temperature. Development of this type has been recorded in *Tortopus incertus* (Tsui and Peters, 1974) and in *Atalophlebia australis* and *Atalonella inconspicua* from South Australia.

Light and photoperiod have little, if any, effect on the incubation period of mayfly eggs in South Australia. Saline conditions and desiccation appear to be deleterious, with reduced viability with increased salinity and non-viability after drying. Of the environmental parameters tested, under normal conditions, i.e. in fresh water, the most important determinant of the duration of egg development periods for the South Australian mayflies was temperature.

CHAPTER 6.

Geographical Distribution of South Australian Mayflies.

VI.1 Introduction

Examination of the published literature demonstrates that the taxonomic understanding of the Australian mayfly fauna is very limited. As a result, detailed geographical distribution data, even for individual species, is virtually non-existent. Many species distribution records are limited to one locality, allowing no possible interpretation of ecological factors controlling their distribution. Similarly, many locality records accompanying taxonomic studies include little, if any, information on the habitat from which the material was collected.

In South Australia the published distribution data for mayflies are limited to three papers, Eaton (1871), Harker (1954) and Timms (1974). Only three species were noted, *Atalonella inconspicua*(described as *Leptophlebia inconspicua* by Eaton) from Adelaide; *Atalophlebia australasica* (recorded by Harker in Tillyard's 1934 collection) from near Mt. Gambier and *Tasmanocoenis tillyardi* recorded by Timms as *Caenis* sp. from the lakes near Mt. Gambier.

From the present taxonomic and ecological study of the South Australian mayfly fauna detailed examination of the geographical distribution of each species is possible, but the overall zoogeographical picture, relative to the rest of the

Australian continent, is still limited by scanty systematic knowledge and collections. Therefore the following discussion of zoogeographical relationships is, at present, tentative.

The distribution of each species in South Australia is based both on collections made during this study, and on material previously collected by colleagues in the Department of Zoology, University of Adelaide. The localities of all collections are recorded in Table VI.1 and illustrated in Fig. VI.1. Records of all mayflies held in the South Australian Museum were also examined, but no new localities were represented.

Collection of mayflies was successful from 131 distinct localities, but many other sites were visited without mayflies being recorded. Distribution data based only on positive records present only part of the information available, therefore the absence records are also included. The localities previously identified and annotated in Fig. VI.1 represent positive Ephemeroptera sites, whereas those marked, but without a corresponding number, represent localities from which collections of benthic invertebrates were made, but at which no mayflies were recorded. At each collecting site salinity, temperature, substrate and flow conditions were recorded in an attempt to compare these physical conditions with mayfly distribution.

TABLE VI.1.

Localities and map grid references of collecting sites at which mayflies were present in South Australia.

The sites are grouped in sub-provinces (see text) and each site is numbered to coincide with Fig. VI.I Grid references all refer to National Map Series 1 : 250,000; Australia.

No.	Locality	Grid Reference
NORTHERN FLINDERS RANGES		
1.	Arkaroola Creek, Arkaroola	229243
2.	Hot Springs Creek, Paralana Hot Springs	237263
3.	Stubbs Waterhole	230244
4.	Nepouie Creek	229226
5.	Balcanoona Creek	222219
6.	Trib. Mt. McKinley Creek, E. of Nepabunna Mission	199211
7.	Trib. Tea Tree Creek, Wearing Gorge	215179
8.	Mt. Chambers Creek, near "Mulga View"	209174
9.	Trib. Mt. Chambers Creek, Little Bodmonie Wells	202164
10.	Bendieuta Creek	198159
11.	Old Wirrealpa Spring	180155
12.	Wirrealpa Creek, 5km W. of Wirrealpa Homestead	182148
13.	Eregunda Creek, Fountain Spring	178148
14.	Emu Creek, Aroona Dam	647211
15.	Willigan Creek, 3rd Spring	148158
16.	Oratunga Creek, 4.5km N.E. of Mt. Mary	143152
17.	Parachilna Creek, at Mt. Mary	141146
18.	Parachilna Creek, 2km E. of Mt. Mary	143145
19.	Wockerawirra Creek	157137
20.	Enorama Creek	158121
21.	Elatina Creek	150121
22.	Brachina Creek	143120
23.	Bunycroo Creek	148110
24.	Oraparinna Creek	162118
25.	Trib. Wilpena Creek, at Wilpena turnoff	156099
26.	Moralana Creek, Blacks Gap	142089
27.	Arkaba Creek, Little Weepowie	145075
28.	Kanyaka Creek, at Death Rock	638031
29.	Warren Gorge	608018
SOUTHERN FLINDERS-NORTHERN MT. LOFTY RANGES.		
30.	Old Woolshed Dam, near Hesso	543029
31.	Nectar Brook Dam, and Creek	601956
32.	Spring Creek	620954
33.	Back Creek in Port Germein Gorge	616924
34.	Wild Dog Creek, 7km N. of Murray Town	629936
35.	Rocky River, N. of Wirrabarra	632917
36.	Rocky River, S. of Wirrabarra	632914
37.	Rocky River, near Tandowie	634908
38.	Rocky River, 5km N. of Laura	634901
39.	River Broughton at Hutt River junction	157855
40.	Hutt River near Clare	159817
41.	Ohlenmeyer Park Reservoir, Sevenhills	159811
42.	Skillogalee Creek, near Sevenhills	159810
43.	Schumachers Creek, Spring Gully	152810
44.	River Wakefield near Leasingham	164799
45.	Julia Creek, W. of Eudunda	199776
46.	North Para River, Chateau Yaldara	188726
47.	Little Para River, Lower Hermitage	177700

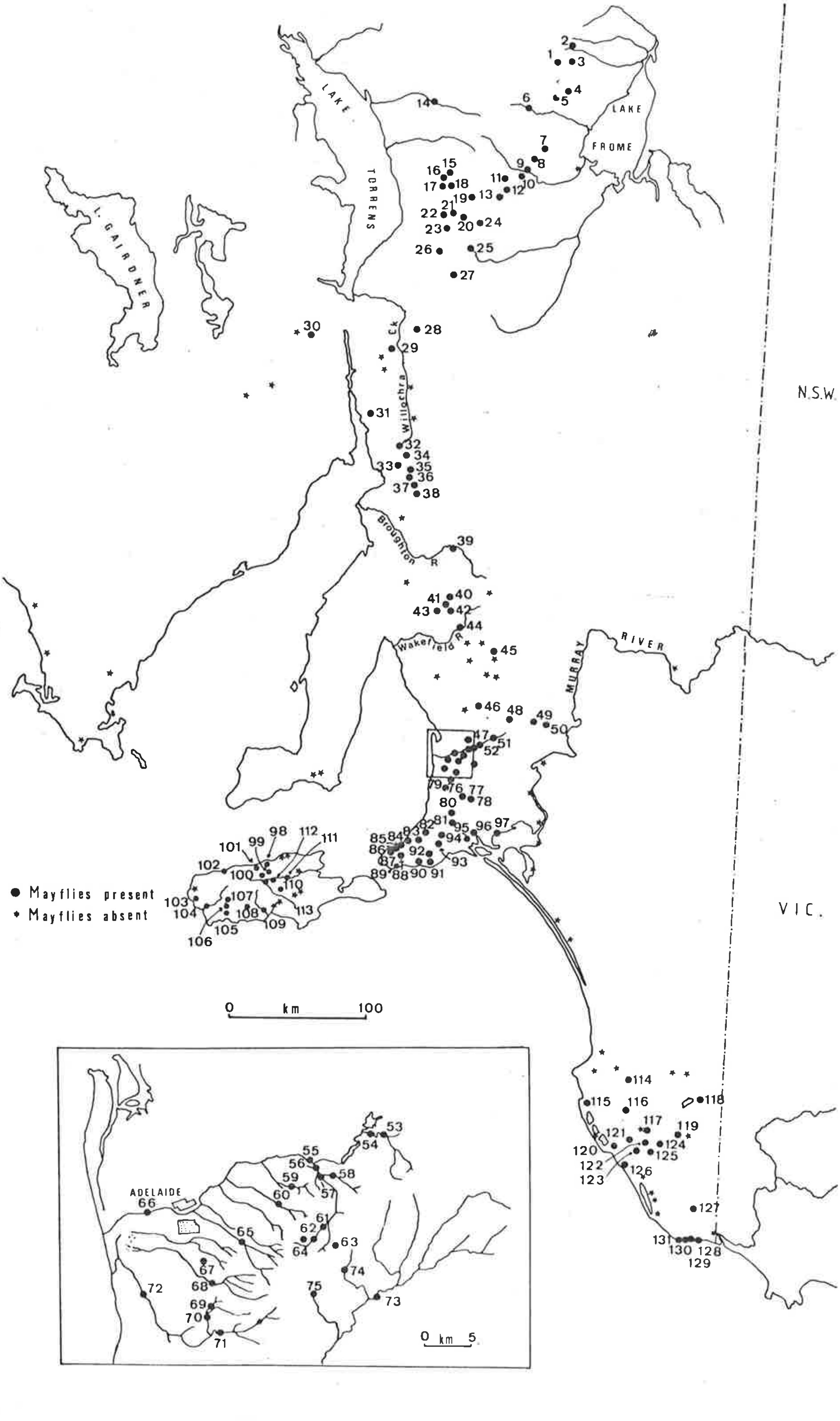
Table VI.1. (Cont.)

No.	Locality	Grid Reference
SOUTHERN FLINDERS-NORTHERN MT. LOFTY RANGES (Cont.)		
47.	Little Para River, Paracombe	179695
48.	The Marne River, S. of Eden Valley	209717
49.	The Marne River, near Cambrai	228718
50.	The Marne River, near Black Hill	246713
MT. LOFTY RANGES-FLEURIEU PENINSULA		
51.	Torrens River at Birdwood	197699
52.	Torrens River, 2km E. of Gumeracha	193698
52.	Torrens River at Gumeracha	189698
53.	Cudlee Creek	185694
54.	Torrens River at Kiosk	184696
55.	Torrens River at road to Priarie	183696
56.	Torrens River, Castambul	176692
56.	Deep Creek, Castambul	176692
57.	Deep Creek at ford	177691
58.	Trib. Deep Creek near Montacute Conservation Park	178690
59.	Fifth Creek near Montacute	174689
60.	Fourth Creek at Morialta Falls	172687
61.	Deep Creek at Knotts Hill Road Bridge	177685
62.	Deep Creek near Ashton	176683
63.	Dam, Carey's Gully	178681
64.	Cock's Dam, Ashton	174684
65.	First Creek, near Waterfall Gully Reserve	167683
66.	Torrens River at Torrens C.A.E.	155686
67.	Pool at Waite Institute, Mitcham	164680
68.	Brownhill Creek, Mitcham	163678
69.	Trib. Sturt River at Blackwood	164675
70.	Sturt River, Coramandel Valley	163671
71.	Chambers Creek, Coramandel Valley	163669
72.	Sturt River below Flinders University	154677
73.	Onkaparinga River at Balhannah	183678
74.	Trib. Onkaparinga River at Carey's Gully	178681
75.	Algate Creek, Algate	173675
76.	Scott Creek at Scott Creek	170668
77.	Blackfellow Creek at Kuipto Colony	172643
78.	Bull Creek on Kuipto Colony Road	178643
79.	Kangarilla Creek, Meadows Road	168658
80.	Finnis River at Mt. Effie	168637
81.	Tookayerta Creek	168631
82.	Myponga River E. of Myponga	648629
83.	Carrickalinga Creek near Wattle Flat	648622
84.	Anacotilla Creek near Yankalilla	631621
85.	Bungala River near Normanville	632618
86.	Yankalilla River near Lady Bay	629619
87.	No Where Else Creek at Rapid Bay	618612
88.	Yankalilla Creek on road to Parawa	636612
88.	Yankalilla Creek at Hay Flat	636612
89.	The Deep Creek, Delamere	622602
90.	Gold Digging Swamp	637608
91.	Coolawang Creek	642603
92.	Inman River, E. of Victor Harbour	651616
93.	Hindmarsh River on Sawpit Road	160619
93.	Inman River on Sawpit Road	155615
94.	Hindmarsh River at Hindmarsh Falls	160622

TABLE VI.1. (Cont.)

No.	Locality	Grid Reference
MT. LOFTY RANGES-FLEURIEU PENINSULA (Cont.)		
95.	Trib. Currency Creek at Bromlé	168622
96.	Finnis River near Finnis	182631
97.	Lake Alexandrina - Milang	200628
KANGAROO ISLAND		
98.	Middle River near Middle River Station	508597
99.	Middle River near Glencorrie	509589
100.	Middle River N.E. of Binnowie	502588
101.	Western River, Karawatha	496596
102.	De Mole River	474589
103.	Breakneck River	461566
104.	Rocky River, Flinders Chase National Park	470563
105.	South West River near Riverdale	484560
106.	South West River at St. Andrews	484566
107.	South West River near Brigadoon	484570
108.	Stunsail Boom River near Karatta	499559
109.	North East River near Carnarvon	499563
110.	Eleanor River near Daws Diggings	524578
111.	Cygnet River	521588
112.	Grassy/Sheep Creek near Moorlands	515585
113.	Tin Hut/Bullock Creek	510586
SOUTH EAST SOUTH AUSTRALIA		
114.	Drain K., West Avenue Range	318431
115.	Drain L., near Robe	284414
116.	Reedy Creek Drain, N. of Greenaways	315428
117.	Eastern Division Diversion Drain at "Ceres"	329394
118.	Mosquito Creek at Robinson's Bridge	380424
119.	Bakers Range Drain, E. of Penola	357393
120.	Sutherland Drain, near Beachport	307381
121.	"Trib." Mt. Hope Drain	327381
122.	Reedy Creek Drain at Furner	335386
123.	Eastern Division Diversion Drain, N.W. of Millicent	323390
124.	Drain near "Keera Park"	349382
125.	Drain at "White Heath"	345378
126.	Mt. Hope Drain near Lake Frome	323368
127.	Brown Lake, Mt. Gambier	378334
127.	Valley Lake, Mt. Gambier	378334
128.	Hitchcock Drain	383309
129.	Eight Mile Creek	381309
129.	Trib. of Eight Mile Creek	381309
130.	Deep Creek at Cheese Factory	379308
130.	Drain W. of Deep Creek	378308
131.	Jerusalem Creek near Port Macdonnell	375308
131.	Cress Creek, Port Macdonnell	373308

Fig. VI.1. Distribution of collecting localities in South Australia showing sites where mayflies were present, and absent.



Distribution of collecting localities

VI.2 The Natural Environment of South Australia.

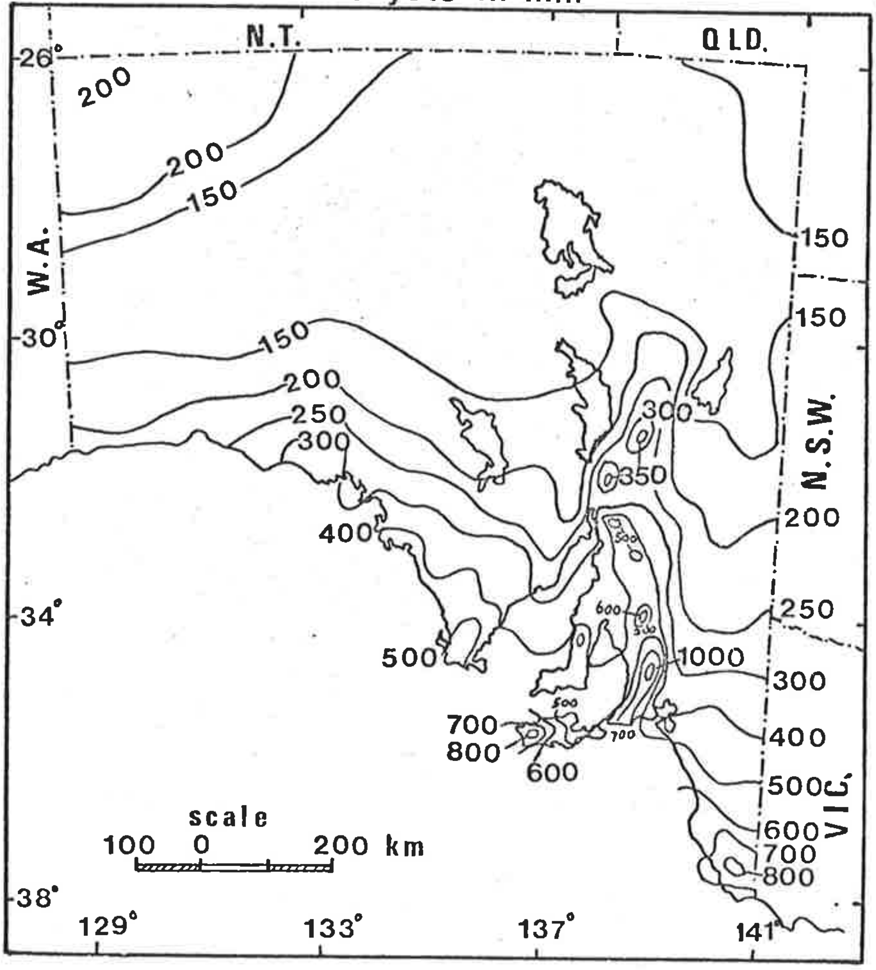
The general physical features of South Australia are documented in the South Australian Year Book (1975) and a brief summary of this article is given below.

South Australia has generally low relief with the inland area predominantly flat, featureless plains or desert. The Mt. Lofty-Flinders Ranges extend up the centre of the State like a central spine. Kangaroo Island is essentially the extension of the southern part of the Mt. Lofty Ranges (known as the Fleurieu Peninsula) which, with the Flinders Ranges, extend some 800 km. from Cape Jervis to Lake Torrens. In the south the Mt. Lofty Ranges are of low altitude, with Mt. Lofty reaching 727 m above sea level. To the north, the Flinders Ranges attain greater height with St. Mary Peak, at 1,166 m the highest peak. Midway along the Mt. Lofty-Flinders Ranges the Barrier Range diverges in a north-easterly direction towards Broken Hill.

The Mt. Lofty-Flinders chain has a dramatic effect on climate, especially rainfall (Fig. VI.2) and temperature (Fig. VI.3). Rainfall exceeds 300 mm per annum throughout the greater part of the Ranges, and exceeds 500 mm in the southern region of the Mt. Lofty Ranges. It rapidly diminishes to the east of the Ranges at about 20 mm per km. In terms of total rainfall, 82.66% of the total area of South Australia receives under 250 mm and only 3.85% more than 500 mm. The seasonal distribution of rainfall is also important in defining the climatic conditions of the state. From November to March,

Fig. VI.2. Isohyets of average annual rainfall (mm.) for South Australia.

South Australia
AVERAGE ANNUAL RAINFALL
Isohyets in mm



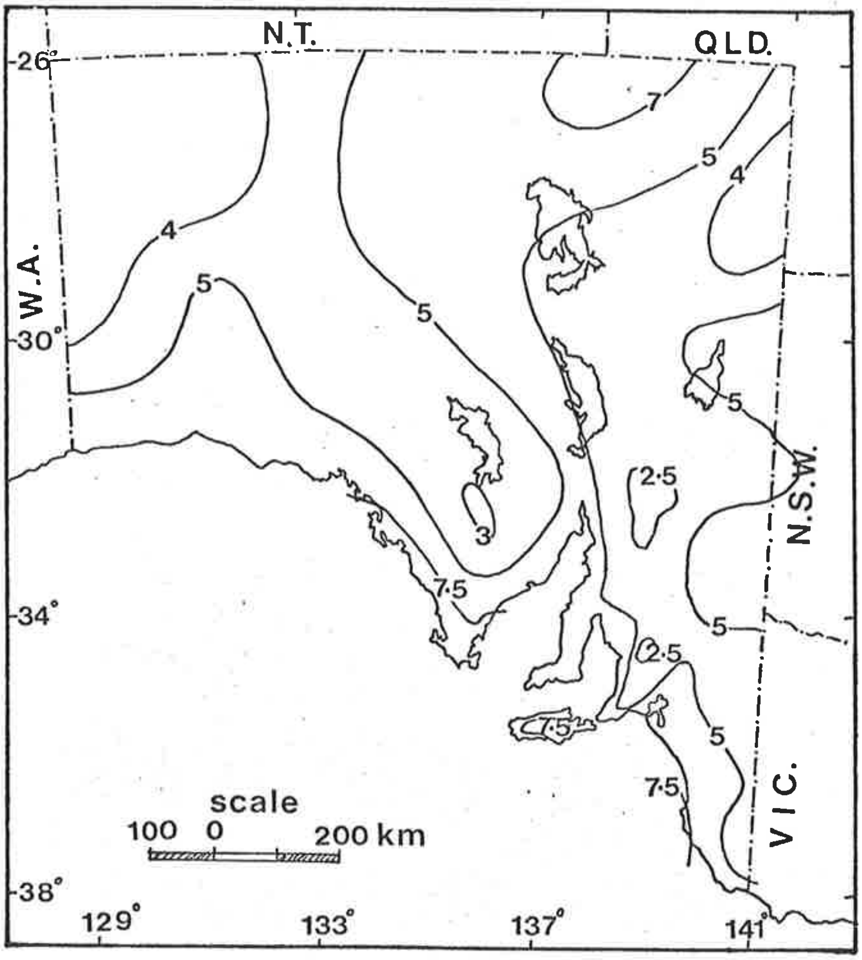
rainfall is slight, but during this time evaporation is intense. In the Southern half of the State 60% of the total precipitation falls between April and October (Specht, 1972) with June to August usually the wettest months. In the interior, however, rainfall is erratic and scanty with little seasonal bias.

In terms of temperature, the isotherms parallel the coastline, but the cooling effect of the mountain ranges is clearly evident (Fig. VI.3). The period December - February is generally warm in the south to very hot in the northern regions (Fig. VI.3a). The winter months are cool (Fig. VI.3b) with June, July and August the coolest months. In the arid north daily temperatures during Winter may exceed 20°C for many days, whereas the mean temperature in the east and south-east of the Ranges is nearer 10°C.

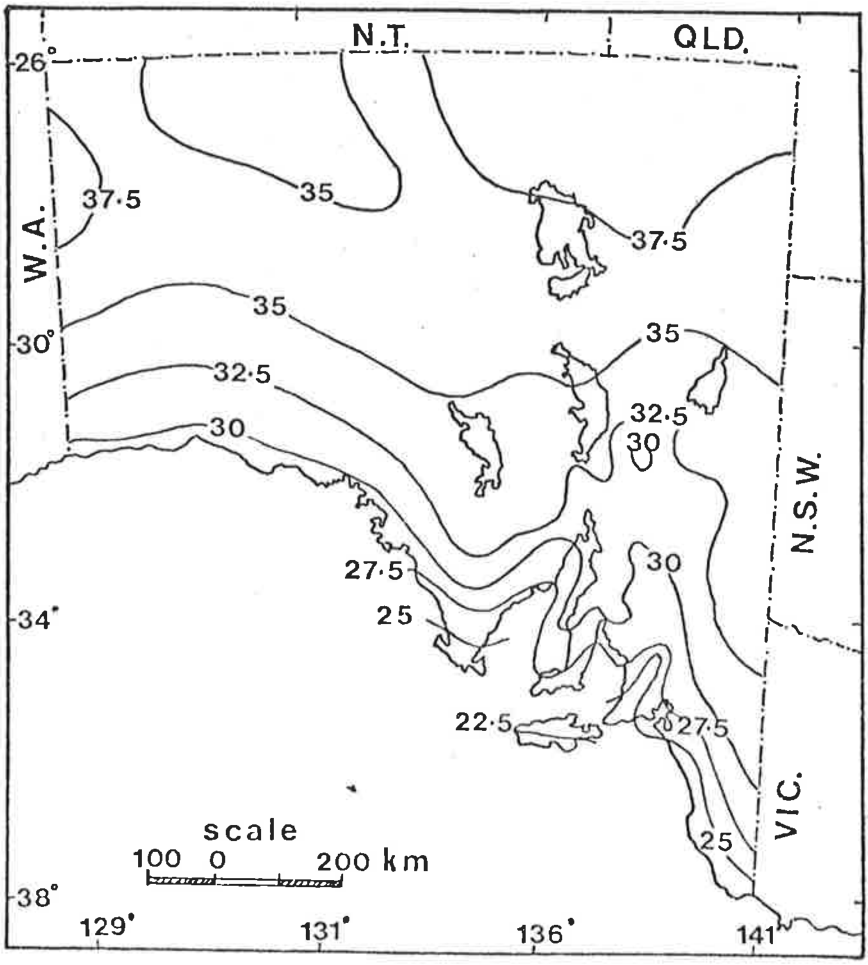
A major feature in the South Australian climate is the annual evaporation. Andrewartha and Birch (1954) divided Australia into a series of bio-climatic zones determined by moisture, with the aridity increasing further from the coastline. These bio-climatic zones were defined in terms of the ratio of precipitation to evaporation (P/E). South Australia was divided into four such zones ranging from warm temperate/desert (P/E > 0.5 for 1 - 3 months) in the north, through warm temperate/arid; warm temperate/semi-arid to warm temperate/semi-humid (P/E > 0.5 for 7 - 9 months). In all these areas evaporation exceeds precipitation, and where these conditions occur the potential for saline lake development is present (Langbein, 1961) as shown by Buckney and Tyler (1976)

Fig. VI.3. Mean maximum (a) and minimum (b) temperatures for South Australia.

