THE COMPARATIVE MORPHOLOGY AND PHYLOGENY OF CERTAIN GONDWANIAN LEPTOPHLEBIIDAE BASED ON THE THORAX, TENTORIUM, AND ABDOMINAL TERGA (EPHEMEROPTERA)

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INTRODUCTION

The Leptophlebiidae comprise the largest family of mayflies, with about 50 nominal genera and approximately 300 described species. The family is cosmopolitan in distribution, and has undergone extensive adaptive radiation, hence occupies a wide variety of aquatic habitats. The greatest diversity of genera occurs in the Southern Hemisphere, especially in certain tropical and cool mountainous regions.

Most taxonomic studies on Southern Hemisphere Leptophlebiidae have been regional in nature. Some of these works are by Harker (1950, 1954, 1957), Penniket (1961), Phillips (1930, 1931), Riek (1970), and Tillyard (1926, 1935) for the Australasian region; Barnard (1932, 1940), Crass (1947), Demoulin (1970), Lestage (1924), Peters and Edmunds (1964) for the Ethiopian region; Lestage (1931), Needham and Murphy (1924), Peters and Edmunds (1972), Traver (1946) for the Neotropical region; and Peters and Edmunds (1970) for the Eastern Hemisphere.

Peters and Edmunds (1964, 1970, 1972) indicated that the Gondwanian (Southern Hemisphere and India) Leptophlebiidae form several distinct holophyletic units. One of these groups occurs throughout Australia, Tasmania, New Zealand, New Caledonia, southern South America, southern Africa, Madagascar, southern India, and Ceylon, thus suggesting one or more Southern Hemisphere dispersal routes in the past. Preliminary studies

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showed that many nominal genera already described in this complex are actually diphyletic or polyphyletic. Nominal genera that we presently include in this complex are: *Atalophlebia* Eaton, 1881, *Atalophlebioides* Phillips, 1930, *Atalomicria* Harker, 1957, *Atalonella* Needham and Murphy, 1924, *Deleatidium* Eaton, 1899, *Jappa* Harker, 1954, *Kirrara* Harker, 1954, *Ulmerophlebia* Demoulin, 1955, and *Zephlebia* Penniket, 1961, from the Australasian region; *Atalonella, Hapsiphlebia* Peters and Edmunds, 1972, *Massartella* Lestage, 1930, *Massartellopsis* Demoulin, 1955, *Meridialaris* Peters and Edmunds, 1972, and *Penaphlebia* Peters and Edmunds, 1972, from the Neotropical region; *Adenophlebia* Eaton, 1881, *Adenophlebiodes* Ulmer, 1924, *Aprionyx* Barnard, 1932, *Atalophlebioides*[3], and *Ulmerophlebia* from the Ethiopian region; and *Kimminsula* Peters and Edmunds, 1970, from Ceylon. However, these groups represent only a portion of the Southern Hemisphere leptophlebiid genera. Some undescribed genera have also been included in this study.

Southern disjunct distributions occur in many other animals and plants. Such distribution patterns have been a subject of great dispute among biogeographers in the past; however, recent hypotheses of sea-floor spreading and plate tectonics have provided a possible clue to this problem. Much interest is now generated among biogeographers to study the probable effect of such tectonic events on the evolution and distribution of the southern biota.

The objectives of this study are: 1) To determine the phylogenetic relationships of the named genera of Leptophlebiidae, based on the comparative morphology of their thorax, tentorium, and the abdominal terga. This is significant in that these morphological structures have never been used by others in studying the phylogeny of the Leptophlebiidae. 2) To compare obtained phylogenetic information with the geological history of the southern continents, and to hypothesize the possible dispersal history of the genera.

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[3] Since this paper was prepared for submission, G. Demoulin (Bull. Inst. Roy. Sci. Nat. Belg. 49(7):1-20, 1973) placed the Madagascan species of *Atalophlebioides* in a new genus, *Petersophlebia*. All *Atalophlebioides* sp. from Madagascar mentioned in this paper should be referred to *Petersophlebia*.

There are often debates as to the suitability of a particular organism for studies in historical biogeography. The Leptophlebiidae is a highly suitable taxon for research of this nature for the following reasons: 1) Among the Ephemeroptera, the Leptophlebiidae are a large group of mayflies with a very ancient evolutionary history. The taxonomic diversity of the group reaches its maximum in the Southern Hemisphere with a high degree of endemism. Based on the fossil data of Demoulin (1965, 1968), Riek (1970), and Tshernova (1970, 1971) the oldest known fossils with presumed leptophlebiid affinities can be dated back to the Jurassic (*Lepismophlebia* Demoulin and *Mesoneta* Tshernova), and recent genera were represented in the Paleocene (*Leptophlebia* Westwood), Oligocene (*Choroterpes* Eaton, *Paraleptophlebia* Lestage), and Miocene (*Atalophlebia* Eaton). It is therefore logical to presume that the Leptophlebiidae lineage can at least be dated back to the Jurassic. Following the geological time-table given by Cracraft (1973), Gaskin (1972), Raven and Axelrod (1972), present separation of Gondwanaland (i.e., a former single Southern Hemisphere landmass) probably began in Jurassic and ended in mid-Cenozoic. This places the occurrence and past dispersal of the Leptophlebiidae into the critical period when Gondwanaland is supposed to have separated. Thus, by studying the phylogeny and distribution of these recent genera in the Southern Hemisphere, we observe the cumulative effect of biological, climatic, and geological processes during possible continental breakup. 2) Nymphs of the selected genera are cool-adapted, inhabiting cool or high-altitude streams and lakes (Agnew, 1961, 1962; Harrison, 1965; Peters and Edmunds, 1972; Riek, 1970; Schoonbee, 1973). In historical biogeography this is significant because: (a) The distribution and dispersal of these insects are limited by their ecological requirements. (b) Geologically, their habitats are relatively unchanged (Brundin, 1965). (c) A cool adapted nature implies that their evolutionary rates have been relatively slow as compared to warm adapted species (Fairchild, 1969; Rensch, 1960). Therefore, evolutionarily, these cool-adapted mayflies are relatively stable in space and time. 3) Eggs or egg-laden females are dispersed by wind; however, mayflies are relatively poor for long range dispersal (Edmunds, 1972;

Mackerras, 1970). Also, the longevity of the mayfly adults is extremely short; they survive for only a few minutes to a few days, depending on the species. Based on the mayfly fauna on various oceanic islands of the world, Edmunds (1972) concluded that the mayflies are particularly useful for the study of zoogeography since chance dispersal over long stretches of ocean is very limited.

METHODS AND MATERIALS

The methods and techniques given by Tsui and Peters (1972) for studying the leptophlebiid thorax were followed. The nymphal tentorium was studied by the methods given in Hudson (1951). The nymphal abdominal terga were studied by both phase-contrast and scanning electron microscopy (SEM). In preparing the nymphal terga for phase-contrast microscopy, the abdomen of the nymph was boiled in 10% KOH