MEAN MINIMUM TEMPERATURE: JULY
Isotherms in °C



South Australia
MEAN MAXIMUM TEMPERATURE: JANUARY
Isotherms in °C



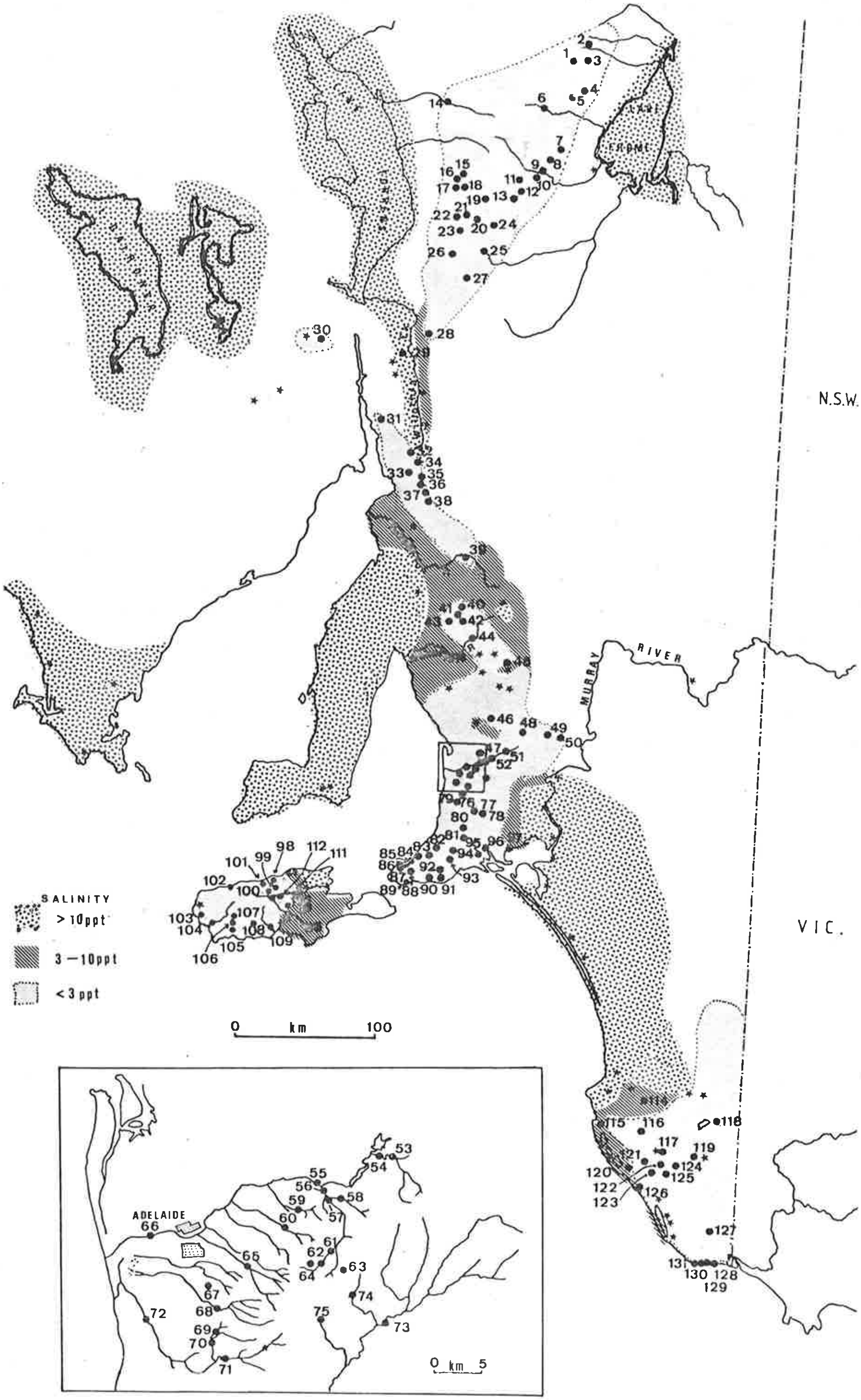
in Tasmania. Compounding this saline lake development potential is the relatively recent emergence (in the Tertiary) of the coastal plains from the sea, especially the Yorke Peninsula, Adelaide Plains and the Coorong. In the arid "centre", saline lake development has occurred, with the innumerable dry salt pans, and frequently-dry Lake Eyre as distinct examples. Where regions of higher rainfall occur along the Ranges and in the south-east, precipitation and ground water discharges maintain relatively fresh surface waters.

In South Australia and the arid areas of the Australian continent the majority of athallasic waters are saline. Williams (1964) adopted an arbitrary dividing line between fresh and saline waters at 3‰ (based on his own taste threshold) and Bayly and Williams (1973) continued the use of this value as a useful criterion for distinguishing fresh and saline waters. Buckney and Tyler (1976) compared the divalent cation proportion of fresh and saline waters from Tasmania and noted wide variation at low total ionic concentration, but much less variation as salinity increased. The range over which this variation decreased was from 1 - 11‰. Using this definition, many of the waters salty to taste would be considered "fresh". However, in the present study the criterion of 3‰, as used by Williams (1964) and Bayly and Williams (1973), has been chosen to deliniate fresh from brackish waters. Combining the criteria a salinity map of South Australia has been compiled from records made from 1970-77 by the Engineering and Water Supply Department, Adelaide, the Zoology Department, University of Adelaide and Williams and Buckney (1976). Freshwater has been defined as below 3‰, slightly brackish waters 3 - 10‰ and saline waters > 10‰. The distribution of these waters is shown in Fig. VI.4 illustrating how freshwaters are limited to the Ranges, Kangaroo Island, the South-East and a limited area on the south-eastern side of Eyre Peninsula. The Musgrave Ranges in the north-west of the state also are known to have permanent fresh water holes, but during this study no sampling for either water or mayflies, was possible.

VI.3 The Distribution of Mayflies in South Australia.

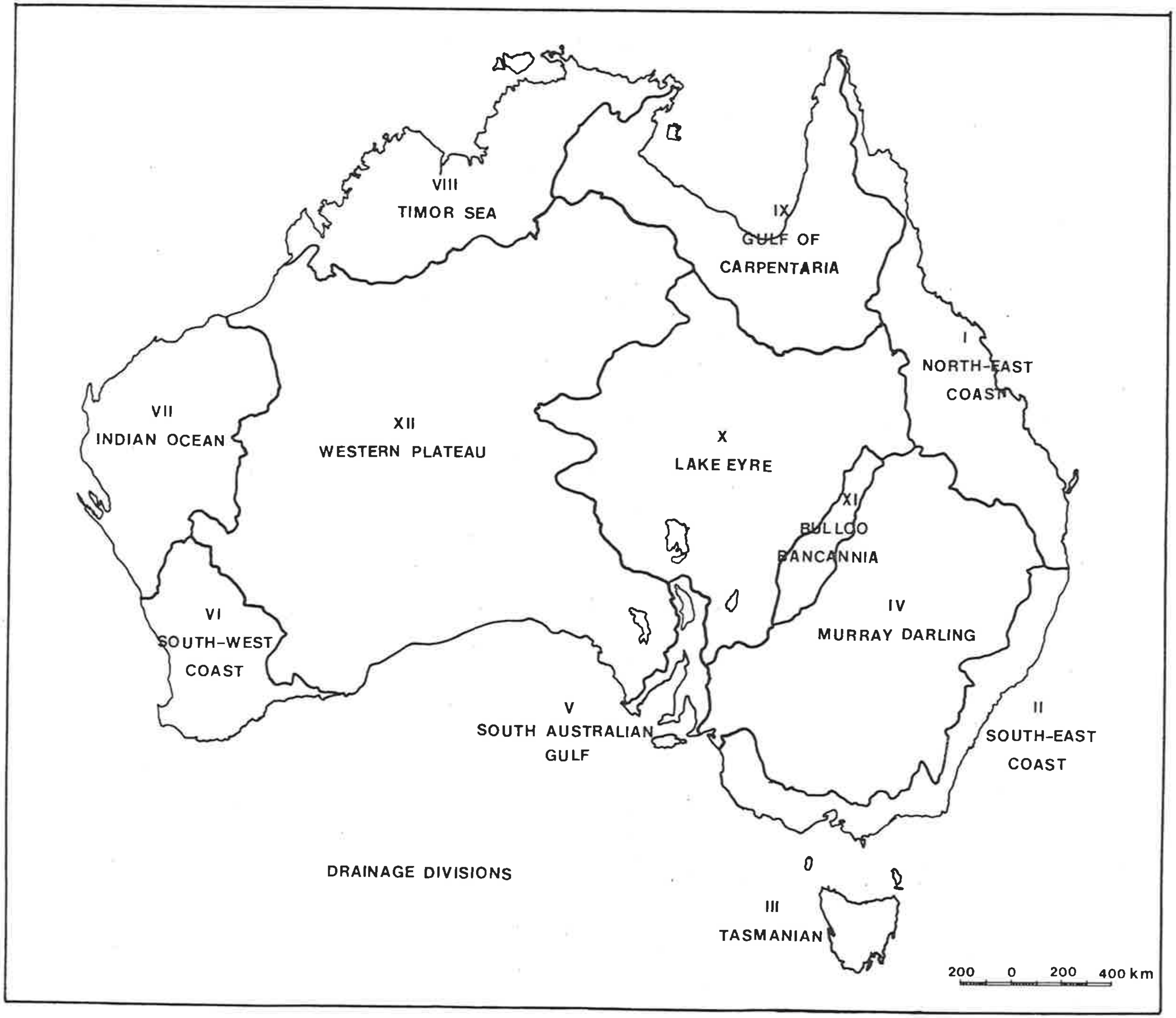
Australian surface water drainage has been grouped into 12 drainage divisions (Fig. VI.5) on the basis of their location along the major physical divides, or their position in major river systems. The Ephemeroptera in South Australia occupy four of the drainage divisions, South Australian Gulf, Lake Eyre, Murray-Darling and South East Coast. Each of these basins can be subdivided into drainage divisions or major river catchments, Fig. VI.6 (after Australian Water Resources Council, 1976). These have been adopted to simplify discussion of the mayfly distribution. A comparison of the salinity map and distribution map clearly shows that the distribution of the mayfly fauna of South Australia is closely correlated with the distribution of water less than 3‰, with rare collections from waters in the 3 - 10‰ regions.

Fig. VI.4. Salinity map of South Australia based on available records from the Engineering and Water Supply Department, Zoology Department, University of Adelaide, and Williams and Buckney (1976). Areas not shaded represent regions which lack water, or lack salinity records.



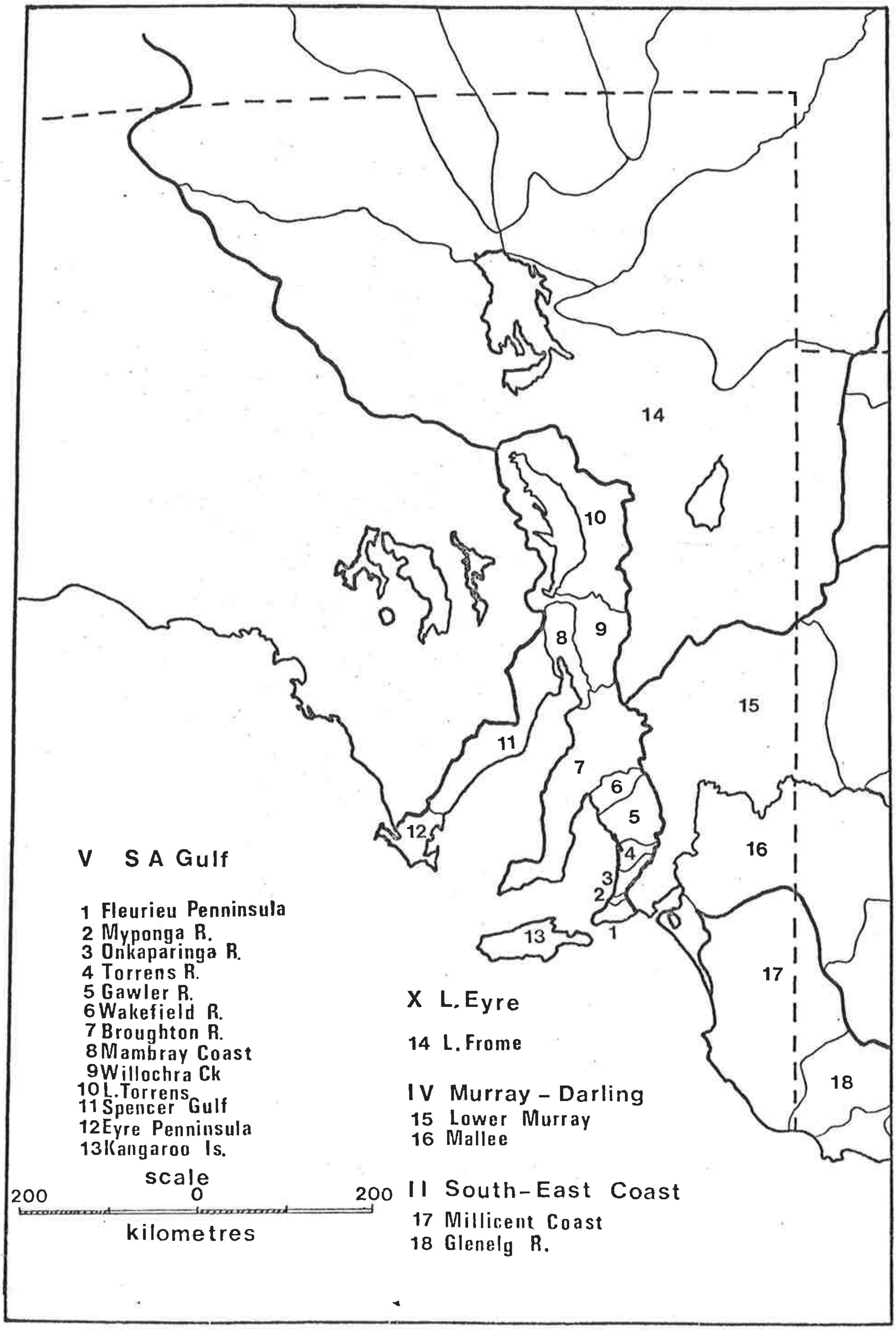
Distribution of collecting localities

Fig. VI.5. Drainage divisions of Australia (after Australian Water Resources Council, 1976).



DRAINAGE DIVISIONS

Fig. VI.6. Major river catchments in South Australia (after Australian Water Resources Council, 1976).


14
10
9
8
15
11
7
6
5
12
4
3
2
16
1
13
17
18
V S A Gulf
1 Fleurieu Penninsula
2 Myponga R.
3 Onkaparinga R.
4 Torrens R.
5 Gawler R.
6 Wakefield R.
7 Broughton R.
8 Mambray Coast
9 Willochra Ck
10 L. Torrens
11 Spencer Gulf
12 Eyre Penninsula
13 Kangaroo Is.
scale
200
0
200
kilometres
X L. Eyre
14 L. Frome
IV Murray - Darling
15 Lower Murray
16 Mallee
II South-East Coast
17 Millicent Coast
18 Glenelg R.

VI.3.1 Distribution of Individual Species

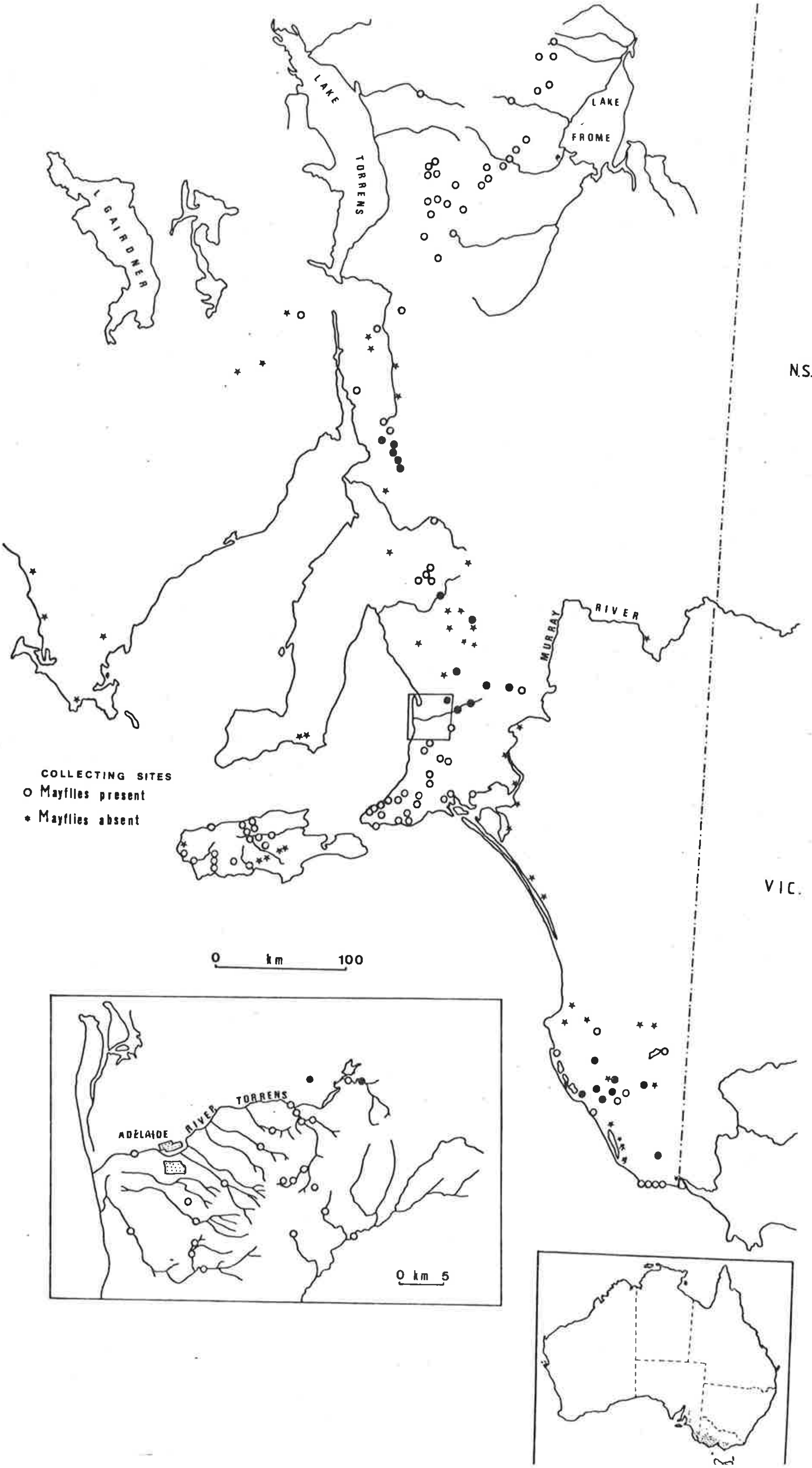
VI.3.1.1 F. Leptophlebiidae:

Atalophlebia australis

The distribution of *A. australis* is illustrated in Fig.VI.7. The records of *A. australis* are limited to the South East of South Australia; the Torrens, Gawler, Broughton Rivers and Mambray Coast Drainage basins. A single record of the species by Dr. J. E. Bishop from Spring Creek in February 1976 was the only record from the Willochra catchment. In the catchments of the Mt. Lofty and Southern Flinders Ranges this species is always limited to the upper catchment tributaries, but this is not the case on the south eastern drainage system, which are lowland drainages.

Not only are the positive records of the species noteworthy; the localities from which it is absent are just as important. With the exception of the River Torrens records, *A. australis* is absent from the Southern Mt. Lofty Ranges, the Fleurieu Peninsula, and Kangaroo Island. To the north, *A. australis* occurs in the Southern Flinders Ranges, but was found in the most southerly streams of the Mambray Coast drainage (Back Creek) and of the Willochra Basin (Spring Creek). Back Creek rises from the same ridge as Rocky River, the northern tributary of the River Broughton. The headwaters of both streams are less than one kilometre apart.

Fig. VI.7. Distribution of *Atalophlebia australis* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution *A. australis* in Australia.



LAKE TORRENS
L. GAIRDNER
LAKE FROME
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

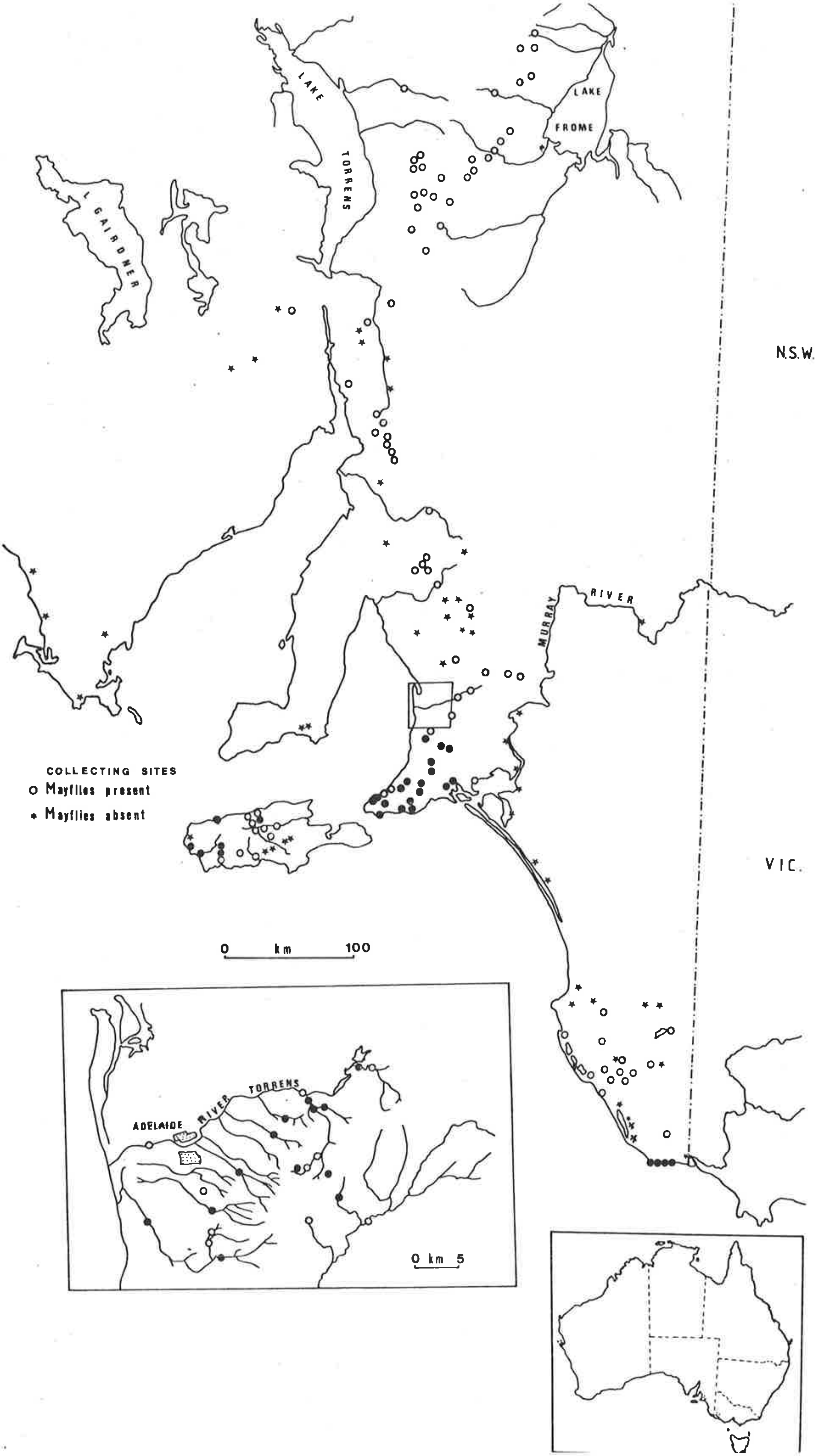
The absence of *A. australis* may be because it has been eliminated from these streams during periods of unfavourable conditions, or alternatively northerly colonisation is still progressing, and the Mt. Remarkable streams have not been successfully colonised. The presence of populations of *Baetis soror*, *Atalonella inconspicua* and *T. tillyardi* in these streams would suggest conditions have not altered enough to eliminate them, and since *B. soror* has specific habitat requirements of flowing water (Chapter 3) it would seem likely conditions unfavourable to *A. australis* would also disadvantage *B. soror*. Also the absence of relictual populations in isolated permanent waters, i.e. Goat Rock in Spring Creek, would also tend to suggest *A. australis* has not successfully colonised these streams.

A. australis was found to co-occur with *Atalonella inconspicua*, *Tasmanocoenis tillyardi* and, in flowing reaches, *Baetis soror*.

Atalophlebia australasica

Fig. VI.8 illustrates the known distribution of *A. australasica* in South Australia; limited to the Southern Mt. Lofty Ranges, Fleurieu Peninsula, Kangaroo Island and the coastal streams of the south east corner of the State. *A. australasica* was not recorded north of the River Torrens, and was never recorded at the same locality as *A. australis*. These two species are therefore discretely distributed, with the River Torrens the only catchment occupied by both.

Fig. VI.8. Distribution of *Atalophlebia australasica* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *A. australasica* in Australia.


LAKE TORRENS
LAKE FROME
L. GAIRDNER
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

A. australasica co-occurred with *Atalonella inconspicua*, *Baetis soror* and *Tasmanocoenis tillyardi*. In Tookayerta Creek and the coastal streams south of Mt. Gambier it also co-occurred with *Atalonella fuscula* and *Atalonella pilosa* respectively.

Atalophlebia auratus

This species was only recorded from the type locality at Bakers Range Main Drain, east of Penola (Fig. VI.9) and it appears to be a South Australian endemic. It is probable that *A. auratus* is present in the upper reaches of Bakers Range Main Drain, but the relative inaccessibility of the area has limited the records to this single locality. Extensive collections from the drain system in the South East did not reveal its presence elsewhere. *A. australis* is also found at this locality emerging at similar times to *A. auratus*.

Atalonella inconspicua

A. inconspicua is also probably endemic to South Australia with its distribution limited to the South Australian Gulf Division (Fig. VI.10). The record by Ulmer (1908) from Western Australia has not been substantiated, although collections have been examined. Therefore *A. inconspicua* is considered to be solely a South Australian species.

Fig. VI.9. Distribution of *Atalophlebia auratus* in South Australia (●), also showing localities at which this species was not recorded. The species is known only from the marked locality.

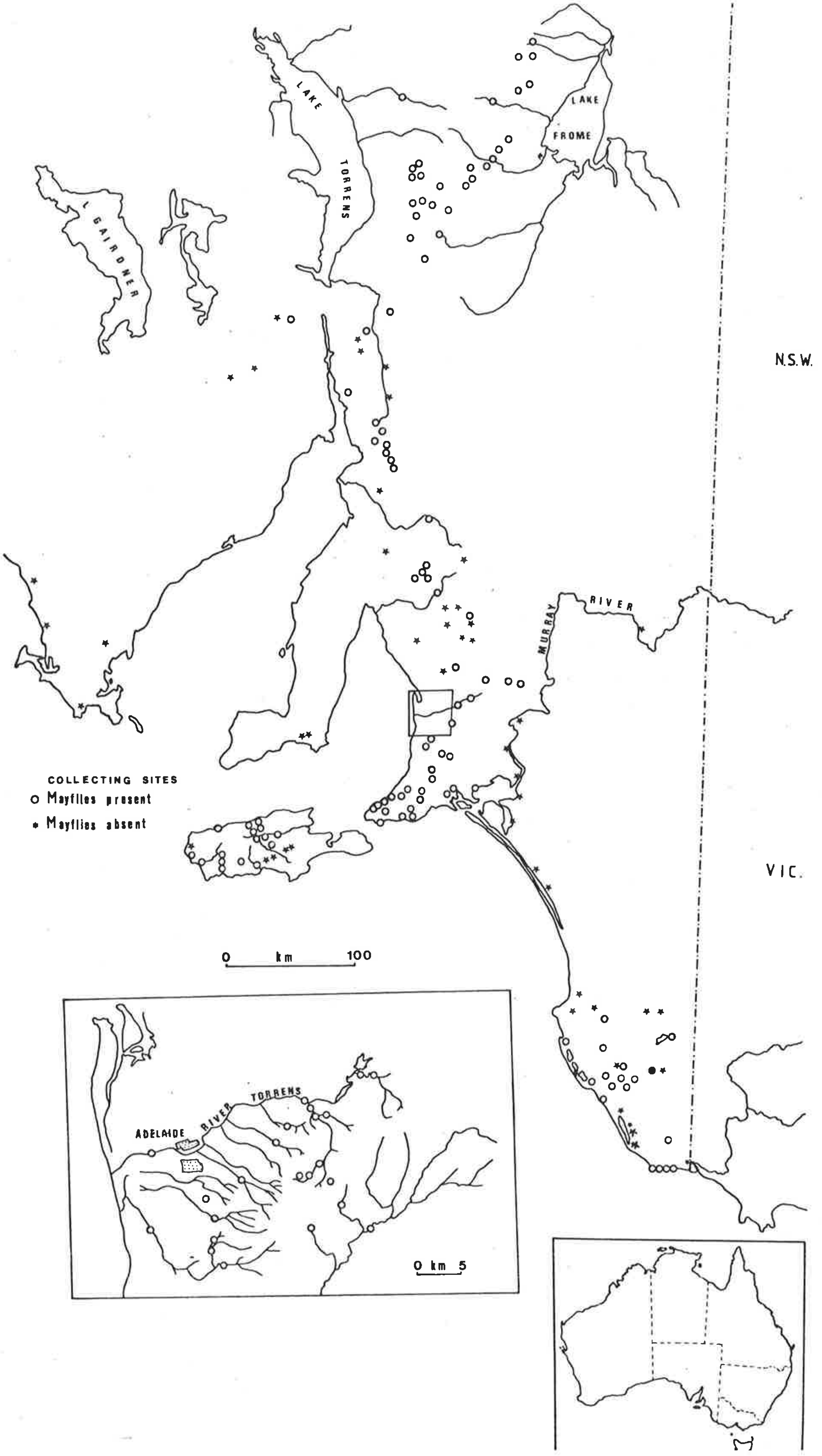
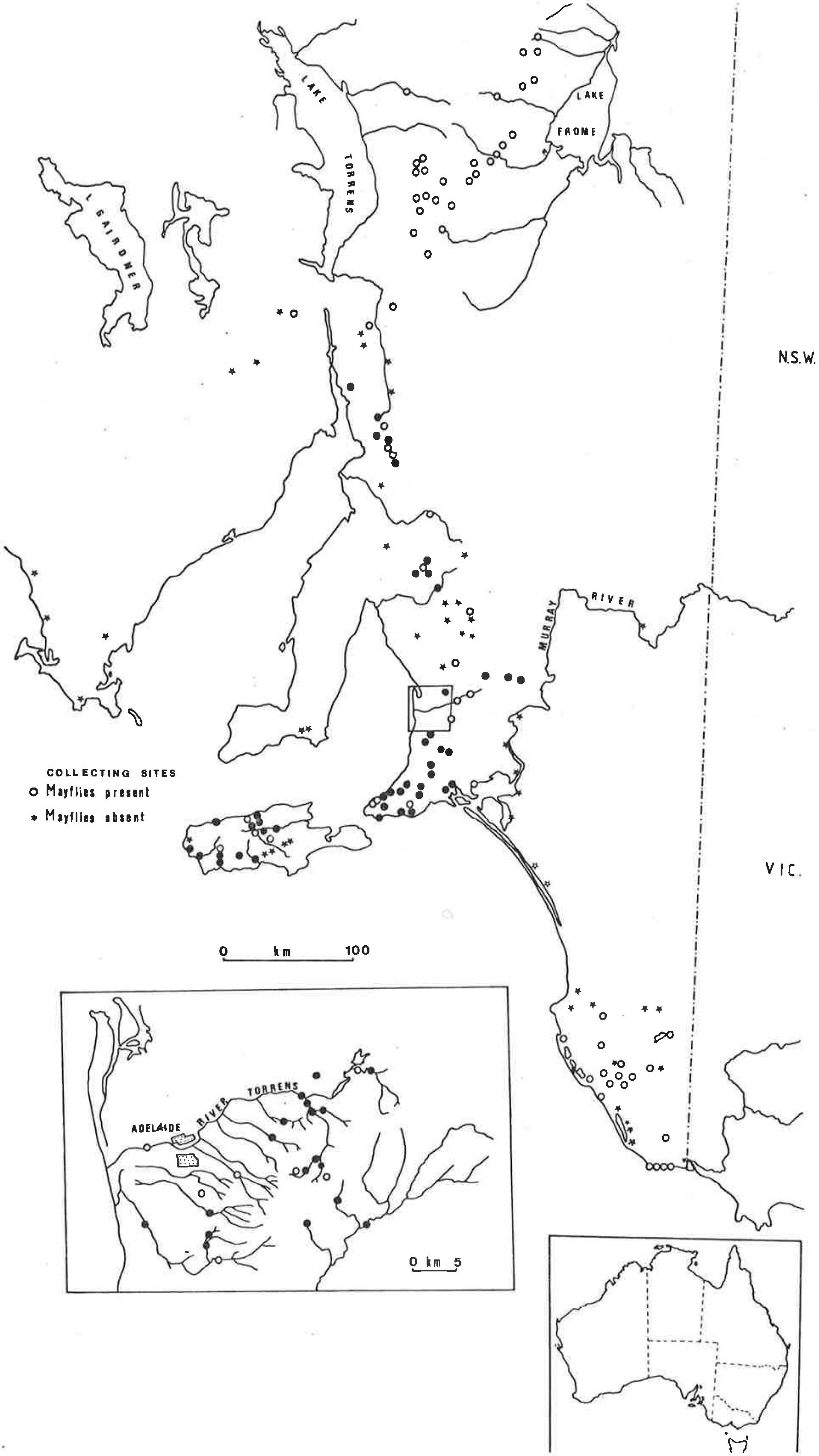

LAKE TORRENS
LAKE FROME
L. GAIRDNER
N.S.W.
VIC.
MURRAY RIVER
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Fig. VI.10. Distribution of *Atalonella inconspicua* in South Australia (●), also showing localities at which this species was not recorded.


LAKE
TORRENS
LAKE
FROME
L. GAIRDNER
N.S.W.
MURRAY
RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER
TORRENS
0 km 5

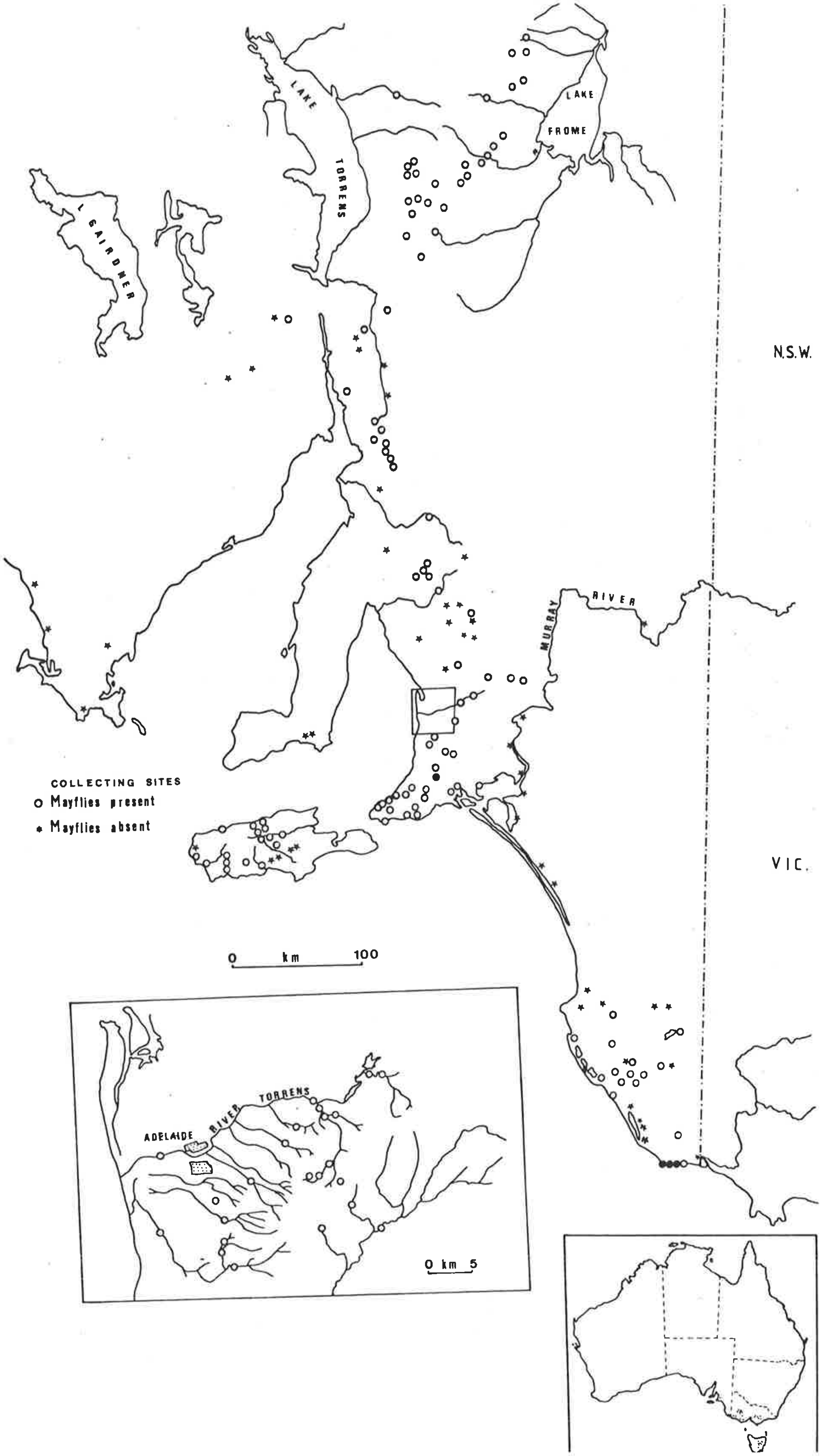
Within the South Australian Gulf Division, *A. inconspicua* is present in almost every freshwater lotic habitat from the Southern Flinders Ranges to Kangaroo Island. In the Southern Flinders this species extends beyond the streams occupied by *Atalophlebia australis* and occupies all streams draining the Mt. Remarkable massif. To the south, only the upper, non-saline catchments of the Broughton and Wakefield Rivers are occupied; the Gawler River and Light River are without populations of *Atalonella inconspicua*. Almost without exception the freshwater streams of the Southern Mt. Lofty Ranges, Fleurieu Peninsula and Kangaroo Island support populations of *A. inconspicua*.

A. inconspicua coincides in distribution with *Atalophlebia australasica* in the southern localities, and with *A. australis* in the north. North of Spring Creek *A. inconspicua* is the only leptophlebiid species occurring in the other streams of the Mt. Remarkable massif. It is therefore the most northerly distributed leptophlebiid recorded in South Australia.

Atalonella fuscula

A. fuscula is limited to only four localities in South Australia; only one on the Fleurieu Peninsula, the others in the coastal streams south of Mt. Gambier (Fig. VI.11). In all cases the streams occupied by *A. fuscula* are cool, permanently flowing, low salinity streams. In Tookayerta Creek on the Fleurieu Peninsula *A. fuscula* co-occurs with *A. inconspicua*

Fig. VI.11. Distribution of *Atalonella fuscula* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *A. fuscula* in Australia.


LAKE TORRENS
L. GAIRDNER
LAKE FROME
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

but the emergence and flight times differ, with swarms of one or other species recorded at any time. In the south-eastern streams it co-occurs with *A. pilosa*. Similarly, recorded flight times do not overlap suggesting an ecological isolation of the species. *Atalophlebia australasica, Jappa pipinna, Baetis soror* and *Tasmanocoenis tillyardi* also co-exist with *A. fuscula*.

Atalonella pilosa

This species can hardly be considered a "South Australian" species as its distribution within South Australia is exclusively the coastal streams south of Mt. Gambier (Fig. VI.12). This species is truly a Victorian immigrant into the political region designated as South Australia, but its presence necessitates its record. *A. pilosa* was found to co-occur with *Atalophlebia australasica, Atalonella fuscula* and *Baetis soror*. Its co-occurrence with *A. fuscula* was also recorded in Northern Tasmania and the Grampian Mountains in Victoria.

Jappa pipinna

J. pipinna, like *Atalonella pilosa,* is a Victorian immigrant found in two streams in the South East coastal system (Fig. VI.13). It is apparently limited to the western Victorian region and the southern Grampians, but more extensive collections in Victoria may broaden its known distribution. In

Fig. VI.12. Distribution of *Atalonella pilosa* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *A. pilosa* in Australia.

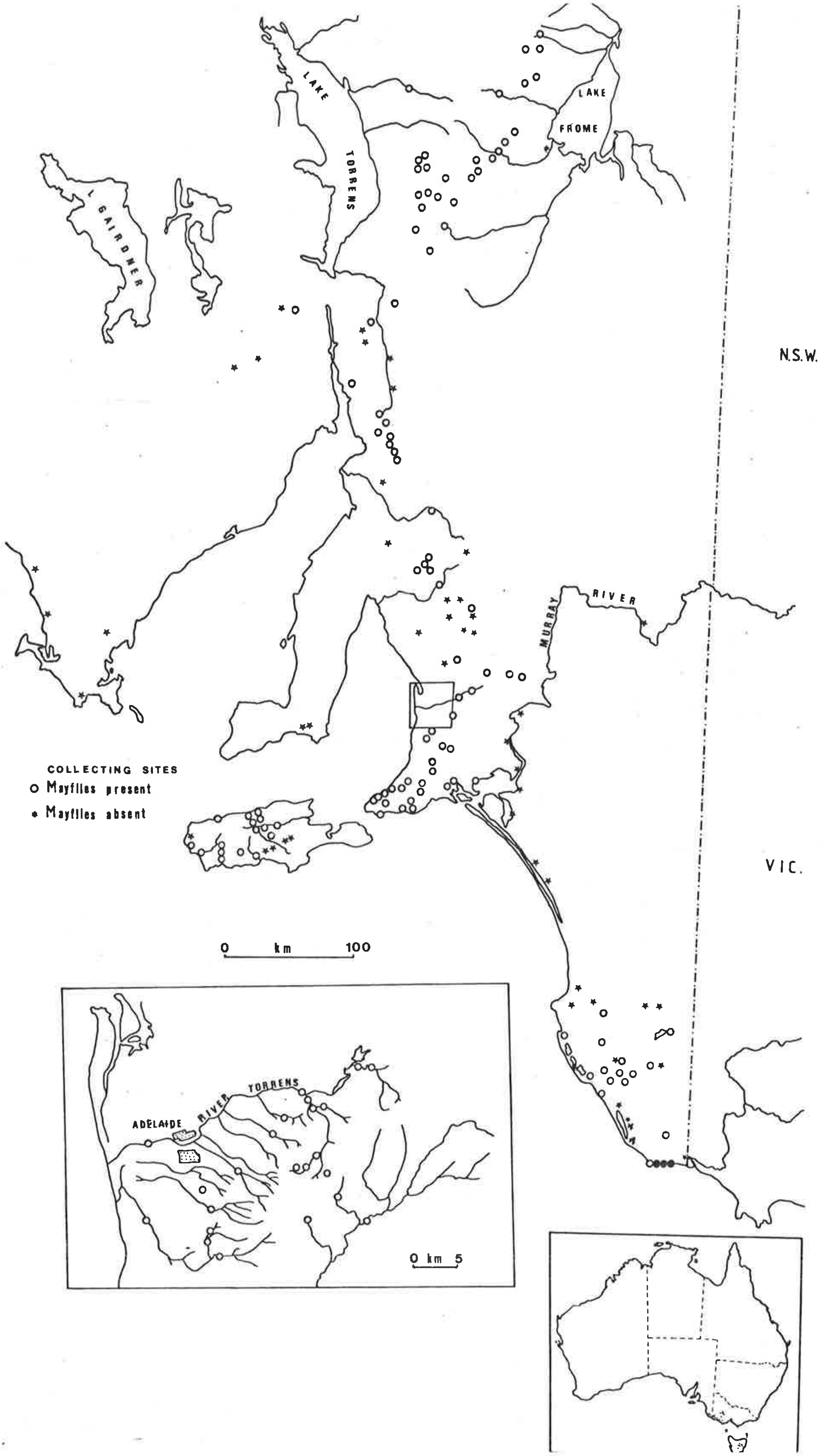
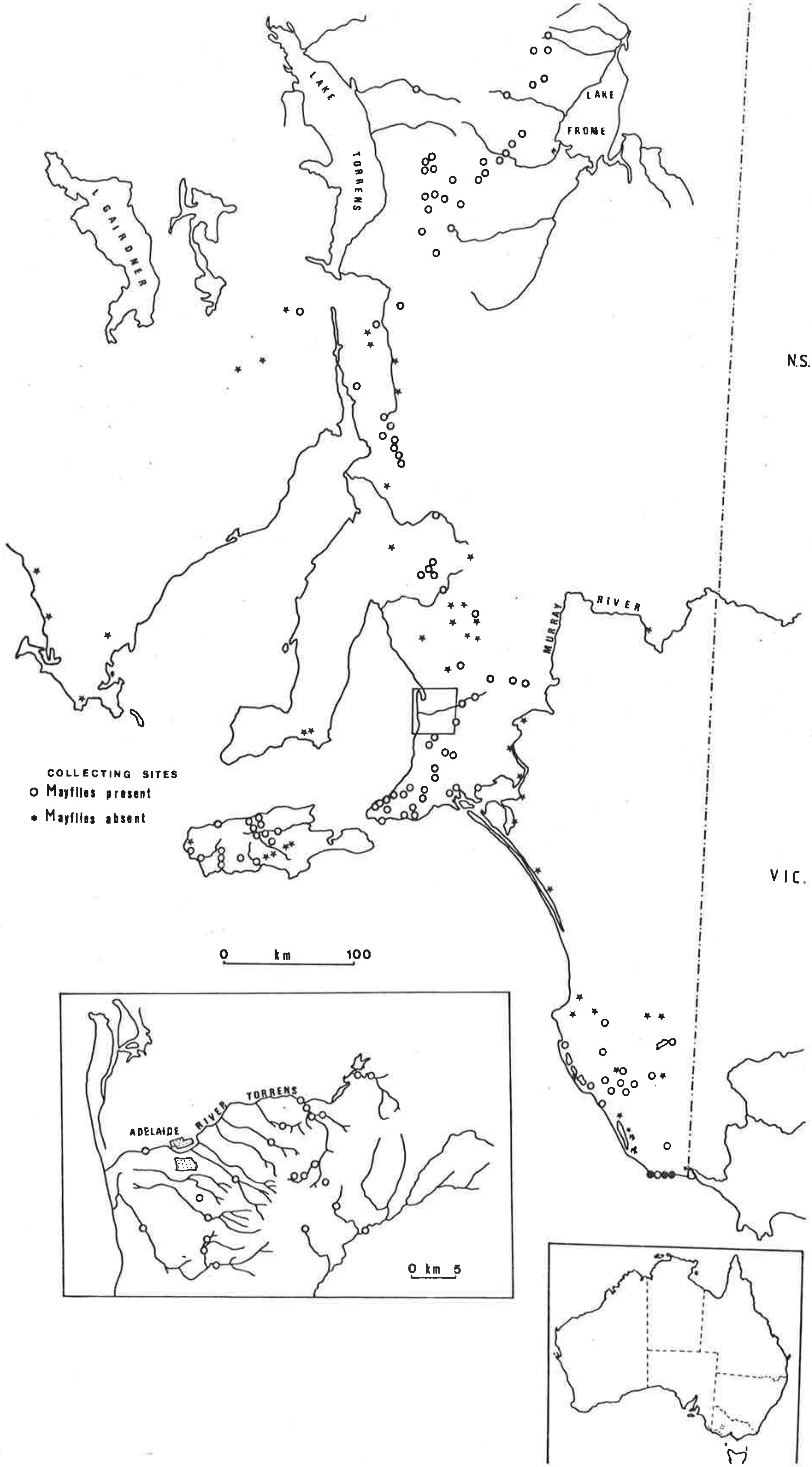

LAKE TORRENS
L. GAIRDNER
LAKE FROME
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
★ Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Fig. VI.13. Distribution of *Jappa pipinna* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *J. pipinna* in Australia.


LAKE TORRENS
LAKE FROME
L. GAIRDNER
N.S.W.
VIC.
MURRAY RIVER
COLLECTING SITES
○ Mayflies present
• Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

South Australia it co-exists with *Atalophlebia australasica, Atalonella pilosa, A. fuscula, Baetis soror* and *Tasmanocoenis tillyardi.*

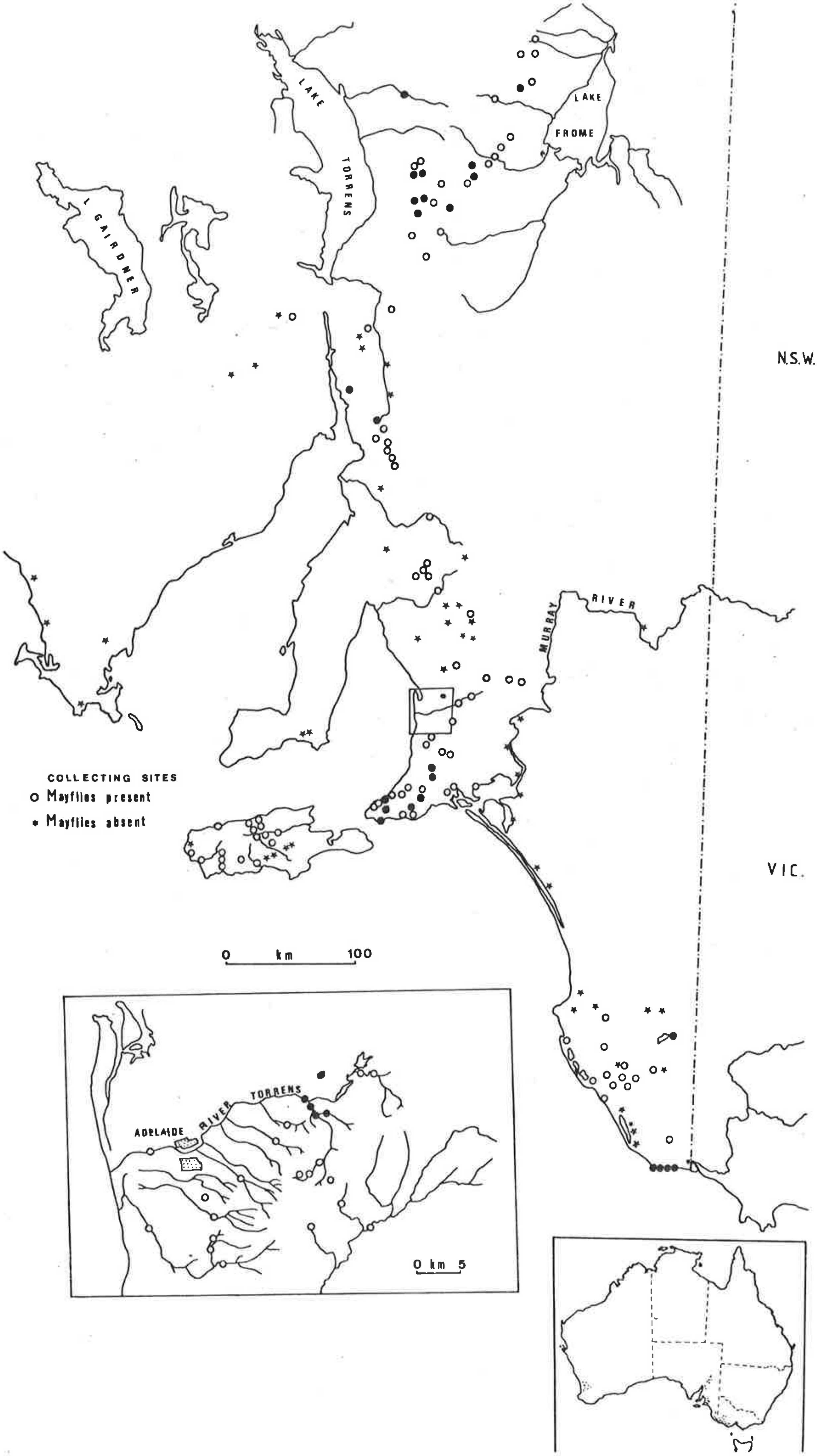
VI.3.1.2 F. Baetidae:

Baetis soror

The distribution of *B. soror* is disjunct, with discrete centres of distribution in the Northern Flinders Ranges, the Mt. Remarkable massif, the Mt. Lofty Ranges, Fleurieu Peninsula and the South East coastal streams (Fig. VI.14). *B. soror* does not occur on Kangaroo Island, nor in any of the upstream sites of the Gawler, Wakefield or Broughton River Drainages. Similarly *B. soror* was not recorded in the extensive man-made drainage system of the South East Region. The distribution of this species is almost strictly limited by the presence of permanent, fresh, flowing water. In all localities in which mayflies are found, but which lack *B. soror*, the flowing requirement is not met all year round.

B. soror was recorded co-existing with almost all species recorded in South Australia with the exceptions of the *Cloeon* species. *Tasmanocoenis tillyardi* was recorded from all streams in which *B. soror* occurred, but *B. soror* appears to be the only species restricted to the permanent flowing streams.

Fig. VI.14. Distribution of *Baetis soror* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *B. soror* in Australia.


LAKE TORRENS
L. GAIRDNER
LAKE FROME
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Centroptilum elongatum

Fig. VI.15 illustrates the distribution of *C. elongatum* in South Australia. In contrast to the wide distribution of *B. soror* this species is limited to two localities on the South Australian mainland, but is the only baetid species recorded on Kangaroo Island. Apart from the wide distribution of this species on Kangaroo Island, the two mainland localities of record are Carrickalinga Creek on the Fleurieu Peninsula, and Mosquito Creek in the South East. At the latter locality *C. elongatum* was found with *B. soror*, but this was the only co-occurrence of these two baetids. *C. elongatum* also co-existed with *Atalonella inconspicua, Atalophlebia australasica* and *Tasmanocoenis tillyardi*.

Cloeon fluviatile

C. fluviatile is widely distributed in the Northern Flinders Ranges, and sparsely distributed throughout the Mt. Lofty and Southern Flinders Ranges (Fig. VI.16). With the exception of the creek records in the Flinders Ranges this species occupies many of the farm dams in the Mt. Lofty and Flinders Ranges. Even in the creek localities *C. fluviatile* was recorded principally from large, standing, stationary, waterholes. No records of this species were made from either Kangaroo Island or the South East Drainage area. In all localities from which *C. fluviatile* was recorded it was the only baetid species found. *Tasmanocoenis tillyardi* occasionally was found to co-occur with *C. fluviatile*.

Fig. VI.15. Distribution of *Centroptilum elongatum* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *C. elongatum* in Australia.

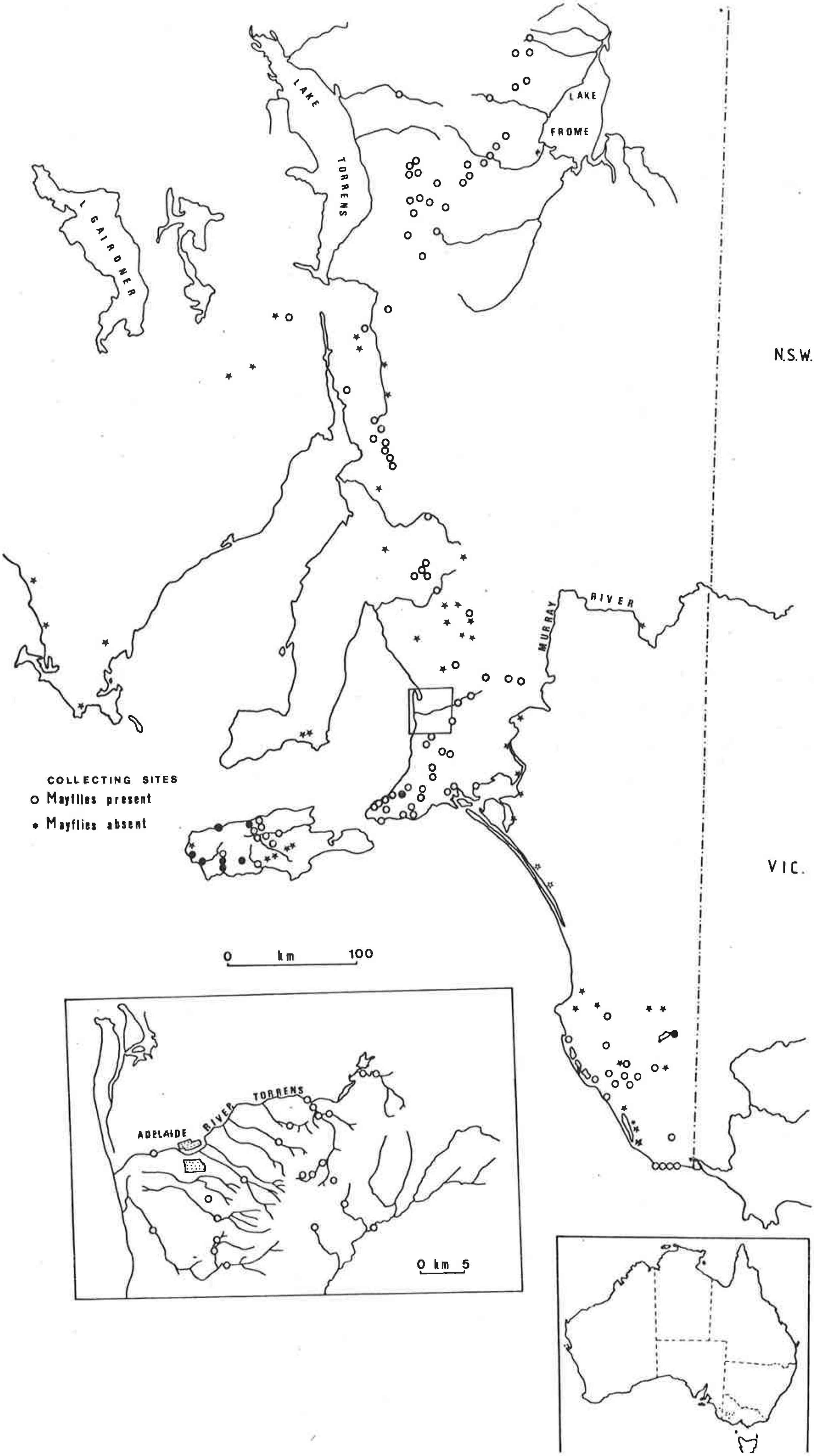
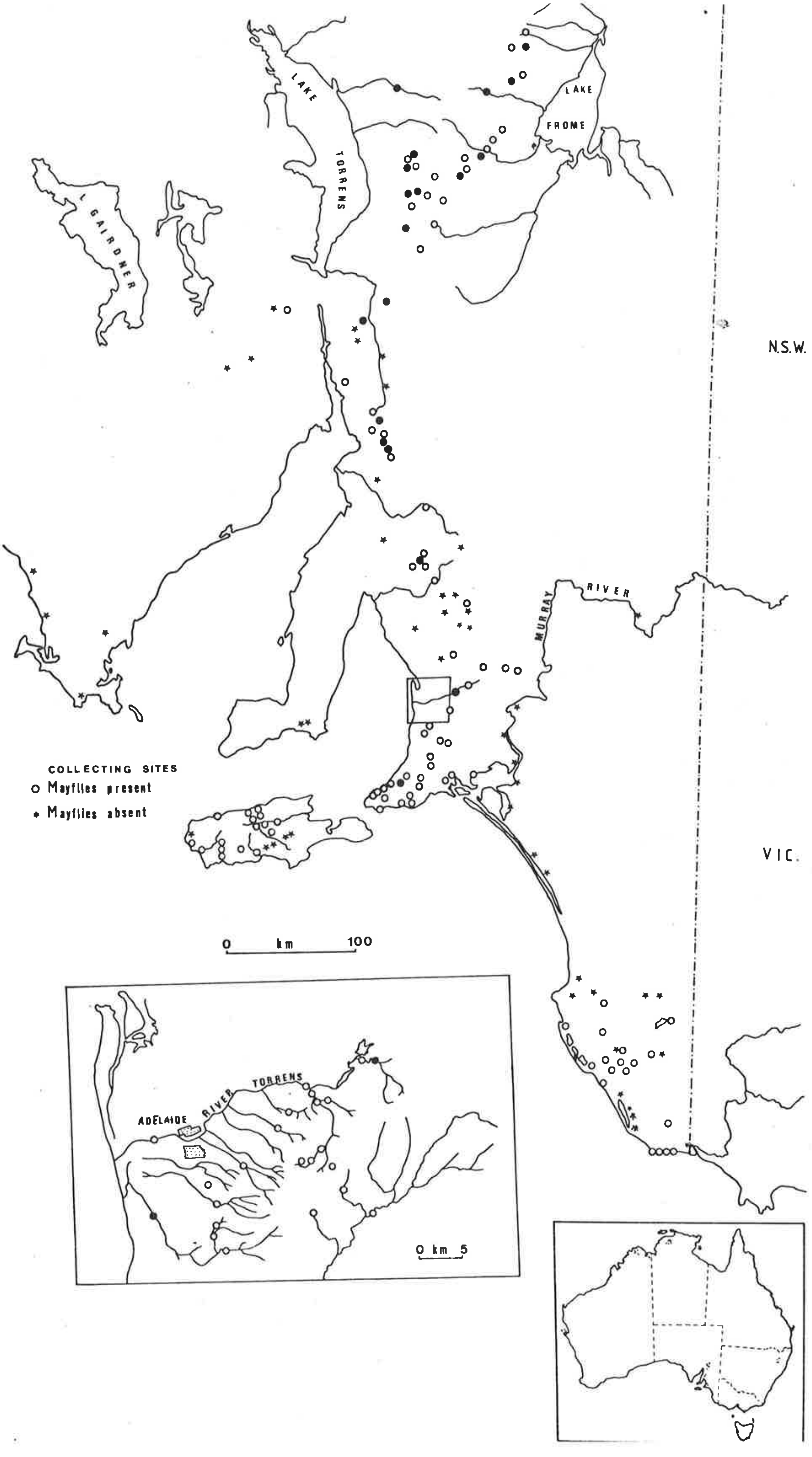

LAKE TORRENS
L GAIRDNER
LAKE FROME
N.S.W.
VIC.
MURRAY RIVER
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Fig. VI.16. Distribution of *Cloeon fluviatile* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *C. fluviatile* in Australia.


LAKE TORRENS
L. GAIRDNER
LAKE FROME
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Cloeon paradieniensis

This species was recorded at only two localities in South Australia, one in the Little Para River in the Gawler River drainage, and one in the agricultural drain system 7 km east of Furner near "Keera Park" in the South East (Fig. VI.17). This species does not appear to occupy farm dams to the same extent as *C. fluviatile* and therefore has not broadened its distribution utilising this man-made habitat. Its very limited distribution may reflect specific habitat requirements or inadequate sampling specifically for this species.

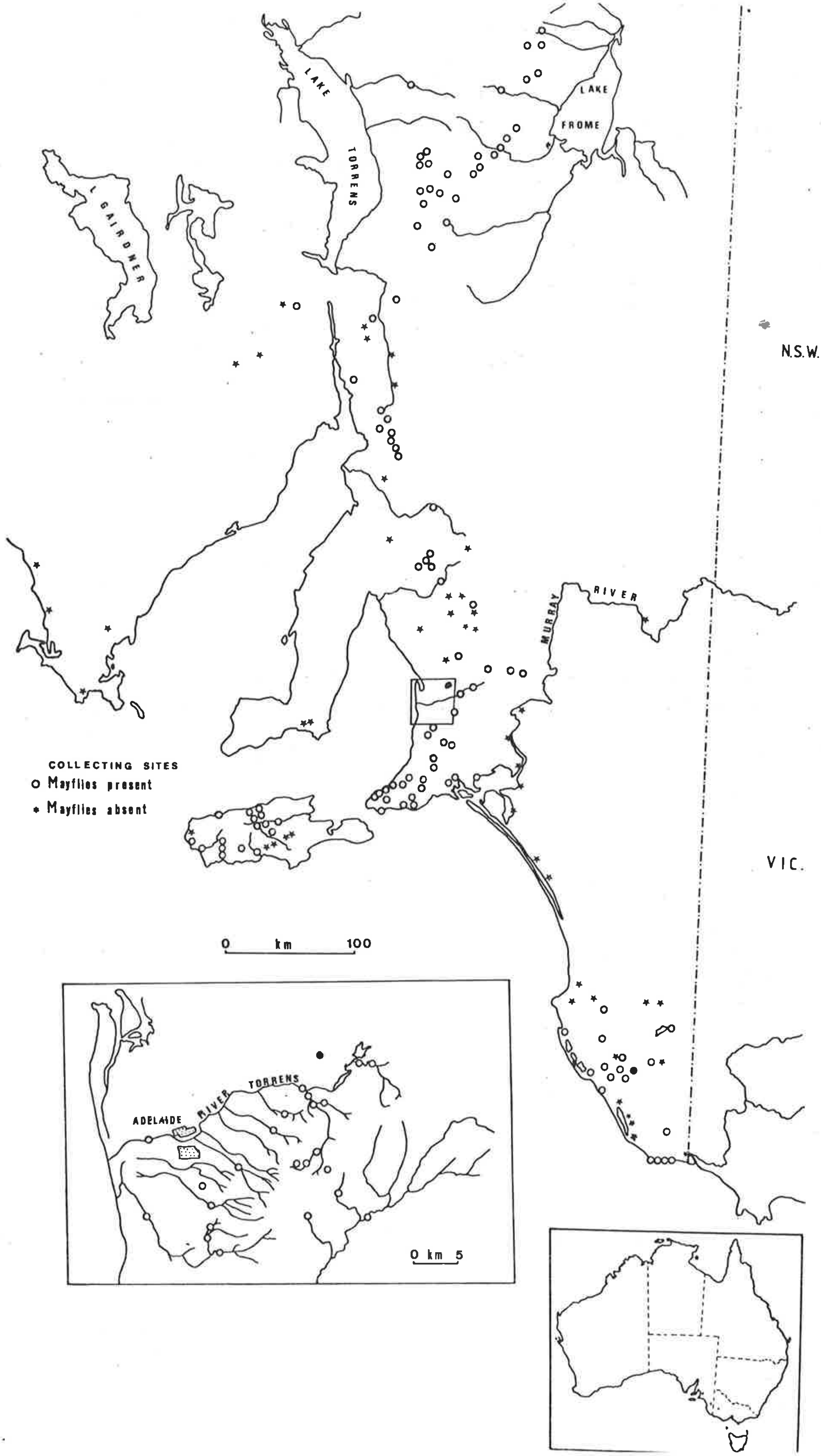
C. paradieniensis was found co-existing with *Atalophlebia australis* at both localities, and in the Little Para River *Atalonella inconspicua* was also recorded.

VI.3.1.3 F. Siphlonuridae:

Tasmanophlebia lacus-coerulei

The only siphlonurid species recorded in South Australia was *T. lacus-coerulei*. It occurs at only two localities within the State borders, both on the Fleurieu Peninsula (Fig. VI.18). Both localities have similar substrates of sand containing fine particulate organic material. Tookayerta Creek differs from Yankalilla Creek in having a high annual discharge and being relatively cool, originating from springs some 2 - 300 m above the collecting locality. Below this site much farming and clearing activity has altered the creek, and

Fig. VI.17. Distribution of *Cloeon paradieniensis* in South Australia (●), also showing localities at which this species was not recorded.


LAKE TORRENS
L. GAIRDNER
LAKE FROME
N.S.W.
MURRAY RIVER
COLLECTING SITES
○ Mayflies present
* Mayflies absent
VIC.
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

no *T. lacus-coerulei* was recorded. In Yankalilla Creek, this species was only recorded in the upper reaches where the substrate is similar to that present in Tookayerta Creek.

Although the streams of the south eastern corner of South Australia have sandy substrates, *T. lacus-coerulei* was not recorded there. The nearest record to these localities was in the Glenelg River near Dartmoor, south western Victoria. These records increase the known distribution of this genus which previously was believed to occur in ".... the lakes and streams at high altitude from Tasmania to the Blue Mountains in N.S.W." (Riek, 1970a). Both records in South Australia are in foothill or lowland localities.

T. lacus-coerulei in South Australia co-occurs with *Atalonella inconspicua,* and *T. tillyardi* at Yankalilla Creek, and in Tookayerta Creek it was recorded with *B. soror, A. inconspicua, A. fuscula* and *Atalophlebia australasica.*

VI.3.1.4 F. Caenidae:

Tasmanocoenis tillyardi

T. tillyardi is the most widely distributed mayfly in South Australia, occupying nearly every freshwater habitat available, with the exception of those on the Eyre Peninsula (Fig. VI.19). *T. tillyardi* was the only species of mayfly recorded west of Port Augusta in a farm dam near Hesso. *T. tillyardi* co-exists with almost all other mayfly species recorded from South

Fig. VI.18. Distribution of *Tasmanophlebia lacus-coerulei* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *T. lacus-coerulei* in Australia.

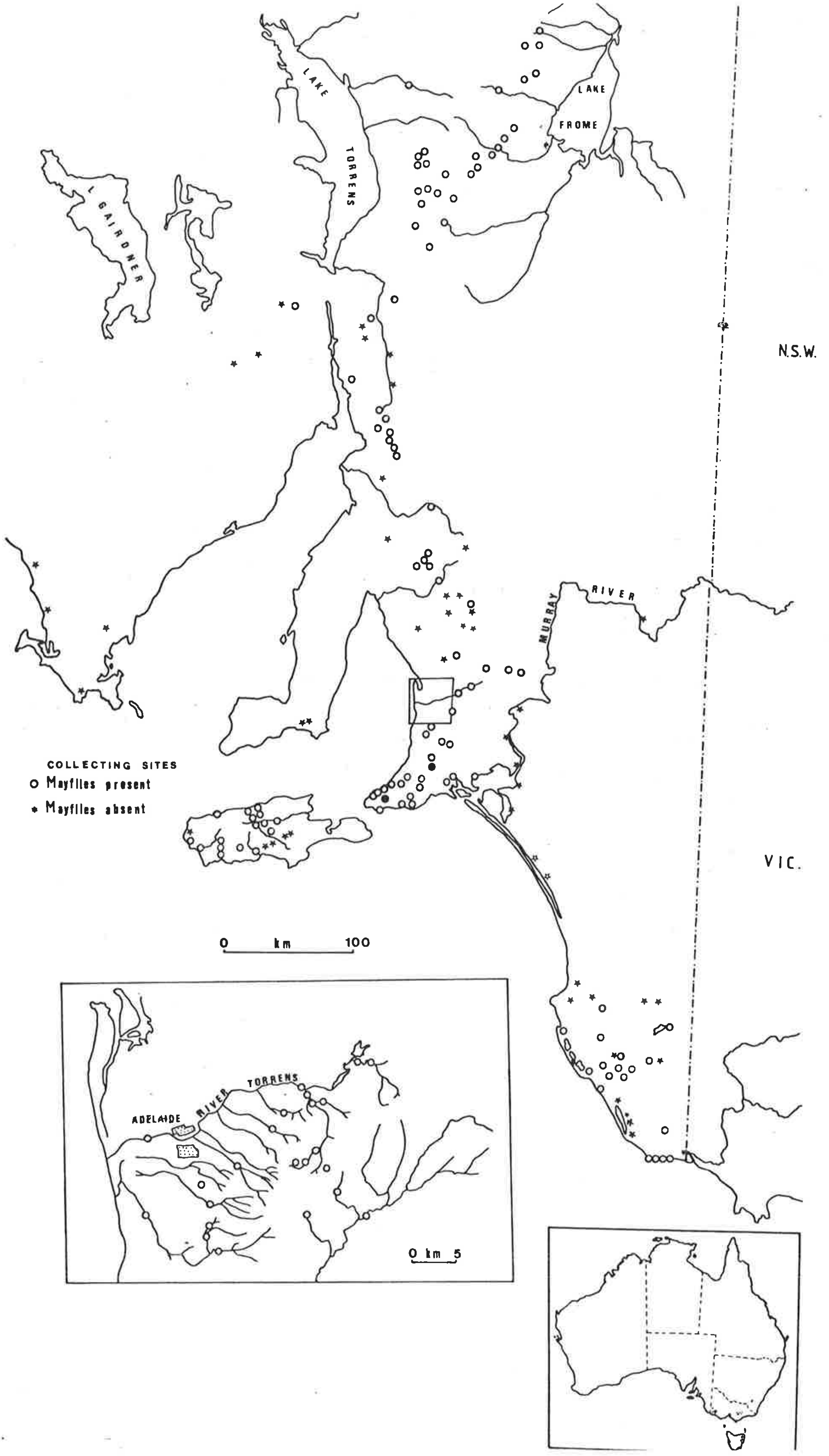
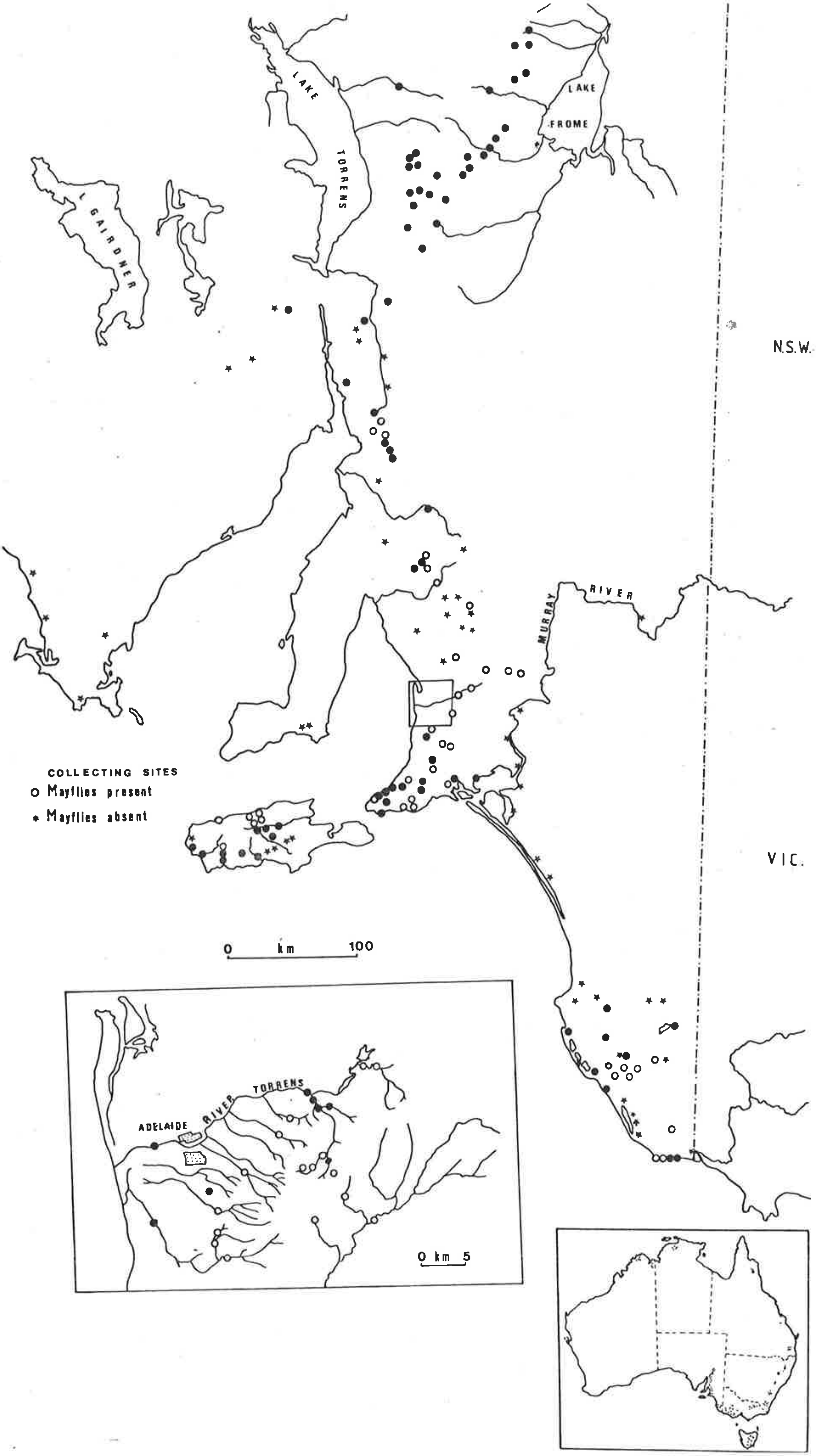

LAKE TORRENS
LAKE FROME
L. GAIRDNER
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Fig. VI.19. Distribution of *Tasmanocoenis tillyardi* in South Australia (●), also showing localities at which this species was not recorded. The inset shows the present known distribution of *T. tillyardi* in Australia.


LAKE TORRENS
LAKE FROME
L GAIRDNER
N.S.W.
MURRAY RIVER
VIC.
COLLECTING SITES
○ Mayflies present
* Mayflies absent
0 km 100
ADELAIDE
RIVER TORRENS
0 km 5

Australia with *Cloeon paradieniensis* the only exception. Its tolerance of a broad range of stream conditions, as recorded in Chapter 3, aids in its wide distribution.

VI.3.2 Discussion of Mayfly Distribution.

The distribution of mayflies in South Australia is clearly limited by the availability of persistent surface fresh water without which completion of their life cycle is impossible. Each species has different environmental pressures exerted on it, and these and geographical barriers to dispersal have influenced the distribution of each species as outlined above.

Documentation of the distribution of each individual species is artificial if interactions of other species are ignored. If an overall view is taken of the distribution of the South Australian mayflies five major faunal regions or sub-provinces within South Australia are evident. Not only does each of the regions possess a particular fauna, but also uniformity of geology, vegetation, climate (especially temperature and rainfall) and drainage. Each sub-province is discrete, being isolated by geographical barriers of either athallassic saline waters, or as on Kangaroo Island, by the sea. These sub-provinces are :

1. Northern Flinders Ranges (Localities 1 - 27)

2. Southern Flinders - Northern Mt. Lofty Ranges (Localities 28 - 50)

3. Mt. Lofty Ranges - Fleurieu Peninsula (Localities 51 - 97)

4. Kangaroo Island (Localities 98 - 113)

5. South East South Australia (Localities 114 - 131)

VI.4 Description of the South Australian Faunal Sub-Provinces

VI.4.1 The Northern Flinders Ranges

This sub-province is geographically isolated from the Southern Flinders Ranges by the flat, open denuded and saline Willochra Plain, which appears to be an effective barrier to mayfly colonization. Climatically the Northern Flinders Ranges are distinct from the Southern Ranges, with rainfall much lower (250-350 mm) and the summer periods tending to be hotter (+5°C) exceeding 37.5°C for more than 20 days annually (South Australian Year Book (1975)). Andrewartha and Birch (1954) included this region in the warm-temperate arid climatic zone, with a precipitation to evaporation ratio $(P/E) > 0.5$ for 1 - 3 months each year. The drainage of this sub-province tends to be spatially and temporally intermittent. Only after extensive rainfalls do the majority of water courses have flowing surface water. For most of the time the "streams" are characterized by short flowing stretches between deep water holes or large shallow pools originating from multiple spring systems. Only a few streams are permanent, but these may also experience periods of drying and form pools in excessively dry years. These streams are usually fresh from their sources to the point at which they debouch onto the western and eastern plains surrounding Lake Torrens and Lake Frome where they rapidly become saline.

In terms of mayfly fauna this sub-province is distinguished by being occupied by only three species, *Tasmanocoenis tillyardi*, *Baetis soror* and *Cloeon fluviatile*. The true distinguishing feature faunistically is not so much the presence of these species, but the absence of any leptophlebiid species. The distribution of both *Atalonella inconspicua* and *Atalophlebia australis* extends into the Southern Flinders Ranges, but does not penetrate beyond the Willochra Plain into the Northern Flinders Ranges. Two possible explanations can be suggested to explain this. Either the Leptophlebiidae have been eliminated from the Northern Flinders, or they have not been able to colonize the drier, warmer, less reliable northern localities. In Chapter 3 it was shown that *Atalonella inconspicua* was capable of occupying any niche available at Spring Creek, depending on the flow regime being experienced at the time. Observations on *Atalophlebia australis* suggest that this species is also opportunistic, being capable of surviving the seasonal flow regimes experienced in the semi-arid streams.

With these capabilities it would seem unlikely that both species have been eliminated from the Northern Flinders Ranges unless the temperature conditions were unfavourable. Normal temperature conditions in the southern streams of the Northern Flinders Ranges differ little (+2°C) from the temperature conditions in northern localities of the Southern Flinders Ranges. However, in terms of survival it is the extreme conditions which determine an animal's capacity of maintaining viable populations. During very hot weather in Summer the Northern Flinders' streams may reach temperatures in excess of 30°C which may be deleterious to both *Atalophlebia australis* and *Atalonella inconspicua*. The thermal tolerances of these species is unknown.

The geological history of the Willochra Basin would suggest this area was adequate mayfly habitat during the early Tertiary. The Willochra Basin sediments are highly leached, reflecting a higher rainfall than at present, and these sediments "were laid down under quiet fluviatile and lacustrine conditions ... " (O'Driscoll, 1955). This geological evidence of higher rainfall is supported by pollen grain studies (Kemp, 1976; Twidale and Harris, 1977) and fossil evidence (Specht, 1972), as discussed in detail in section VI.5. Central Australia had abundant conifer forests during the early Tertiary, indicative of high rainfall and a sub-tropical climate. With increased aridity and erosion as the Tertiary progressed, the sub-tropical forests were eliminated and replaced by the present dune system characteristic of Central Australia (Specht, 1972).

With the climatic changes of the late Tertiary the Willochra Basin changed from a wet, freshwater stream and lake system to a dry saline basin. O'Driscoll (1955) stated that "weathered bedrock invariably contains quite a high proportion of soluble salts which are dissolved by surface water during flow, the salinity of the water being increased when flat gradients prolong the time of contact, and also increase the evaporation rate".

During the early Tertiary the Willochra Basin was probably suitable habitat for mayflies. If leptophlebiid mayflies occupied the Central Australian region during this time it might be expected that relictual populations could exist in the drainages of the Northern Flinders Ranges, as is the case for *B. soror*, *C. fluviatile* and *T. tillyardi*. But the high temperature conditions which may periodically occur could have eliminated the leptophlebiid mayflies. However, based on the present day southern distributions of *Atalophlebia australis* and *Atalonella inconspicua* it is suggested that they are probably recent invaders into the Northern Mt. Lofty and Southern Flinders Ranges; the Willochra Plain acting as a barrier to their northerly invasion. In contrast, the three species which occupy this sub-province are widely distributed throughout Australia (see insets Fig. VI.14, VI.16 and VI.19), and probably occupied the freshwater habitats of Central Australia during the early Tertiary. With the increased aridity they are now restricted to the freshwater streams of the mountain chains.

Tasmanocoenis tillyardi occupies all habitats available in the Northern Flinders drainage, but *C. fluviatile*, although widely distributed, was never recorded in any flowing water. This latter species is well adapted to the stream conditions of the Northern Flinders, which, for most part of the year, are a series of stationary pools. Unlike *C. fluviatile*, *B. soror* was found in the limited flowing stretches of the northern creeks. As discussed in Chapter 3, *Baetis* requires flowing water to allow oxygen replenishment along the surface of its immobile gills. Consequently the distribution of *B. soror* in this sub-province is considerably narrower than either *T. tillyardi* or *C. fluviatile*.

VI.4.2 Southern Flinders/Northern Mt. Lofty Ranges Sub-Province

This sub-province has as its northern edge the barrier of the Willochra Plains, and to the south the Gawler River catchment. The precipitation in this area ranges between 500 - 600mm per annum and the temperature is similar to that experienced in the northern sub-province, but 2 - 5°C cooler during Summer. The P/E ratio exceeds 0.5 for 4 - 6 months, and the region is zoned as warm temperate, semi-arid (Andrewartha and Birch, 1954). The relief is low with the mountains rounded, unlike the steep rugged scarps of the Northern Flinders Ranges. Within this sub-province Mt. Remarkable is the highest peak rising some 950 m above sea level.

Drainage of the region is to the west into the Gulf St. Vincent with the Broughton, Wakefield and Gawler River catchments draining the majority of the area. The eastern slopes drain into the Willochra Creek, and the Lower Murray River Basin. The streams within these catchments are characterized by fresh upper reaches with the salinity increasing near the foothills as they flow onto their respective eastern and western plains. Similarly many streams are temporary, flowing on the surface for only short periods, and becoming a series of pools during the summer months, similar to those creeks of the Northern Flinders sub-province.

At the southern boundary of the Southern Flinders/Northern Mt. Lofty Ranges there is no apparent geographical boundary to ephemeropteran colonization, but faunistically this sub-province is distinct from the Southern Mt. Lofty Ranges/ Fleurieu Peninsula sub-province. The species occupying the mid-northern region include two leptophlebiids, *Atalophlebia australis* and *Atalonella inconspicua*; three baetid species, *B. soror*, *Cloeon fluviatile* and *C. paradieniensis*; and the ubiquitous caenid *Tasmanocoenis tillyardi*. Again the major distinguishing feature of this sub-province is the absence of species, especially *Atalophlebia australasica*, *Atalonella fuscula*, *Centroptilum elongatum* and the siphlonurid *Tasmanophlebia lacus-coerulei*. With the exception of *Atalophlebia australasica* all the other species have limited distribution in the Southern Mt. Lofty Ranges and Fleurieu Peninsula sub-province. Therefore, separation of the two Mt. Lofty Ranges sub-provinces may appear quite artificial. However, *C. paradieniensis* was not recorded in the southern sub-province, and the two widely distributed *Atalophlebia* species do not overlap in their distribution. It appears that *A. australis* is better adapted to occupy the less reliable streams of the mid-northern sub-province, whereas *A. australasica* occupies the more certain habitats of the southern Mt. Lofty Ranges and the Fleurieu Peninsula. Both species occur in the River Torrens Catchment, but were never recorded at the same locality. The reliability of stream habitat may explain the discrete distribution of the two species. There is some circumstantial evidence for competitive exclusion between the species but no experimental evidence to support or test this hypothesis. Distribution evidence supporting this hypothesis comes from the River Torrens, where *A. australis* is present in the upper reaches which are semi-permanent, but *A. australasica* is absent. Below Kangaroo Creek dam on the River Torrens the reverse is the case. Since *A. australis* is capable of inhabiting both permanent and intermittent streams there would seem to be no reason why this species could not occupy the generally more reliable Southern Mt. Lofty Ranges drainage. Conversely, if *A. australasica* requires consistent stream habitat, characteristic of the southern sub-province, it would tend to be limited to its present distribution.

The circumstantial evidence for competitive exclusion is reasonably strong. Exclusion of *A. australis* to the otherwise favourable southern stream suggests direct competition with *A. australasica*, but this is not necessarily so. Competition may come from other Insect Orders with similar distributions and habitat requirements. Since no investigation of comparative stream faunas (with the exception of the mayflies) was performed, no evidence for or against this suggestion can be presented. However, the absence of *A. australis* in the Southern Mt. Lofty Ranges/Fleurieu Peninsula sub-province is considered to be biologically influenced rather than geographically determined.

The distribution of species within the mid-northern sub-province is closely correlated with the distribution of fresh water (< 3‰). In the majority of cases the increase of salinity as the streams flow onto the plains tends to limit all species to the upper catchment streams. *Cloeon fluviatile* occupies similar habitats to those in the Northern Flinders Ranges sub-province, but in addition utilises the farm dams and reservoirs that are frequently found within the Southern Flinders/Northern Mt. Lofty Ranges sub-province. The distribution of *C. fluviatile* has probably been influenced by farm dam construction, which has allowed effective colonization.

Unlike *C. fluviatile*, *C. paradieniensis* has a very limited known distribution in the North Para River. The distribution in the Para River catchment may be greater than collections suggest, as a result of the apparent disappearance of this species during winter months. During Winter, when the creek was flowing, no specimens were collected either from the type locality or from nearby. The relationship between the two *Cloeon* species is unclear, but both species were never recorded together at any one locality.

The distribution of *Baetis soror* is again limited to permanent flowing streams comprising only the Mt. Remarkable drainage (i.e. Spring Creek), and the upper reaches of the Rocky River. The sluggish temporary system of the Light, Wakefield and Gawler Rivers do not possess populations of *B. soror*.

Tasmanocoenis tillyardi is almost ubiquitous, occurring in the upper reaches of all systems where salinity was below 3‰. However, *T. tillyardi* was not recorded in the eastern flowing Marne River catchment, this is surprising since the species is the most widely distributed in South Australia.

Possible explanations for its absence may be either periods of high salinity of the Marne River waters during Summer, or historically it has not recolonized the stream after a period of severe drought. During the egg development study (Chapter 5) it was shown the eggs of *A. inconspicua* can survive salinities up to 7‰, but to explain the absence of *T. tillyardi* the eggs of this species would have to be incapable of surviving in brackish waters. No eggs of *T. tillyardi* could be collected, and therefore no salinity tolerance was determined. The alternative explanation that *T. tillyardi* has not recolonized, is quite likely. The life span of adult *T. tillyardi* is very short, certainly less than eight hours, and more likely less than three hours. Since the species flies only at night, when wind is absent, the recolonization potential is limited. The Marne River has probably been dry at periodic intervals thereby eliminating most freshwater species. The presence of *Atalonella inconspicua* and *Atalophlebia australis* is not inconsistent with this idea, because their recolonization potential is much higher than that of *T. tillyardi*. The duration of adult life is measured in days, rather than hours, and they swarm, mate and oviposit during the day at which time wind is more likely to be present. Recolonization from the River Torrens catchment is likely to occur. The distribution of *Atalonella inconspicua* is similar to that of *T. tillyardi*, with the Marne River the obvious exception.

VI.4.3 Southern Mt. Lofty Ranges/Fleurieu Peninsula Sub-Province.

As mentioned above, this sub-province lacks a distinct northern barrier but is geographically isolated to the West by Gulf. St. Vincent, by Backstairs Passage to the South and by the dry, saline Murray Plains to the East. The Southern Mt. Lofty Ranges are of low relief with Mt. Lofty the highest peak at 727 m above sea level. Although of low altitude, the orographic effect on the climate of the sub-province is obvious, with conditions cool and wet compared to the northern sub-provinces. Precipitation is at its maximum on Mt. Lofty, where observations from 1972-1974 suggested the mean annual rainfall may be as high as 1600 mm (Schwerdtfeger, 1976), but decreases to below 500 mm in the rain shadow on the eastern slopes. The majority of the province, however, receives in excess of 600 mm per year. Although rainfall is relatively high, it is concentrated during the winter months, and the summer months are characterized as hot and dry.

Summer average temperatures for the sub-province are near 25°C with average winter minima between 2 - 5°C on Mt. Lofty and 5°C over much of the Fleurieu Peninsula. More detailed climatic discussion for the sub-province can be found in the South Australian Year Book (1975); Schwerdtfeger (1976) and Bureau of Meteorology "Climate of Adelaide" (1978). Andrewartha and Birch (1954) include this region in the warm-temperate, semi-humid bioclimatic zone where $P/E > 0.5$ for 7 - 9 months of the year.

The drainage of the sub-province is primarily to the west and south with the four drainage basins of the Torrens River, Onkaparinga River, Myponga River and the Fleurieu Peninsula. The streams in these drainage basins are permanent, although not always flowing during Summer, and reliably contain water throughout the year. On the eastern slopes of the Mt. Lofty Ranges is the Lower Murray River drainage. Mayflies were recorded in the Finniss River catchment which flows south into Lake Alexandrina, but to the north the numerous small watercourses are predominantly dry, as the region is in the rain shadow of the Ranges. The creeks only flow after heavy rain, but since the soil around Lake Alexandrina north of the Finnis River is highly saline, they are very salty. No mayflies were recorded from this area.

Four mayfly species are widely distributed: *Atalophlebia australasica*, *Atalonella inconspicua*, *Tasmanocoenis tillyardi* and *Baetis soror*. As in all other sub-provinces *B. soror* was only recorded in streams which had permanently flowing stretches, whereas the other species were found wherever fresh water occurred. The absence of *Atalophlebia australis* was discussed above.

Two comparatively rare species also occur in this sub-province, although their distribution is very limited: *Tasmanophlebia lacus-coerulei* and *Centroptilum elongatum*. *T. lacus-coerulei* was only recorded in South Australia from two streams, in a 200 m length of Tookayerta Creek, and a similar small stretch of the Yankalilla River. Both localities have sandy substrates rich in fine particulate organic material.

In the case of Tookayerta Creek, the stream is unique in the South Australian ranges, as it is a permanent spring-fed stream which has a high all year discharge, low summer temperature (< 18°C) and a high winter temperature (> 6°C). During Summer a luxuriant growth of watercress (*Nasturtium* sp.) occurs, trapping large amounts of fine particulate organic material and creating a stable environment for *T. lacus-coerulei*. Temperature and discharge data were not collected for Yankalilla Creek as the presence of *T. lacus-coerulei* was not recorded here until near the end of the present study. However, summer discharge was less and more variable, and temperature higher than at Tookayerta Creek.

In Tookayerta Creek, *Atalonella fuscula* another species uncommon in South Australia, co-occurred with *T. lacus-coerulei*. In the Southern Mt. Lofty Ranges/Fleurieu Peninsula sub-province this species was found only in Tookayerta Creek. As mentioned *A. fuscula* and *A. inconcpicua* co-occurred, but were reproductively isolated by emergence and flight times. *A. inconspicua* emerged in early Spring, while *A. fuscula* emerged later in Summer and Autumn.

That *A. fuscula* is restricted to Tookayerta Creek, suggests that this is the only stream which satisfies its environmental requirements. Tookayerta Creek resembles the more southern, South East sub-province streams, permanently flowing and relatively cool. The distribution of *A. fuscula* in the Southern Mt. Lofty Ranges therefore appears limited by the distribution of permanent, cool stream habitats.

Centroptilum elongatum is also limited to one locality in this sub-province; Carrickalinga Creek. This stream was temporary in 1977 with the type locality being dry in the Summer. Upstream the surface water was restricted to small areas of spring influence with pools and short inter-connecting wet stretches. The upper reaches of other streams in this sub-province may also contain this species, but until more collections are made this is speculation.

The only other species recorded in this sub-province was *Cloeon fluviatile*; recorded in large stationary pools in the River Torrens and Sturt River during the summer months. These were the most southerly records of this species.

VI.4.4 Kangaroo Island Sub-Province

Kangaroo Island is the largest island off the coast of South Australia separated from the Fleurieu Peninsula by Backstairs Passage. Structurally it is part of the Mt. Lofty Ranges and Fleurieu Peninsula (Daily *et al*, 1979), but has been isolated from the mainland since the sea level rose at the end of the Pleistocene.

Rainfall on Kangaroo Island is similar to that of the Fleurieu Peninsula with precipitation concentrated during the winter months. Rainfall is highest on the western half of the island, exceeding 600 mm annually (with higher altitude regions receiving some 900 mm), decreasing to 500 mm or less in the east (Burrows, 1979). Evaporation is also high, and the salinity of surface waters reflect the west-east rainfall effect, with fresh waters in the west and saline waters in the east (Fig. VI.4). Summer average temperature for the island is approximately 22.5°C and winter average 7.5°C. Thus the climate is temperate, with a relatively mild wet Winter and a warm dry Summer. For a detailed climatic discussion see Burrows (1979). The island has a similar bioclimatic classification as the Fleurieu Peninsula, with $P/E > 0.5$ for 7 - 9 months of the year (Andrewartha and Birch, 1954).

Clearly isolated geographically, Kangaroo Island has a distinct mayfly fauna made noteworthy by the complete absence of *Baetis soror*, and its replacement by *Centroptilum elongatum*. The distribution of *C. elongatum* is restricted to the freshwater streams of the western half of the island, but unlike the sparse distribution on the South Australian mainland this species is present in almost all available streams. The absence of *B. soror* may be the result of the temporary nature of the Kangaroo Island creeks, which during Summer often become a series of spatially isolated pools. Although the winter conditions in the streams would suit the flow requirement of *B. soror* this may not be met in the dry summer months. On the Fleurieu Peninsula *C. elongatum* occupied the temporary Carrickalinga Creek, which had a similar annual flow regime to that of the Kangaroo Island creeks. The distribution of *B. soror* and *C. elongatum* appears mutually exclusive except at Mosquito Creek in the South East where both species were recorded. It appears that *B. soror* has an advantage in permanent flowing streams, and *C. elongatum* an advantage in temporary streams.

Only three other species of mayfly were recorded on Kangaroo Island; *Atalophlebia australasica, Atalonella inconspicua* and *Tasmanocoenis tillyardi*. These species are widely distributed in the Southern Mt. Lofty Ranges and Fleurieu Peninsula, and the similarity to the Kangaroo Island fauna is obvious. All three species were found co-occurring at many localities, but the distribution in the Cygnet River is worthy of particular mention. Unlike the majority of streams on Kangaroo Island the Cygnet River drains to the east and is fresh at its source, grading to saline along the lowland reaches. This natural salinity gradient could be useful in describing the salinity tolerance of the various mayfly species. Records of salinity have not been made in the river and therefore definite values cannot be expressed. However, in the lowland reaches the water is salty to taste and therefore exceeds 3 - 5‰. No mayflies were recorded in these lowland reaches. Upstream at locality 111 the water was just salty to taste (salinity 3 - 5‰) and only *A. inconspicua* was recorded. Further upstream at localities 112, and 113 the water was fresh (< 3‰) and both *T. tillyardi* and *A. inconspicua* were recorded. The less saline western and southern drainages were occupied by all four species. It therefore appears that the widespread *T. tillyardi* and the South Australian endemic *A. inconspicua* are capable of occupying waters of higher ionic content than *A. australasica* and *C. elongatum*.

VI.4.5 South East Sub-Province

The fifth ephemeropteran sub-province consists of the south-east of South Australia. This sub-province is geographically isolated from the other sub-provinces by the northern boundary of the large Murray Artesian Basin extending throughout New South Wales, South Australia and Victoria. This basin has a complex history of sedimentation during the Mesozoic and Tertiary (Glaessner and Parkin, 1958). In South Australia the Basin can be divided into two divisions; the northern Murray Basin proper and the Gambier Embayment (Glaessner and Parkin, 1958; Alderman, 1973) separated by a higher structure, the Padthaway Horst. The Padthaway Horst is the northern boundary of the South East sub-province.

The geology of the Gambier Embayment is dominated by the Mt. Gambier limestone deposited by Oligocene seas which covered the entire Murray Basin. During the Quaternary, regression of the seas occurred, caused by uplifting of the region, notably during the Pleistocene (Alderman, 1973), and a series of coastal dunes were deposited at each successive water level. These low northwest-southeast trending dunes, separated by level plains, are the dominant geomorphological feature of the South East, with the notable exception of the few extinct Quaternary volcanoes in the Mt. Gambier-Millicent area.

The climate of the Murray Basin is predominantly semi-arid whereas high winter rainfall occurs in the Gambier Embayment, with annual rainfall exceeding 500 mm over the entire region and 800 mm in the Mt. Gambier and Millicent area. The temperature regime is temperate, with a mean maximum summer temperature less than 30°C, and a mean minimum winter temperature greater than 5°C over much of the sub-province. The region was classified as warm-temperate, semi-humid by Andrewartha and Birch, and $P/E > 0.5$ for 7 - 9 months per year.

As recorded in Section VI.2, evaporation exceeds precipitation over the whole State. However, the South East sub-province differs from the rest of the State in predominantly overlying permeable limestone. This limestone and the sand-dune ranges become charged with water by the high winter rainfall, and from various marginal intake areas, the most important being the Goroke-Edenhope district in Victoria (Glaessner and Parkin, 1958; Williams, 1974). Ground water movement is towards the north-west, with high quality in the south-east deteriorating, in terms of salinity, to the north-west.

The low topography of the South East sub-province and the absence of surface drainage characterized this region before European settlement of South Australia. The plains between the sand-dune ranges were subject to prolonged and extensive flooding during the high rainfall Winters because of the obstructions of natural drainage by the dunes, and a high ground water level. Williams (1974) has reviewed man's activities in these regions from 1863 when the first moves were made to drain portions of the South East. Since then a series of drainage channels have been cut between the ridges and at right angles to the direction of the dunes (i.e. NE-SW). These have effectively drained the area, so that the former swamp-lands of the South East are no longer subjected to extensive flooding. The swamps have now been replaced by streams.

Although the water quality, i.e. salinity, still tends to deteriorate towards the north-west along the dune system, the direction of surface flow has been somewhat modified, with the north flowing water intercepted at several points and diverted westward to the sea. Two major drains, Bakers Range Main Drain and Reedy Creek Drain both flow south-east to north-west until reaching the right angle Eastern Division Diversion Drain where the drainage alters, to northeast-southwest to the sea. The northern extensions of both these drains flow northwest-southeast to the Eastern Division Diversion Drain. This directional flow (i.e. north-west direction of the southern sections and south-east direction of the northern sections) has had an obvious effect on the mayfly fauna which will be discussed below.

Clearly the South East sub-province is distinct in morphology and drainage from the other four sub-provinces. In terms of the mayfly fauna it is also distinct, possessing a distinctly "Victorian" fauna. Only two species are fairly widely distributed; *T. tillyardi* and *Atalophlebia australis*. Both species are distributed in such a way as to appear almost mutually exclusive, but this appears to be caused by the water quality (salinity) and the direction of the surface drainage. *T. tillyardi* occupies the lower quality north-west waters which flow south-easterly to the Eastern Division Diversion Drain, while *A. australis* occupies the lower salinity southern waters. The southern drainage tends to the north-west and therefore passively assists colonization in this direction until the Eastern Division Diversion Drain is reached. The south-east flowing Reedy Creek Drain and Biscuit Flat Drain, because of their directional flow, obstruct further northerly colonization by *A. australis*. These two species are the only ones which have successfully utilized the man-made drainage system of the dune ranges. *Cloeon paradieniensis* was also recorded in a "tributary" of Reedy Creek Drain near "Keera Park", but this was the only record of this species in the drains.

To the north-east of the dune drains is Bool Lagoon, filled by Mosquito Creek which rises in Victoria. The Bool Lagoon Outlet Drain on the western side of Bool Lagoon connects to the Eastern Division Diversion Drain to maintain a relatively static water level in the Lagoon. *T. tillyardi* occupies the inlet and outlet of Bool Lagoon, but *A. australis* was not recorded there. *Centroptilum elongatum* was also recorded in Mosquito Creek, but not in the Bool Lagoon Outlet Drain. This was the only record of this species in the South East sub-province.

Only one other species was recorded in the man-made drainages of the dune ranges, the endemic *Atalophlebia auratus*. This species was recorded from one locality in Bakers Range Main Drain, where it was found in association with *A. australis*. This limited distribution appears to be the result of the drainage of the swamps. *A. auratus* is morphologically distinct from both *A. australis* and *A. australasica*, not only in the male genitalia, but also in the nymphal morphology. The leg measurements of *A. auratus* are similar for all legs, with the ratios of femur length to tibia and tarsal lengths similar for the fore, mid and hind legs (i.e. 1.00 : 0.98 : 0.49; 1.00 : 0.96 : 0.48; 1.00 : 0.96 : 0.47 respectively). In contrast, both *A. australis* and *A. australasica* have leg lengths that progressively increase from the fore to the hind leg. The short fore legs and longer hind legs tend to orient the nymphs of *A. australis* and *A. australasica* with the head lower than the rest of the body. In a stationary body of water (i.e. swamp) this inclined orientation would have no obvious advantage over the horizontal orientation of *A. auratus*. However, under flowing conditions this inclined orientation would effectively utilize the forces of the flowing water to push the nymphs onto the substrate, whereas the horizontal stance of *A. auratus* would be a disadvantage. *A. auratus* is perhaps adapted to the swamp-like conditions which predominated in the South East before European settlement, and to which it is apparently endemic. Since the building of the artificial drains the swamp environment has been altered, giving an advantage to those species adapted to a lotic environment. Therefore, the limited distribution of *A. auratus* may be a result of the drainage activities of man. Although Bakers Range Main Drain was dredged in the 1880s, its effect was limited until the Eastern Division Diversion Drain was constructed between 1944-1970 (Williams, 1974). The change from swamp to flowing "river" is therefore only recent, and Bakers Range Main Drain services one of the last areas drained. It may therefore be the last refuge of *A. auratus* which now appears to be in direct competition with the invading *A. australis*. The limited distribution of *A. australis* in the drains suggest a recent colonization.

Along the southern coast of the South East sub-province are a series of spring-fed streams which have high permanent discharges. These streams, of which Eight Mile Creek is the major system, were all channelled in the 1900-1943 period. Accessory drains were also constructed during this period, to encourage drainage of the groundwater and therefore decrease flooding of the area. These permanent coastal drains and streams have the richest mayfly fauna of any streams in South Australia, with the exception of Tookayerta Creek. Species occupying these streams and drains include *T. tillyardi*, *Atalophlebia australasica*, *Atalonella fuscula*, *A. pilosa*, *Jappa pipinna* and *Baetis soror*. *Jappa pipinna* and *A. pilosa* were only recorded in the South East sub-province, but this apparently limited distribution is because the present study was confined predominantly to the South Australian political borders. In the Glenelg River catchment, the southern streams of the Grampians (i.e. Wannon River catchment) and adjacent Victorian coastal streams these two species are ubiquitous. Similarly the other species, with the exception of *A. auratus* are also common in these Victorian streams. The South East sub-province of South Australia is therefore more correctly considered as a "Victorian" sub-province, as the aquatic fauna are not limited by political boundaries.

Atalophlebia australis and *A. australasica* both occurred in the South East sub-province, but were never recorded from the same locality, a situation parallel to that in the River Torrens and the Northern and Southern Lofty Ranges sub-provinces.

VI.5 Origins of the South Australian Mayfly Fauna.

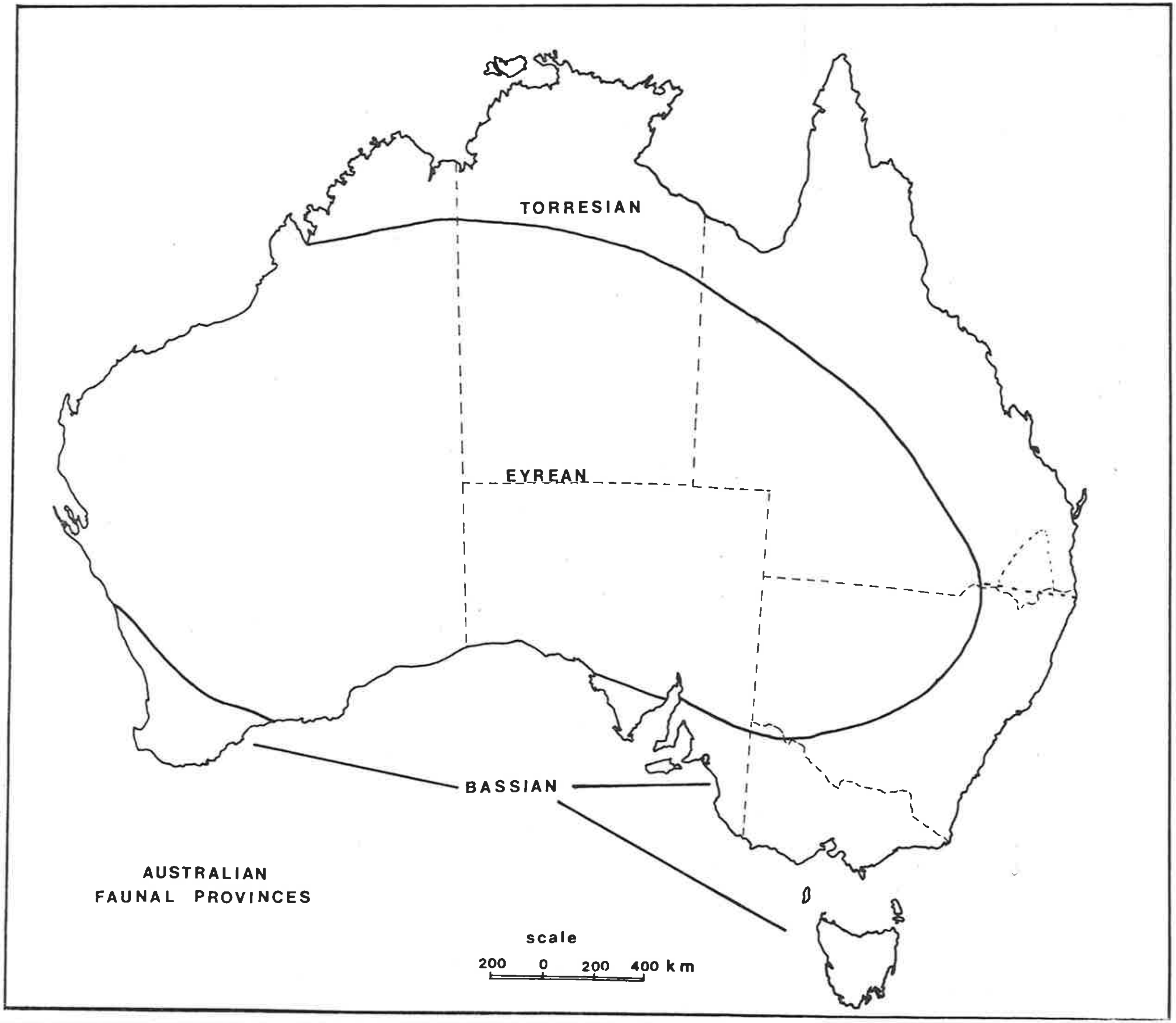
The Ephemeroptera are useful insects for the study of biogeography as they require water throughout their nymphal life, and tend to have low tolerance to saline waters. The adult reproductive stage is very short, which greatly inhibits its ability to disperse widely in the only stage not totally dependent on water. Barriers of marine areas, arid land, saline athalassic waters and high mountain ranges are effective and dispersal therefore only occurs when habitats are available for colonization, or aerial mechanisms, i.e. wind dispersal, can act over a short distance in a relatively short time. Dispersal would therefore be relatively slow unless barriers were reduced by changing climate, or the creation of suitable habitat occurred by alteration of the *status quo* e.g. by drain construction.

The study of zoogeography involves interpretation of present day distributions and, with botanical, geological and zoological evidence, the elucidation of the origins of this distribution. The technique obviously has inherent problems, especially in regions where fossil records are absent, and therefore no direct evidence exists. Also man's activity has, in many regions, altered the environment in such a way that the faunal assemblage is no longer a product of natural historical interactions, but rather a very recent event.

The Australian zoogeographical region can be sub-divided into three faunal provinces, which can be classified both ecologically and by faunal characteristics (Fig. VI.20). These were described and discussed by Mackerras (1970) and Tyler (1976). The Bassian Province is the moist temperate region consisting of south-western Western Australia, the south-east coastal region of the Australian mainland, and Tasmania. The Torresian Province has a wet-moist tropical to sub-tropical climate and consists of the northern and north-eastern coastal belt of Australia. The arid central region of the continent, with rainfall below 500 mm per year comprises the Eyrean Province. Mackerras (1970) left the limits of the Bassian Province open in the South Australian region, but Tyler (1976) considered that the Bassian Province ended in the South East corner of South Australia, leaving the Mt. Lofty-Flinders Ranges in the Eyrean Province. The uncertainty of the limits to each province is caused by the mosaic of species composition at the boundaries. Fauna from each province interact and mix forming transitional zones. Therefore, the general position of the limits of each province is probably of more value than a specific position, unless there is an obvious physical barrier.

With the limited available distribution records of Australian mayflies collated from the taxonomic papers, very little zoogeographical interpretation can be made. Similarly the absence of a fossil record, with the exception of a record in southern Tasmania from Triassic fluvial deposit (Riek, 1962), make zoogeographical discussion very conjectural. In an attempt to clarify the origins of the South Australian mayfly

Fig. VI.20. The zoogeographical provinces of Australia.


TORRESIAN
EYREAN
BASSIAN
AUSTRALIAN
FAUNAL PROVINCES
scale
200
0
200
400 km

fauna, additional collections from Victoria, Tasmania and south-west Western Australia and north-west Western Australia were examined. Material held in the South Australian Museum, and the National Museum of Victoria was also studied, but collections in the National Insects Collection of C.S.I.R.O. in Canberra were not available for examination. From the examined material, and published records, the distribution of many of the South Australian species throughout the whole Australian region were traced, and the possible origins of the South Australian fauna are discussed. It is stressed that the following discussion is conjectural and is supported only by present day distributions, pollen grain and fossil plant evidence, and geological evidence.

Of the thirteen species of mayfly present in South Australia, two are endemic (*Atalonella inconspicua* and *Atalophlebia auratus*) and one (*Cloeon paradieniensis*) appears endemic, but this may only reflect poor collection of *Cloeon* in the material examined. The other species have wide distributions throughout the Bassian Province (see insets of Figs. VI.7 - VI.19) with *T. tillyardi* having an ubiquitous coastal distribution in the Bassian and Torresian Provinces. None of the South Australian species were present in the south-west Western Australian material examined, although *B. soror* is described from this area. The species with the relatively wide Australian distributions are those that give more complete information on the factors affecting their present day distribution.

Of possible factors determining the distribution of the South Australian Ephemeroptera, two appear to have been extremely important, namely climate and eustatic changes in sea level. When the climate and sea level changes in the South Australian region are examined, the South Australian mayfly fauna appears to consist predominantly of a relictual fauna, influenced, as has been the vegetation of the area, by increasing aridity and the invasion of the seas. Although limited fossil evidence of Australian mayflies is available (Riek, 1962, 1970b), fossil evidence from paleo-botanical studies is useful in determining the past climatic conditions of the arid regions which today are totally unsuitable for mayfly colonization. Studies of pollen grains have shown that during the early Tertiary the main elements of the extant flora of Australia were present on lateritic, podsolic soils which were developed under a sub-tropical climate of high rainfall and high temperatures (Specht, 1972). Kemp (1976) found no indication of marine influence in Central Australia during the early Tertiary, but did find an abundance of conifer pollen of *Microcachrys* and *Podocarpus*, both forms indicative of high rainfall. Twidale and Harris (1977), in a study of Ayers Rock and the Olgas in Central Australia, found the Tertiary flora, as indicated by pollen grains, to closely resemble the extant vegetation of the Gippsland and Otway Basins of Victoria.

As the Tertiary progressed, the climate of northern South Australia changed and became less humid, until by the end of the Tertiary early Quaternary, the climate was arid to desertic (Jessup, 1961). Throughout the Quaternary, interspersed with wet periods, were a number of severe arid periods occurring predominantly in the Pleistocene and up to the present. During the arid periods of the Pleistocene widespread erosion occurred and in the present-day arid regions the sub-tropical vegetation was destroyed, and replaced by the extensive dune systems which are characteristic of Central Australia (Specht, 1972).

Aridity was not the only major destructive influence on the early Tertiary flora and Fauna. During the Tertiary (Oligocene and Miocene) there was a major invasion by the sea onto the Murray-Otway Basin, the St. Vincent Basin and the Eucla Basin of South Australia. It was during this time that the Gambier limestone assemblages were deposited. The Murray-Otway Basin seas are the most important in terms of the South Australian mayfly fauna as they probably destroyed any freshwater faunal assemblages previously occupying these regions, and created an extensive barrier between central Victoria and South Australia, thus isolating the respective fauna. The freshwater fauna were therefore probably restricted to the Mt. Lofty-Flinders mountain chain, bordered to the east, and south by the Oligocene seas, and to the north and west by arid deserts. Towards the end of the Miocene, and continuing into the Pliocene, the seas receded and the Basins began to upwarp in relation to the sea (Kenley, 1971). During the Pleistocene glaciation (which was only of indirect influence on the South Australian fauna) the sea level dropped, because water was locked in the ice masses. The extent of the drop is uncertain, but Davies (1974) considered that 125 m below present-day levels would not be an over-estimation. During this time Kangaroo Island was continuous with the Fleurieu Peninsula (Daily, *et al*, 1979) and further to the south, Tasmania was continuous with the Victorian mainland. At the end of the Pleistocene the sea level again rose and reached its present level some 9,000-10,000 years B.P.

The consequence of the climatic changes, eustatic sea level changes and man-made environmental alterations as documented by Williams (1974) can each be considered as factors determining the South Australian mayfly distribution. The mayfly fauna consists of three groups of species: the endemics (*Atalonella inconspicua* and *Atalophlebia auratus*); the species widely distributed, but isolated to mountain ranges (*Atalophlebia australis*, *A. australasica*, *Atalonella fuscula*, *Baetis soror*, *Cloeon fluviatile*, *C. paradieniensis*, *Centroptilum elongatum*, *Tasmanocoenis tillyardi* and *Tasmanophlebia lacus-coerulei*); and the recent invaders from Victoria (*Jappa pipinna* and *Atalonella pilosa*). Some species occur in more than one group, e.g. *Atalophlebia australis*, *A. australasica*, *Atalonella fuscula*, *Tasmanocoenis tillyardi*, *Centroptilum elongatum* and *Baetis soror*, all of which were isolated to the Ranges, but have also re-invaded from Victoria.

The distribution of *T. tillyardi* and *C. fluviatile* overlap at least two Australian zoogeographical provinces (Figs. VI.16 and VI.19). The records of *C. fluviatile* are limited because the permanent pools and dams in Australia have not been extensively collected. As mentioned in Chapter 2, this species was described from New Guinea (Ulmer, 1919) and recorded at

Armidale by Harker (1950a). None of this material could be examined, therefore conclusions drawn about this species are perhaps tentative. Conversely, the distribution of *T. tillyardi* as illustrated in Fig. VI.19 is based on examined material and its distribution includes the Bassian and Torresian provinces. The other widespread Bassian species with a predominant south-eastern distribution (with the exception of *B. soror*) have been affected, and isolated by similar factors to the two species discussed above.

During the early Tertiary when Australia was predominantly tropical-sub-tropical, with extensive coniferous and *Nothofagus* forests in the south-east of the continent, the ancestors of *T. tillyardi* and *C. fluviatile* were probably extensively distributed throughout the freshwater habitats of Australia with extensive populations from the Central areas to the northern, eastern and southern coasts. In contrast, the ancestors of *Atalophlebia australis, A. australasica, Atalonella fuscula, B. soror, Cloeon paradieniensis, Centroptilum elongatum* and *Tasmanophlebia lacus-coerulei* were probably restricted to, but widely distributed throughout the southern regions of the continent. Whether these species, or their ancestors, were present in Tasmania during the Tertiary is unclear, but of those that do occur in Tasmania, their present day distribution in the northern half of the State would suggest that they are more recent invaders.

With the onset of the arid period in the late Tertiary the distribution of freshwater habitats probably was restricted to the Ranges and coastal belts of the Australian continent.

The distributional ranges of all the above species decreased. The climate changes affected the flora in a similar fashion. "During the arid periods much of the vegetation died of drought and the soils became unstable and subject to wind erosion and then to water erosion whenever storms occurred. In South Australia much of the early Tertiary flora was destroyed:- *Nothofagus* and Malaysian closed-forest communities no longer exist" (Specht, 1972). Specht also noted that many of the more humid elements of the Australian sclerophyll flora also suffered. The flora of the Grampians of Victoria has a close affinity with the vegetation of the south-west corner of Western Australia (Willis, 1974), and this disjunct distribution was a result of the changes in climate.

Tyler (1971, 1976) discussed the distribution of two closely related species of frogs, *Pseudophryne occidentalis* and *P. bibroni* from Western Australia and south-east Australia respectively. He recorded the Western Australian species *P. occidentalis* in the north-west of South Australia in the Everard Ranges. This record suggested that the two species were once components of a continuous distribution, now limited by extensive drought and arid conditions. *P. occidentalis* and *P. bibroni* are now isolated within regions where permanent water occurs. In South Australia *P. bibroni* is found in the Ranges and on Kangaroo Island. The south-eastern Australian distribution also extends into the south-east of South Australia. As the extent of desert increased in South Australia the mayfly and frog species were probably forced back into the wetter ranges and coastal belts. Combined with the decrease in fresh water habitats during the Tertiary, was the onslaught of the Oligocene-Miocene seas which separated the Mt. Lofty/Flinders Ranges area from the Victorian region. The Murray-Otway Basin seas created an enormous barrier to distribution of any freshwater fauna, separating not only the mayflies, but also the distribution of *Pseudophryne bibroni*. Crocker and Wood (1947) showed that many *Eucalyptus* spp. which now have disjunct remnants in South Australia had a continuous distribution with south-east Australia.

The ancestors of the widely distributed South Australian mayfly species were probably restricted to the Flinders/Mt.Lofty Ranges, Fleurieu Peninsula and Kangaroo Island. During this period of isolation the endemic species *Atalonella inconspicua* may have evolved to occupy the restricted freshwater habitats. The distribution of *T. tillyardi* and *Cloeon fluviatile* suggests that their ancestors were also restricted to the mountain ranges and coastal streams of the north-western Western Australia and northern Queensland. Further collections may reveal that these two species are distributed all along the northern coast and down the north-east coast of Australia. The ancestors of *T. tillyardi* probably also occurred along the Victorian coast and Dividing Ranges into New South Wales and Queensland. No records of this species have been made in south-west Western Australia. In contrast, *C. fluviatile* has not been recorded further south than Armidale near the east coast of northern New South Wales and therefore, with the exception of the South Australian records, this species appears to have a predominant Torresian distribution.

Of the Bassian species, *B. soror* is the only one that also occurs in south-west Western Australia. The distribution of this species is similar to that of the frog *Pseudophryne* and the Grampians flora, all of which were apparently isolated by the increased aridity. The other species which were also isolated during the late Tertiary probably had an extensive distribution throughout the south-eastern region of the Bassian Province.

As the seas receded there was a reinvasion from the distributional refuges of the Grampians, and Great Dividing Range. Once freshwater habitats became available the ancestors of *B. soror*, *Atalophlebia australasica*, *Atalonella fuscula*, and *T. tillyardi* re-occupied the coastal streams. In South Australia they probably invaded the South Eastern coastal streams south of Mt. Gambier. The extensive swampland which developed between the sand-dune ranges as a result of the increasing rainfall and high ground water were invaded by an *Atalophlebia* species from which *A. auratus* probably evolved. *T. tillyardi* or its ancestors also probably invaded these swamps.

Other species invaded from Victoria, and these make up the recent invading group, *Atalonella pilosa*, and *Jappa pipinna*. These species colonized the southern flowing streams along the Victorian and South Australian coastline. This series of invasions probably occurred since the Pleistocene when the sea levels were below their present day levels. Also during this period *T. tillyardi*, *Atalonella fuscula*, *Atalophlebia australis* and *Tasmanophlebia lacus-coerulei* perhaps invaded

Tasmania explaining their restricted northern limits of distribution on that island.

Kangaroo Island, which during the Pleistocene was continuous with the Fleurieu Peninsula, may also have been colonized at this time by the ancestors of *Atalophlebia australasica*, *Atalonella inconspicua*, *Centroptilum elongatum* and *Tasmanocoenis tillyardi*. If flowing streams existed on this extension of the Peninsula *B. soror* probably colonized as well, but with the recent arid climate throughout South Australia, and the temporary nature of the Kangaroo Island creeks, *B. soror* has not maintained viable populations. Conversely *Centroptilum elongatum* now occupies all available habitats on Kangaroo Island, and only maintains a relictual population in a temporary stream on the Fleurieu Peninsula. The other species that invaded Kangaroo Island are all capable of surviving the temporary nature of the streams, and therefore remain part of the island mayfly fauna.

Climatic changes and eustatic sea level changes have therefore been instrumental in determining the present day distributions of the South Australian mayflies, either by isolation or by increasing the salinity of the athalassic water, i.e. in the Murray Basin, Spencer Gulf Basin and Adelaide Plains. One other factor has also been important for colonization, especially in the South East of the State. As mentioned in discussing the distribution of *Atalophlebia auratus*, the influence of man in draining the swamps has disadvantaged this species, and has created a suitable habitat for *A. australis*. Since effective drainage was not accomplished until the east-west drains L, K, and M were completed (1900-1943) the extent of *A. australis* distribution in this area has almost certainly occurred in less than 80 years.

In conclusion, the mayfly fauna of South Australia consists of three groups, a small endemic group of two species, a recent invading group of two species and the relictual group which are isolated in the streams of the Mt. Lofty and Flinders Ranges, including nine species. Within this latter group are species which are also widely distributed in the south-east of Australia, and which have recolonised the water courses of South East South Australia since the withdrawal of the Tertiary seas, and the construction of the extensive drain system. The two disjunct faunas of the Ranges, and the South East are the result of the extensive decrease in freshwater habitats caused by increased aridity, by marine invasion and by man's activities in the alteration of the natural environment.

CHAPTER 7.

Conclusions.

VII.1 General Conclusions

Previous to this study only three publications had recognised the presence of a mayfly fauna in South Australia. Eaton (1871) described a mayfly from Adelaide, *Leptophlebia inconspicua*, later to be placed in the genus *Atalophlebia* (Eaton, 1884). Harker (1954) recognised *Atalophlebia australasica* in Tillyard's 1934 collection from Mt. Gambier, and Timms (1974) recorded a *Caenis* sp. from the volcanic lakes of south-eastern South Australia.

After extensive examination of freshwater habitats in South Australia, thirteen species of mayflies from four families and eight genera have been recognised. All of these species have been determined from adult males and associated mature nymphs. Five new species have been recognised and described; *Atalophlebia auratus*, *Atalonella pilosa*, *Jappa pipinna*, *Cloeon paradieniensis*, *Centroptilum elongatum*, and one species transferred from the genus *Atalophlebia* to *Atalonella* (*Atalonella inconspicua* (Eaton) comb. nov.). The first associated nymphal descriptions of five previously described species have been included [*A. inconspicua* (Eaton), *A. fuscula* (Tillyard), *Baetis soror* Ulmer, *Cloeon fluviatile* Ulmer and *Tasmanocoenis tillyardi* (Lestage)].

A. fuscula was associated with a nymph by Tillyard (1936), but this study has shown that Tillyard's description was probably of the nymph of *A. pilosa* sp. nov., which co-occurs with *A. fuscula*. The adults and nymphs of *Atalophlebia australis* (Walker), *A. australasica* (Pictet) and *Tasmanophlebia lacus-coerulei* Tillyard have been re-described in detail from South Australian material.

The character expression of all species was examined to document any variation occurring within the South Australian populations. Qualitative characters, especially genitalia, were consistently expressed in male imagos, and those of gill structure, mouthpart structure and abdominal tergite spination were consistently expressed in the nymphs. In nymphs, the mandibular dentition and prosthecal structure, labrum shape, labial and maxillary palp structure were all valuable specific characteristics. The major wing venation was considered valuable at the generic level with the features of the hind wing most useful. The cross vein systems varied extensively, even within an individual, and therefore were not considered useful taxonomic characters. Abdominal colour pattern of nymphs also was variable, although a basic pattern in each species was determinable. Very little reliance was placed on this character.

An analysis of variation of morphometric character expression was made for the common South Australian species. Many characters were geographically and sexually variable, with the range of expression so great that their value as taxonomic characters was doubtful at the species level. Those characters which were statistically inconsistent at the species level also had a wide range of expression and could only be used as 'secondary' characters, supporting the classification based on male imago genitalia and nymphal morphology.

In South Australia many of the freshwater systems are near the limits of permanency. Two streams were selected; one cool, permanently flowing (Deep Creek) and one warm and intermittent (Spring Creek); to examine how their respective mayfly faunas had adapted to these two environments. The streams were compared in terms of physical environment; geology, temperature, discharge, substrate, pH, conductivity (or salinity) and water chemistry. Their mayfly faunas differed; two species were common to both streams, *Tasmanocoenis tillyardi* and *Baetis soror*, while *Atalophlebia australasica* occupied only the permanent stream, and *Atalonella inconspicua* only the intermittent stream.

The habitats occupied and life cycles of this group of species were examined by using a dual net box-sampler with an inner coarse net of 480 μm aperture, and an outer fine net of 110 μm mesh aperture. This sampler enabled collection of first instar nymphs of all species, and since at each locality all species were from different families, identification of the early instar nymphs was relatively simple.

The habitats occupied by each species from both streams indicated that *Baetis soror* was the most specific, with the greatest number of nymphs collected in the flowing water habitats.

Atalophlebia australasica occupied most habitats, but the majority of specimens was collected in slower, deeper 'pools' or 'flats', with reduced numbers in 'riffles' and fast flowing habitats. *Atalonella inconspicua* and *Tasmanocoenis tillyardi* occupied all habitats, except fast 'riffles', equally, but the greatest numbers were recorded in slower flowing reaches. In Spring Creek both *A. inconspicua* and *T. tillyardi* were recorded in the hyporheos below the dry stream bed in March 1977. These species also occurred in the spatially isolated pools in the watercourse. Early instars apparently enter the hyporheos to avoid the high water temperatures that occur in the pools during Summer. Recolonization, once the stream recommenced flowing, was most probably from the fauna occupying the hyporheos, and by downstream drift of animals from the isolated pools.

Examination of life cycles of each species showed that in the cool permanent Deep Creek *T. tillyardi* had two generations per year with immature nymphs from both generations developing throughout the winter months. In the warmer Spring Creek, *T. tillyardi* had a polyvoltine life cycle with two winter generations plus a summer generation. *Baetis soror* showed a similar increase in the number of generations, with three generations in Deep Creek (one winter, and two summer) and four generations in Spring Creek (two winter, two summer). *Atalophlebia australasica* in Deep Creek and *Atalonella inconspicua* in Spring Creek both had polyvoltine life cycles with three generations per year.

During the life cycle study first instar nymphs of *Atalophlebia australasica* and *T. tillyardi* were recorded in early Spring before a preceeding adult emergence, but first instar nymphs of *B. soror* were always recorded after an emergence period. The development of eggs of four species, unfortunately not including *A. australasica* or *T. tillyardi*, was examined to determine if there were more than one development strategy. Eggs of *A. australis* and *Atalonella inconspicua* did not hatch in water below 11°C, but remained viable until the temperature increased above this level. In contrast, *Atalonella fuscula* and *B. soror* eggs did not have a quiscent stage, and development was continuous over the examined temperature range (9 - 24°C). In all cases development was directly related to water temperature above either a threshold temperature, or a quiescent induced temperature. A third strategy, obligatory diapause, was not recorded for any species examined. Light and/or photoperiod have little if any effect on the length of the incubation period.

The ability of eggs to remain viable under conditions of elevated salinity and after dessication was examined for comparison with conditions that occur in the temporary stream habitat. Reduced viability of *A. fuscula* eggs occurred with increased salinity, and eggs of neither *A. fuscula* or *B. soror* survived dessication. This strategy was therefore unlikely to operate, and survival of mayflies in the temporary habitats of South Australia was probably by entry into the hyporheos, or by isolation in the pools associated with springs, from which locations recolonization took place once the stream recommenced flowing.

The distribution of each species in South Australia was documented, and compared with the distribution of fresh and saline waters. All species were apparently limited by the availability of persistent surface fresh water, without which completion of their life cycle was impossible.

Comparative distribution of species groups indicated five distinct faunal components in South Australia. These sub-provinces within the Bassian zoogeographical province not only have distinctive mayfly faunas, but also distinctive climatic conditions (temperature, rainfall, evaporation) vegetation and geology. By examining the distribution of each species within these sub-provinces, and in a wider context throughout Australia, an attempt was made to determine the origins of the South Australian species.

Three distinct components of the South Australian mayfly fauna were apparent, the endemics, *Atalophlebia auratus* and *Atalonella inconspicua*; the species restricted to the central mountain chain of the Mt. Lofty-Flinders Ranges (including the Fleurieu Peninsula and Kangaroo Island), *Atalophlebia australasica*, *A. australis*, *Atalonella fuscula*, *Baetis soror*, *Centroptilum elongatum*, *Cloeon paradieniensis*, *C. fluviatile*, *Tasmanophlebia lacus-coerulei* and *Tasmanocoenis tillyardi*; and the species which are probably more recent invaders from Victoria: *Jappa pipinna*, *Atalonella pilosa*, *A. fuscula*, *Atalophlebia australis*, *A. australasica*, *Cloeon paradieniensis*, *Baetis soror* and *Tasmanocoenis tillyardi*. The 'invading' fauna closely resembles the isolated species group suggesting that the faunas were once continuous, and have been separated by two major factors, climatic change and eustatic sea level changes during the Tertiary. Geological, floral and zoological evidence demonstrates that the climate of Central Australia was much wetter in the early Tertiary than at present, but that as the Tertiary progressed the climate changed, becoming more arid, eliminating the previously lush flora of Central Australia. Combined with this, sea levels also rose, encroaching on the low lying areas of the Murray-Otway Basin, the St. Vincent Basin and the Eucla Basin in South Australia. These two changes restricted fauna and flora to the refuge areas of the hills and mountain ranges. The sea level change isolated the South Australian 'ranges" fauna and the 'Victorian' fauna. With the recession of the sea and subsequent uplifting of the land since the Pleistocene, re-invasion of the coastal streams has occurred. However, the now saline Murray Plains have maintained effective isolation of the two faunas.

More recently, man-made alterations to the natural environment have had noticeable effects on the mayfly fauna. *Cloeon fluviatile* is commonly found in farm dams and may have moved into these water bodies to exploit a widespread and vacant habitat that occurs throughout the State. Numerous channels have been constructed to drain the extensive swamps and marsh lands of the South East. *Atalophlebia auratus*, which was probably endemic to the swamp lands, appears adversely affected by the new flowing habitat and is apparently being replaced by *A. australis*.

VII.2 Areas of Future Research

The present study has indicated several possible areas for future work on the Australian Ephemeroptera.

1) Further examination of species' survival strategies in intermittent streams is required, with emphasis on recolonization after the dry summer periods, occupation of the hyporheos, size distribution of animals in the hyporheos, and resistance to dessication of the nymph and egg stages. The present study has shown that *Atalonella inconspicua* and *Tasmanocoenis tillyardi* definitely enter the hyporheos during the dry summer months, but this behaviour was not examined in detail. The inability of eggs of *Baetis soror* and *A. fuscula* to survive dessication suggests that these mayflies do not utilise drought resistant eggs to survive. Also the presence of a generation of *A. inconspicua* and *T. tillyardi* that originated during the period of zero surface discharge in Spring Creek, suggests that these species also do not utilise drought resistant eggs as a survival mechanism. However, more detailed examination may record this strategy in other species of the Australian mayfly fauna.

2) Further life history studies are required to determine whether more Australian species have flexible life cycles similar to those displayed by the South Australian species. If this is the case, the systems developed in the Northern Hemisphere for classifying life histories may be inapplicable to the Australian mayfly fauna.

3) More detailed examination of micro-habitat occupation and requirements of different species from different genera are necessary. Some information on the South Australian species was obtained, but demonstrated a broad, ecological tolerance. This may not be true of all species, especially of those occupying the alpine streams of eastern Australia.

4) Further studies on egg development under constant and fluctuating temperature conditions, and the applicability of the results to field conditions would be valuable. Examination of thermal summation and day degree development of *B. soror* eggs indicated some similarities between calculated development rates and field observations, but some discrepancies were apparent, especially over the Winter-Spring period. The technique of thermal summation could prove a useful predictive method for life cycle studies.

5) All the preceeding require a functional systematic framework that enables reliable identification of genera and species. Without this framework, ecological comparisons are hampered, and information can be lost, especially when comparisons at the specific level are necessary, but conclusions can only be based on family identifications. Changes in species composition can be unobserved and therefore loss of definition may be extensive.

With the taxonomic study on mayflies nearly complete in South Australia, ecological studies are now possible, but no other Australian State has this required taxonomic framework yet. The major objective for research on the Australian Ephemeroptera must be to establish this taxonomic understanding, both for adult and nymphal specimens, the latter being most important for ecologists.

VII.3 Recommendations

Three important recommendations have come from the present study :

(1) Extensive evaluation of character variation within a species throughout its distribution range must be carried out to give adequate taxonomic definition.

(2) Ethanol preserved adult material should be used in preference to dry pinned imagos.

(3) A net mesh size which will collect representatives of early, preferably first instar nymphs has to be used in life history and ecological studies to avoid erroneous conclusions based on incomplete data.

Evaluation of many morphometric and non-morphometric (i.e. qualitative) characteristics of the South Australian mayflies illustrated wide variation, and therefore limited value in species identification. Morphometric characters were found to vary sexually and geographically, however, those that were significantly different also exhibited wide variation within a population. Therefore, as many specimens as possible from as many localities as possible should be examined to gain some insight into the amount of variation that can exist within each species. In a few cases this was not possible with the species studied, especially for those species that had very restricted distributions. However, these were distinctly different from the other species present, and could therefore be described.

Genitalia, the major characteristic of the male imagos used for specific identification, showed great structural differences when air-dried and ethanol preserved specimens were compared. Air-drying usually resulted in distortion due to shrinkage, separation of semi-fused penes and occasionally extensive contraction of lateral lobes. In ethanol preserved material the genitalia were consistently expressed, and retained the true structure of the genitalia of living males. Only ethanol preserved specimens should therefore be described and illustrated in future work. For producing scanning electron micrographs of male genitalia drying is a necessity, but Critical Point Drying is the method of choice, as the structure of the genitalia is not distorted, resembling living or ethanol preserved material.

Use of a fine mesh, which will collect early instar animals, has been advocated many times (see Appendix 12), but many life history and production studies are still conducted using meshes which collect only late instars. From the data that are obtained conclusions are drawn on egg hatching and duration of generations. Both aspects require direct observation of first instar nymphs. The present study was able to define the life cycles of *Tasmanocoenis tillyardi* and *Baetis soror* in Deep Creek, South Australia, and showed that the conclusions based only on the 480 μm mesh data were inaccurate when compared with the combined 480 μm and 110 μm collections which sampled all instars (Suter and Bishop, 1980, Appendix 12). Therefore it is imperative that autecological studies on mayflies, and other benthic macro-invertebrates, rely only on data collected with nets capable of collecting the smallest size classes, the first instar.

Appendix 1

Localities, Dates and Collectors of Ephemeroptera in South Australia.

Locality	Date	Collectors
NORTHERN FLINDERS RANGES		
Arkaroola Ck. - Arkaroola	25.7.76	PS, RM, BM.
Hot Spring Ck., Paralanna Hot Springs	27.9.75	JEB.
Stubbs Waterhole Ck.	24.7.76	PS, RM, BM.
Stubbs Waterhole	24.7.76	PS, RM, BM.
Nepouie Ck.	24.7.76	PS, RM, BM.
Balcanoona Ck.	24.7.76	PS, RM, BM.
	27.9.75	JEB.
Trib. Mt. McKinley Ck. 19 km E. of Nepabunna Mission	24.7.76	PS, RM, BM.
Trib. Tea Tree Ck, Wearing Gorge	25.7.76	PS, RM, BM.
Mt Chambers Ck.	25.7.76	PS, RM, BM.
Trib. Mt. Chambers Ck. near Little Bodmonie Well	25.7.76	PS, RM, BM.
Bendieuta Ck.	25.7.76	PS, RM, BM.
	15.12.76	JEB, JHD.
Old Wirrealpa Spring	16.12.76	JEB, JHD.
Wirrealpa Ck. 5 km W. of Wirrealpa	25.7.76	PS, RM, BM.
	25.8.76	WDW.
Eregunda Ck. Fountain Spring	10.4.77	PS
Emu Ck, Aroona Dam	16.12.76	JEB, JHD.
	7.10.76	JEB.
	23.7.76	PS, RM, BM.
Willigan Ck, Third Spring	15.12.76	JEB, JHD.
	9.4.77	PS.
Woodendimna Ck. Nirrana	16.12.76	JEB, JHD.
Oratunga Ck. N.E. of Mt. Mary	25.7.76	PS, RM, BM.
Parachilna Ck, Mt. Mary	8.10.75	JEB.
	26.7.76	PS, RM, BM.
	26.8.76	WDW.
	26.12.76	JEB, JHD.
	8.4.77	PS.
Wockerawirra Ck.	26.7.76	PS, RM, BM.
Enorama Ck.	26.7.76	PS, RM, BM.
Elatina Ck.	26.7.76	PS, RM, BM.
Brachina Ck.	29.8.76	WDW.
Bunyeroo Ck.	26.7.76	PS, RM, BM.
	17.12.76	JEB, JHD.
	17.7.77	PS.
Oraparina Ck.	8.10.75	JEB.
Trib. Wilpena Ck.	26.7.76	PS, RM, BM.
Moralana Ck, Blacks Gap	15.12.76	JEB, JHD.
Arkaba Ck, Little Weepowie	26.7.76	PS, RM, BM.
	17.12.76	JEB, JHD.
Kanyaka Ck.	16.7.77	PS.
Warren Gorge	15.12.76	JEB, JHD.

SOUTHERN FLINDERS RANGES - NORTHERN MT. LOFTY RANGES

Old Woolshed Dam, Hesso	11.12.76	JEB, JHD.
Nectar Brook Ck.	10.12.76	JEB, JHD.
Nectar Brook Dam	11.12.76	JEB, JHD.
Spring Ck.	9.10.75	JEB.
	17.4.76	AW.
	10.12.76	JEB, JHD.
	17.12.76	JEB, JHD.
Back Ck, Port Germein Gorge	12.9.76	PS.
	2.10.76	PS, AS.
	10.12.76	JEB, JHD.
	4.10.77	PS, JHD.
Wild Dog Ck, N. of Murray Town	5.7.77	PS
	10.8.77	PS, JHD.
Rocky R, N. of Wirrabarra	12.9.76	PS.
	4.10.77	PS.
Rocky R, S. of Wirrabarra	1.9.76	PS, AS.
	10.8.77	PS, JHD.
	4.10.77	PS.
Rocky R, N. of Stone Hut	11.9.76	PS.
	10.8.77	PS, JHD.
Rocky R, N. of Laura	10.12.76	JEB, JHD.
Broughton R. at Hutt R. Junction	22.10.76	JEB.
	26.11.76	JEB.
Hutt R. near Clare	26.11.76	JEB.
Ohlenmeyer Park Reservoir	27.8.77	PS, AS, AMMR.
Skillogalee Ck.	27.8.77	PS, AS, AMMR.
Schumacher Ck.	27.8.77	PS, AS, AMMR.
R. Wakefield near Leasingham	26.11.76	JEB.
Julia Ck	14.12.76	PS, MB.
North Para R.	28.8.76	PS.
Little Para R., Paracombe	10.10.76	JHD.
	20.10.76	PS, JHD.
Little Para R, Lower Hermitage	1.4.76	JEB, JHD.
Marne R. S. of Eden Valley	28.8.76	PS.
Marne R., Cambrai Picnic Ground	26.5.76	PS, AW.
Marne R., Black Hill	26.5.76	PS, AW.

MT. LOFTY RANGES - FLEURIEU PENINSULA

Torrens R. at Gumeracha	27.1.78	PS, BM.
Torrens R. 2 km E. of Gumeracha	2.7.76	RS.
Torrens R. at Birdwood	11.8.76	PS.
Cudlee Ck.	28.10.76	JEB.
Torrens R. at Kiosk	4.1.77	PS.
	6.2.77	PS.
	12.10.77	PS.
	16.12.77	PS.
Torrens R. near road to Priarie	9.12.76	PS.
	22.12.76	PS.
	12.10.77	PS.
Torrens R. at Castambul	17.3.76	JEB.
	20.10.76	PS.
	18.3.76	JEB.
Deep Ck., Castambul	9.4.76	JEB.
	12.4.76	JEB.
	28.10.76	JEB.
	4.3.77	JEB, AW.
Deep Ck., at Ford	28.3.76	JEB.

	1.5.76	PS, AS.
	6.8.76	PS.
Trib. Deep Ck.	11.11.75	JEB.
	1.5.76	PS,AS.
	4.3.77	JEB, AW.
Fifth Ck, Montacute	12.2.77	JEB.
	23.9.77	JEB.
Fourth Ck, Morialta Falls	12.11.76	JEB.
	24.8.77	PS.
Deep Ck., Knotts Hill Rd.	6.8.76	PS.
Deep Ck., Ashton	15.7.76	PS.
Dam, Carey's Gully	31.3.75	JEB.
Cock's Dam, Ashton	- .10.75	JEB.
First Ck. Waterfall Gully	3.11.77	PS.
Pool at Waite Institute	30.11.77	MG.
Brownhill Ck.	3.3.76	JEB.
	20.3.76	JEB.
	12.8.76	AW.
Trib. Sturt R., Blackwood	29.4.76	PS.
	31.8.76	PS.
Sturt R., Coramandel Valley	29.4.76	PS.
Chambers Ck, Coramandel Valley	31.8.76	PS.
Sturt R., below Flinders University	22.4.76	PS, AW.
	29.4.76	PS.
	27.8.76	AW.
Onkaparinga R., Balhannah	1.12.76	RB.
Trib. Onkaparinga R., Carey's Gully	28.3.76	AW.
Algate Ck., Algate	6.6.76	PS.
Scott Ck., at Scott Ck.	23.9.77	JEB.
Blackfellow Ck, Kuitpo Colony	27.10.76	JEB.
	16.12.76	AW.
Bull Ck. on Kuitpo Colony Rd.	27.10.76	JEB.
Kangarilla Ck., Meadows Rd.	27.4.76	JEB.
	11.11.76	JEB.
Finnis R. at Mt. Effie	27.6.76	PS.
	16.12.76	JEB.
Tookayerta Ck.	6.10.76	JEB.
	27.10.76	JEB.
	29.12.76	JEB.
	11.1.77	PS, TL.
	25.1.77	JEB, AW.
	8.2.77	PS.
	8.2.77	JEB, AW.
	17.4.77	PS.
	28.4.77	JEB.
	26.8.77	PS.
	6.10.77	JEB, AW.
	14.11.77	PS.
	21.12.77	PS, JEB.
	28.2.78	PS, JEB, AW.
	5.4.78	PS.
	8.4.78	PS.
	17.4.78	PS, JEB.
Myponga Ck., E. of Myponga	26.8.77	PS, AMMR.
	21.12.77	PS, JEB.
Carrickalinga Ck, near Wattle Flat	14.11.77	PS.
	21.12.77	PS.
	13.3.78	PS.

Anacotilla Ck., near Yankalilla	1.9.76	JEB.
	11.10.76	JEB.
	20.10.76	JEB, AW.
	21.7.77	JEB, AW.
	6.10.77	JEB, AW.
Bungala R. near Normanville	15.4.76	JEB.
	1.9.76	JEB.
	20.10.76	JEB.
	7.12.76	JEB.
	15.11.77	JEB, AW.
Yankalilla R., near Lady Bay	23.8.77	PS, AMMR, BM.
No Where Else Ck, Rapid Bay	23.8.77	PS, AMMR, BM.
Yankalilla R., on Rd to Parawa	6.11.77	JEB, AW.
	14.11.-7	PS.
Yankalilla R., at Hay Flat	16.12.76	PS, JEB.
	14.11.77	PS.
The Deep Ck, Delamere	1.9.76	JEB.
	11.10.76	JEB.
	7.12.76	JEB.
	15.2.77	JEB, AW.
	21.7.77	JEB, AW.
	23.8.77	PS, AMMR, JEB.
Gold Digging Swamp	15.2.77	JEB.
Coolawang Ck.	16.12.76	AW.
	6.7.77	JEB, AW.
	16.11.77	JEB, AW.
Inman R. on Prouse Road.	5.6.76	PS.
Inman R. on Sawpit Rod.	20.10.76	JEB.
Hindmarsh R. at Falls	26.3.76	JEB, AW.
	29.8.76	PS.
	20.8.76	PS.
	11.10.76	JEB.
	20.10.76	JEB.
	27.10.76	JEB.
	8.2.77	PS.
	26.8.77	PS, AMMR.
Hindmarsh R. on Sawpit Rd.	25.1.76	JEB, AW.
Finniss R. near Finnis	11.1.77	PS, TL.
Trib. Currency Ck, at Bromlé	6.11.77	JEB.
L. Alexandrina, Milang	5.4.77	JHD, MG.
Ck., below Knobs Hill, near Normanville	20.10.76	JEB.
	8.11.77	JEB, AW.

KANGAROO ISLAND

Middle R, Middle R. Station	20.11.77	JEB.
Middle R., Glencorrie	20.11.77	JEB.
Middle R., N.E. of Binnowie	20.11.77	JEB.
Western R., Karawatha	20.11.77	JEB.
DeMole R.	20.11.77	JEB.
Breakneck R.	20.1177	JEB.
	15.12.76	WDW.
Rocky R. Flinders Chase National Park	13.12.76	WDW.
	18.12.76	WDW.
	20.11.77	JEB.
South West R. near Riverdale	19.12.76	WDW.
	19.11.77	JEB.

South West R. at St. Andrews	19.11.77	JEB.
South West R. near Brigadoon	19.11.77	JEB.
Stunsail Boom R.	12.12.76	WDW.
	19.11.77	JEB.
North East R. near Carnarvan	19.11.77	JEB.
Eleanor R. near Daws Diggings	19.11.77	JEB.
Cygnet River	20.11.77	JEB.
	16.12.76	WDW.
Grassy/Sheep Ck. near Moorlands	20.11.77	JEB.
Tin Hut/Bullock Ck.	20.11.77	JEB.

SOUTH EAST SOUTH AUSTRALIA

Drain K West Avenue Range	20.11.77	PS, DS.
Drain L near Robe	20.11.77	PS, DS.
Reedy Ck. Drain, Greenaways	20.11.77	PS, DS.
Eastern Division Diversion at "Ceres"	20.11.77	PS, DS.
Eastern Division Diversion near Beachport	24.4.77	PS, DS.
Mosquito Ck.	23.11.77	PS, DS.
Bakers Range Drain, W. of Penola	22.11.77	PS, DS.
Sutherland Drain near Beachport	24.4.77	PS, DS.
	18.11.77	PS.
Trib., Mt Hope Drain, NW of Millicent	20.11.77	PS, DS.
Reedy Ck. Drain at Furner	20.11.77	PS, DS.
Drain near 'Keera Park'	20.11.77	PS, DS.
Drain at "White Heath"	20.11.77	PS, DS.
Mt. Hope Drain near L. Frome	21.11.77	PS, DS.
Brown Lake Mt. Gambier	15.1.77	PS
	23.4.77	PS, DS.
Valley Lake Mt. Gambier	15.1.77	PS.
Hitchcock Drain	22.11.77	PS, DS.
	15.1.77	PS.
Eight Mile Ck.	22.11.77	PS, DS.
Trib. Eight Mile Ck.	22.11.77	PS, DS.
Deep Ck., at cheese factory	23.4.77	PS, DS.
	22.11.77	PS, DS.
Drain West of Deep Ck.	22.11.77	PS, DS.
Jerusalem Ck.	23.4.77	PS, DS.
	22.11.77	PS, DS.
Cress Ck, Pt. Macdonnell	22.11.77	PS, DS.

ABBREVIATIONS

JEB	J. E. Bishop
MB	M. Brock
RB	R. Buckney
JHD	J. H. Diener
MG	M. Geddes
TL	T. Laver
RM	R. Marchant
BM	B. Mitchell
AMMR	A. M. M. Richardson
RS	R. Shiel
AS	A. Suter
DS	D. Suter
PS	P. Suter
AW	A. Wells
WDW	W. D. Williams

Appendix 2

List of morphometric characters of male and female nymphs of *Atalophlebia australis* from Mt. Hope Drain, which did not show significant differences when compared by "t" test.

Significant characters are presented in Table 11.4.

Character	Males $\bar{x}$	SD	Range	Females $\bar{x}$	SD	Range	d.f.
NL/HW	1.45	0.06	1.40-1.58	1.42	0.07	1.34-1.52	12
PNW/HW	0.96	0.07	0.85-1.04	1.02	0.08	0.88-1.14	12
MNW/PNW	1.14	0.07	1.06-1.24	1.16	0.10	1.08-1.35	12
FFL/FFW	3.16	0.15	3.00-3.48	3.18	0.13	3.01-3.48	25
MT_iL/MFL	0.97	0.02	0.94-1.00	0.97	0.02	0.94-0.99	25
MT_aL/MFL	0.43	0.02	0.35-0.44	0.43	0.01	0.41-0.44	25
HT_iL/HFL	1.02	0.02	0.97-1.05	1.03	0.02	0.99-1.06	22
HT_aL/HFL	0.43	0.01	0.39-0.44	0.42	0.02	0.38-0.43	22
MFL/FFL	1.01	0.01	0.99-1.03	1.03	0.03	0.96-1.07	24
Labial Palpi							
BL/BW	1.81	0.16	1.50-2.10	1.77	0.08	1.67-1.92	26
ML/BL	0.80	0.04	0.75-0.86	0.78	0.08	0.65-0.90	26
AL/BL	0.60	0.08	0.48-0.73	0.57	0.10	0.40-0.71	25
Paraglossae							
L/W	0.97	0.06	0.86-1.06	1.02	0.11	0.86-1.25	23
Maxillary Palpi							
MBL/MBW	2.24	0.30	1.50-2.57	2.05	0.24	1.63-2.40	24
MML/MBL	1.22	0.14	0.88-1.53	1.24	0.10	1.05-1.35	20
MAL/MBL	0.66	0.09	0.50-0.77	0.63	0.10	0.50-0.82	20
Labrum L/W	0.36	0.02	0.33-0.38	0.35	0.02	0.33-0.38	12

List of morphometric characters of male imagos of *Atalophlebia australis* which did not display significant geographical variation when compared by "t" test.

Significant characters are presented in Table 11.5.

Character	Rocky R. Population $\bar{x}$	SD	Range	Reedy Ck. Drain. Population $\bar{x}$	SD	Range	d.f.
NL/BL	0.34	0.03	0.29-0.39	0.33	0.02	0.31-0.35	16
MNW/BL	0.18	0.01	0.16-0.20	0.17	0.01	0.16-0.19	16
PNW/BL	0.13	0.01	0.13-0.15	0.13	0.01	0.12-0.14	9
NL/MNW	1.86	0.13	1.75-2.08	1.91	0.08	1.81-2.00	9
MNW/PNW	1.35	0.09	1.26-1.47	1.32	0.08	1.21-1.42	9
FWL/FWW	2.83	0.09	2.68-2.92	2.71	0.23	2.40-3.12	16
HWL/HWW	1.61	0.05	1.54-1.69	1.65	0.16	1.50-1.89	16
FT$_i$L/FFL	1.33	0.06	1.28-1.43	1.34	0.04	1.29-1.40	14
FT$_1$L/FFL	0.50	0.03	0.45-0.54	0.51	0.03	0.48-0.53	14
MT$_2$L/MFL	0.11	0.01	0.10-0.12	0.11	0.01	0.10-0.12	13
MT$_5$L/MFL	0.19	0.02	0.16-0.22	0.19	0.02	0.15-0.21	13
HT$_{i+}$T$_1$ L/HFL	1.03	0.03	0.97-1.06	1.04	0.07	0.93-1.09	13
HT$_2$L/HFL	0.10	0.01	0.08-0.11	0.10	0.01	0.09-0.11	13
HT$_3$L/HFL	0.09	0.01	0.08-0.10	0.08	0.01	0.07-0.10	12
HT$_4$L/HFL	0.08	0.01	0.07-0.09	0.07	0.01	0.06-0.08	13
HT$_5$L/HFL	0.17	0.01	0.16-0.19	0.17	0.02	0.15-0.20	13

Appendix 4

List of morphometric characters of male and female nymphs of *Atalophlebia australisica*, from Jerusalem Ck, which did not show significant differences when compared by "t" test.

Significant characters are presented in Table 11.7.

Character		Males			Females		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	d.f.
MFL/MFW	3.56	0.14	3.32-3.72	3.48	0.14	3.30-3.69	14
MT$_i$L/MFL	1.00	0.02	0.97-1.02	0.99	0.02	0.96-1.01	14
MT$_a$L/MFL	0.38	0.01	0.36-0.40	0.38	0.01	0.36-0.40	14
HT$_i$L/HFL	1.08	0.02	1.05-1.11	1.07	0.02	1.05-1.09	14
HT$_a$L/HFL	0.37	0.02	0.34-0.39	0.36	0.02	0.32-0.37	14
HFL/FFL	1.19	0.02	1.17-1.23	1.21	0.02	1.18-1.25	12
Labial palpi							
BL/BW	1.71	0.10	1.55-1.82	1.78	0.14	1.58-2.00	14
ML/BL	0.71	0.07	0.63-0.77	0.74	0.05	0.68-0.84	13
AL/BL	0.73	0.03	0.70-0.78	0.70	0.05	0.64-0.74	11
Maxillary palpi							
MBL/MBW	2.96	0.14	2.71-3.14	2.91	0.52	2.75-3.57	13
Labrum L/W	0.30	0.03	0.25-0.33	0.32	0.01	0.31-0.32	6

List of morphometric characters of male nymphs of *Atalophlebia australasica* which did not display significant geographical variation when compared by "t" test.

Significant characters are presented in Table 11.8.

Character	Sturt R. Population $\bar{x}$	SD	Range	Jerusalem Ck. Population $\bar{x}$	SD	Range	d.f.
HFL/HW	1.02	0.02	0.98-1.05	1.03	0.02	1.00-1.06	18
FT_iL/FFL	1.02	0.05	0.88-1.08	1.03	0.02	1.01-1.06	19
FT_aL/FFL	0.50	0.03	0.46-0.55	0.51	0.02	0.48-0.53	18
MT_iL/MFL	0.97	0.02	0.96-1.00	1.00	0.02	0.97-1.02	19
MT_aL/MFL	0.37	0.03	0.35-0.38	0.38	0.01	0.36-0.40	19
HT_aL/HFL	0.36	0.01	0.35-0.37	0.37	0.02	0.34-0.39	16
MFL/FFL	1.05	0.03	1.01-1.09	1.03	0.01	1.01-1.05	16
Labrum L/W	0.29	0.02	0.28-0.33	0.30	0.03	0.25-0.33	9

Appendix 6

Details of morphometric characters of male and female nymphs of *Atalonella inconspicua* from Deep Creek which did not show significant differences when compared by "t" test.

Significant characters are presented in Table 11.11

Character	Males			Females			d.f.
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	
NL/HW	1.20	0.04	1.12-1.25	1.29	0.11	1.11-1.35	11
NL/MNW	1.26	0.05	1.20-1.33	1.22	0.10	1.06-1.32	11
MNW/PNW	1.06	0.05	1.00-1.12	1.03	0.06	0.96-1.10	11
FFL/FFW	3.17	0.18	2.91-3.55	3.22	0.30	3.00-3.81	17
FT_iL/FFL	0.92	0.03	0.88-0.94	0.93	0.03	0.88-0.96	17
MFL/MFW	3.20	0.21	2.96-3.57	3.11	0.13	2.92-3.25	15
MT_iL/MFL	0.92	0.04	0.85-0.97	0.94	0.02	0.91-0.96	15
HFL/HFW	3.35	0.22	3.04-3.81	3.37	0.21	3.12-3.63	20
HT_iL/HFL	0.98	0.03	0.91-1.01	0.97	0.02	0.93-1.00	18
HT_aL/HFL	0.36	0.03	0.33-0.40	0.37	0.02	0.33-0.39	17
MFL/FFL	0.99	0.03	0.95-1.03	1.00	0.02	0.99-1.02	11
HFL/FFL	1.08	0.02	1.03-1.11	1.10	0.01	1.08-1.11	15
Labial palpi							
BL/BW	1.98	0.08	1.78-2.13	1.92	0.17	1.70-2.25	24
ML/BL	0.79	0.07	0.61-0.88	0.80	0.04	0.72-0.88	23
AL/BL	0.64	0.07	0.50-0.71	0.60	0.05	0.55-0.71	23
Maxillary palpi							
MML/MBL	0.92	0.08	0.80-1.09	0.88	0.10	0.73-1.10	22
MAL/MBL	0.80	0.05	0.70-0.90	0.78	0.12	0.64-1.00	19
Labrum L/W	0.50	0.04	0.45-0.57	0.47	0.02	0.45-0.50	11

Appendix 7

Details of morphometric characters of male imagos and nymphs of *Atalonella inconspicua* which did not show significant geographical variation when compared by "t" test.

Significant characters are presented in Table 11.13.

Character	Spring Ck.			Deep Ck.			d.f.
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	
Male Imago							
MNW/BL	0.16	0.01	0.15-0.17	0.17	0.02	0.14-0.19	14
PNW/BL	0.13	0.01	0.12-0.14	0.13	0.02	0.11-0.16	14
MNW/PNW	1.24	0.06	1.17-1.33	1.23	0.11	1.11-1.43	14
NL/MNW	1.89	0.12	1.75-2.10	2.04	0.23	1.78-2.52	14
CL/BL	1.44	0.08	1.36-1.54	1.52	0.20	1.33-1.80	9
AD/BL	1.67	0.12	1.51-1.78	1.87	0.22	1.64-2.28	8
AD/CL	1.16	0.05	1.08-1.23	1.25	0.07	1.05-1.31	8
FWL/FWW	3.20	0.37	2.60-3.68	3.39	0.19	3.21-3.78	14
HWL/HWW	1.56	0.14	1.36-1.75	1.55	0.12	1.44-1.73	14
FFL/BL	0.30	0.04	0.22-0.33	0.26	0.04	0.20-0.31	10
FT$_i$L/FFL	1.42	0.03	1.38-1.46	1.48	0.09	1.28-1.55	10
FT$_4$L/FFL	0.33	0.01	0.31-0.34	0.33	0.04	0.26-0.35	10
MT$_2$L/MFL	0.09	0.01	0.08-0.09	0.08	0.01	0.06-0.09	14
MT$_3$L/MFL	0.08	0.01	0.07-0.09	0.08	0.01	0.07-0.10	14
MT$_4$L/MFL	0.07	0.01	0.06-0.08	0.07	0.02	0.04-0.10	14
HT$_2$L/HFL	0.08	0.01	0.07-0.09	0.08	0.01	0.07-0.10	13
HT$_4$L/HFL	0.07	0.01	0.06-0.08	0.08	0.01	0.06-0.08	13
Nymphs							
NL/HW	1.28	0.15	1.00-1.48	1.24	0.09	1.11-1.35	21
NL/MNW	1.22	0.12	1.00-1.43	1.24	0.08	1.06-1.34	21
MNW/PNW	1.04	0.05	0.96-1.15	1.04	0.05	0.96-1.12	21
HT$_i$L/HFL	0.93	0.03	0.96-1.06	0.93	0.03	0.91-1.01	35
MFL/FFL	0.99	0.06	0.80-1.05	1.00	0.03	0.95-1.03	29
HFL/FFL	1.08	0.04	1.00-1.15	1.09	0.02	1.03-1.11	28
Labial palpi							
BL/BW	1.99	0.23	1.67-2.57	1.95	0.13	1.70-2.25	44
AL/BL	0.59	0.05	0.47-0.73	0.62	0.06	0.50-0.71	43
Maxillary palpi							
MBL/MBW	2.05	0.17	1.80-2.50	1.99	0.15	1.81-2.50	47
MML/MBL	0.89	0.07	0.73-1.00	0.90	0.09	0.73-1.10	40
Labrum L/W	0.51	0.03	0.39-0.56	0.49	0.04	0.45-0.57	21

Details of morphometric characters of male and female nymphs of *Atalonella fuscula* which did not show significant differences when compared by "t" test.

Significant characters are presented in Table 11.15.

Character	Males			Females			d.f.
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	
NL/HW	1.19	0.07	1.04-1.25	1.27	0.08	1.14-1.37	12
PNW/HW	0.93	0.05	0.87-1.00	0.98	0.04	0.92-1.06	12
NL/MNW	1.25	0.07	1.11-1.30	1.25	0.12	1.18-1.31	12
MNW/PNW	1.04	0.04	0.96-1.08	1.04	0.08	0.99-1.22	12
FFL/FFW	2.74	0.10	2.62-3.00	2.76	0.21	2.48-3.08	16
MFL/MFW	2.82	0.18	2.61-3.17	2.67	0.14	2.41-2.78	18
MT_aL/MFL	0.39	0.01	0.37-0.40	0.38	0.01	0.37-0.40	18
HFL/HFW	3.12	0.14	2.96-3.29	3.07	0.19	2.75-3.27	14
HT_iL/HFL	0.91	0.03	0.85-0.94	0.93	0.02	0.91-0.98	14
HT_aL/HFL	0.38	0.01	0.36-0.39	0.38	0.01	0.37-0.39	14
MFL/FFL	1.02	0.02	0.98-1.06	1.04	0.03	1.00-1.08	16
HFL/FFL	1.19	0.05	1.11-1.26	1.23	0.03	1.19-1.29	14
Labial palpi							
BL/BW	1.57	0.07	1.44-1.67	1.55	0.06	1.46-1.67	14
ML/BL	0.70	0.06	0.64-0.78	0.71	0.04	0.65-0.77	14
AL/BL	0.71	0.05	0.63-0.79	0.68	0.03	0.65-0.73	14
Paraglossae L/W	0.97	0.07	0.88-1.07	0.92	0.04	0.85-0.95	16
Maxillary palpi							
MBL/MBW	2.14	0.21	1.80-2.50	2.13	0.13	2.00-2.36	16
MML/MBL	0.69	0.06	0.60-0.78	0.66	0.07	0.54-0.75	15

Appendix 9

Details of morphometric characters of male and female nymphs of *Baetis soror* which did not show significant differences when compared by "t" test.

Significant characters are presented in Table 11.18.

Character	Males $\overline{x}$	Males SD	Males Range	Females $\overline{x}$	Females SD	Females Range	d.f.
NL/MNW	1.20	0.05	1.13-1.30	1.30	0.14	1.09-1.50	16
MNW/PNW	1.46	0.14	1.29-1.74	1.33	0.13	1.21-1.55	16
FFL/FFW	3.23	0.24	2.86-3.64	3.08	0.21	2.73-3.42	24
FT_iL/FFL	0.71	0.04	0.65-0.79	0.72	0.02	0.68-0.76	23
FT_aL/FFL	0.64	0.06	0.56-0.74	0.61	0.02	0.58-0.63	23
MFL/MFW	3.54	0.36	3.15-4.10	3.61	0.31	3.21-4.09	24
MT_iL/MFL	0.70	0.03	0.66-0.74	0.69	0.03	0.66-0.73	24
HFL/HFW	3.81	0.42	3.08-4.44	3.82	0.31	3.17-4.18	22
HT_iL/HFL	0.66	0.02	0.63-0.71	0.66	0.04	0.62-0.76	22
HT_aL/HFL	0.55	0.03	0.51-0.60	0.54	0.03	0.49-0.61	22
MFL/FFL	1.02	0.05	0.95-1.14	1.04	0.07	0.88-1.12	24
Labial palpi							
ML/BL	0.68	0.04	0.60-0.70	0.71	0.05	0.67-0.80	19
glossae L/W	3.55	0.26	3.25-4.00	3.58	0.12	3.50-3.75	20
Labrum L/W	0.58	0.04	0.53-0.64	0.59	0.04	0.53-0.64	12

Appendix 10

Details of morphometric characters of male imagos and nymphs of *Baetis soror* which did not show significant geographical variation when compared by "t" test.

Significant characters are presented in Tables 11.19 and 11.20.

Character	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	d.f.
Male Imagos							
MNW/BL	0.16	0.02	0.13-0.20	0.18	0.01	0.16-0.20	10
NL/MNW	1.73	0.11	1.59-1.89	1.85	0.23	1.58-2.08	10
MNW/PNW	1.47	0.12	1.29-1.63	1.35	0.11	1.18-1.43	10
FWL/FWW	2.67	0.11	2.49-2.86	2.67	0.15	2.49-2.96	29
FT$_i$L/FFL	1.84	0.10	1.71-1.98	1.75	0.18	1.56-1.98	16
FT$_1$L/FFL	0.07	0.01	0.06-0.10	0.09	0.03	0.06-0.15	16
FT$_2$L/FFL	0.79	0.04	0.75-0.87	0.76	0.09	0.63-0.90	15
MT$_i$L/MFL	0.98	0.04	0.91-1.03	0.98	0.04	0.90-1.02	21
MT$_1$L/MFL	0.16	0.03	0.13-0.21	0.17	0.02	0.11-0.20	21
MT$_2$L/MFL	0.13	0.02	0.11-0.16	0.13	0.01	0.11-0.15	21
MT$_3$L/MFL	0.07	0.01	0.06-0.09	0.08	0.01	0.08-0.10	21
HT$_i$L/MFL	0.98	0.02	0.95-1.03	0.96	0.06	0.82-1.05	20
HT$_1$L/MFL	0.16	0.02	0.14-0.19	0.16	0.03	0.12-0.23	20
HT$_2$L/MFL	0.13	0.01	0.11-0.15	0.12	0.02	0.09-0.15	19
HT$_3$L/MFL	0.07	0.01	0.06-0.09	0.07	0.02	0.05-0.10	19
HFL/MFL	0.98	0.09	0.76-1.06	1.01	0.03	0.93-1.05	23
MFL/FFL	0.81	0.03	0.78-0.85	0.81	0.04	0.77-0.87	16
HFL/FFL	0.84	0.06	0.73-0.97	0.82	0.05	0.77-0.91	16
Nymphs							
FFL/HW	0.88	0.08	0.76-1.00	0.88	0.10	0.76-1.00	25
MFL/HW	0.90	0.11	0.76-1.05	0.88	0.15	0.66-1.08	26
HFL/HW	0.95	0.10	0.79-1.07	0.89	0.11	0.79-1.05	23
FFL/FFW	3.16	0.23	2.85-3.64	3.02	0.28	2.68-3.58	38
FT$_i$L/FFL	0.71	0.03	0.65-0.79	0.73	0.04	0.65-0.79	37
MFL/FFL	1.03	0.06	0.88-1.14	1.03	0.04	0.87-1.08	34
HFL/FFL	1.07	0.06	0.90-1.19	1.08	0.03	1.05-1.14	29
Labium L/W	0.59	0.04	0.53-0.64	0.55	0.07	0.44-0.67	21
Labial palpi							
BL/BW	2.07	0.20	1.80-2.50	1.96	0.24	1.67-2.75	35
AL/BW	0.35	0.05	0.27-0.40	0.37	0.06	0.30-0.46	36

Appendix 11

The number of mayflies collected on each sampling date from each habitat as defined by water depth and velocity.

a) Deep Creek. Mayfly species present were *Baetis soror, Atalophlebia australasica, Tasmanocoenis tillyardi* and *Atalonella inconspicua*.

Date	Depth (cm)	Velocity (cmS^{-1})	Habitat	SPECIES			
				B.soror	*A.australasica*	*T.tillyardi*	*A.inconspicua*
20.10.76	25	76.7	Fast riffle	16	4	164	15
	35	31.3	Flat	12	32	332	2
	34	50.5	Run	49	26	186	45
10.11.76	29	19.8	Flat	151	27	334	21
	31	34.3	Riffle	75	37	724	6
24.11.76	32	20.0	Flat	476	101	782	9
	37	24.2	Flat	296	25	412	2
	19	59.4	Fast riffle	376	46	420	2
9.12.76	31	20.0	Flat	388	5	588	-
	26	28.0	Flat	1274	650	1145	8
	22	31.1	Flat	105	32	170	2
	21	39.6	Riffle	578	-	8	-
22.12.76	32	12.6	Flat	440	277	456	12
	34	8.0	Pool	534	148	1408	4
	23	28.0	Flat	573	36	451	2
	20	31.3	Flat	258	1	13	-
6.1.77	30	4.5	Shallow pool	-	320	5121	-
	15	15.5	Flat	662	17	432	-
	12	48.5	Riffle	324	56	115	-
20.1.77	22	15.4	Flat	-	101	466	-
	18	44.3	Riffle	2	104	197	-
	15	54.2	Fast Riffle	-	-	3	-
10.2.77	28	1.4	Shallow pool	-	161	826	-
	18	3.5	Shallow pool	-	103	1603	-
	12	14.0	Flat	52	31	152	-

Appendix 11 continued

Date	Depth (cm)	Velocity (cmS^{-1})	Habitat	SPECIES			
				B.soror	*A.australasica*	*T.tillyardi*	*A. inconspicua*
10.3.77	17	4.4	Shallow Pool	48	149	1050	2
	11	31.0	Flat	-	393	1177	3
	31	5.2	Shallow Pool	-	61	544	1
	11	37.0	Riffle	276	164	417	7
7.4.77	31	31.3	Flat	9	35	954	1
	16	34.3	Riffle	8	25	255	-
	35	32.0	Run	-	60	275	-
	25	62.6	Fast Riffle	6	16	61	1
5.5.77	21	25.0	Flat	13	51	351	-
	12	39.6	Riffle	138	12	153	-
	37	8.0	Pool	28	12	173	-
	13	62.6	Fast riffle	233	37	398	1
1.6.77	26	37.0	Riffle	10	43	295	1
	33	39.6	Run	22	7	172	-
	31	44.3	Riffle	23	15	183	5
	21	67.1	Fast riffle	110	23	151	4
6.7.77	23	31.3	Flat	9	23	304	-
	32	25.0	Flat	10	19	118	-
	20	54.2	Fast riffle	59	23	264	-
	24	93.9	Fast riffle	4	2	108	-
3.8.77	32	44.3	Run	13	25	364	-
	34	76.7	Fast riffle	22	15	184	2
	34	85.2	Fast riffle	6	4	194	-
	32	54.2	Fast riffle	14	36	189	2
7.9.77	23	34.3	Riffle	3	10	198	3
	34	34.3	Run	6	61	310	6
	23	44.3	Riffle	4	5	214	2
	25	65.7	Fast riffle	4	6	20	-

b) Spring Creek. Mayfly species present were *Baetis soror, Atalonella inconspicua* and *Tasmanocoenis tillyardi*.

				B.soror	*A.inconspicua*	*T.tillyardi*
11.9.76	17	3.4	Shallow pool	-	17	370
	11	20.0	Flat	2	1	10
	14	33.3	Riffle	134	202	32
	31	5.3	Shallow pool	1	39	3
2.10.76	11	2.6	Shallow pool	-	457	2368
	11	7.9	Shallow pool	180	166	224
	9	10.5	Flat	84	55	-
	31	0	Stationary pool	-	134	33

Appendix 11 continued

Date	Depth (cm)	Velocity (cmS^{-1})	Habitat	SPECIES		
				B.soror	*A.inconspicua*	*T.tillyardi*
6.11.76	43	33.3	Run	7	16	8
	23	88.5	Fast riffle	52	127	40
	27	50.5	Fast riffle	6	30	20
	15	34.3	Riffle	24	40	11
4.12.76	40	1.6	Pool	129	322	656
	8	28.0	Flat	17,724	98	96
	17	13.3	Flat	320	222	579
	12	3.1	Shallow pool	69	76	482
1.1.77	5	1.5	Shallow pool	1	2	-
	20	0	Stationary pool	-	782	890
	11	1.3	Shallow pool	4	304	362
2.2.77	20	0	Stationary pool	-	19	439
5.3.77*	20	0	Stationary pool	1	468	132
2.4.77	16	0	Stationary pool	-	34	491
	19	0	Stationary pool	-	636	1012
	45	31	Flat	164	102	2
30.4.77	15	0	Stationary pool	1	15	586
	6	10.0	Shallow pool	2144	327	742
3.6.77	40	22.2	Flat	-	44	277
	13	44.3	Riffle	12	24	179
	24	16.7	Flat	-	1152	2151
	23	24.3	Flat	99	349	2748
5.7.77	48	9.0	Pool	-	65	135
	16	50.5	Fast riffle	121	73	33
	27	24.3	Flat	214	242	194
	27	10.0	Shallow pool	129	267	4932
10.8.77	34	10.5	Pool	47	193	36
	10	44.3	Riffle	68	87	-
	21	28.0	Flat	324	290	178
	28	7.9	Shallow pool	236	456	2664
4.9.77	21	3.1	Shallow pool	2	260	213
	10	34.3	Riffle	64	139	16
	20	6.0	Shallow pool	38	184	134
	24	0	Stationary pool	5	282	2132
4.10.77	28	0	Stationary pool	17	196	108
	8	42.0	Riffle	1560	98	17
	15	4.5	Shallow pool	16	624	1028
	22	4.5	Shallow pool	4	972	1693

* Fine net sample not taken into account on this date.

Appendix 12

The Effect of Mesh Size on the Interpretation of the Life History of Two Mayflies from South Australia.

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Suter, P.J., and Bishop, J.E., (1980) The effect of mesh size on the interpretation of the life history of two mayflies from South Australia.
In Flannagan, J.F., and Marshall, K.E., (eds.) *Advances in Ephemeroptera Biology,* Springer, pp. 381-403.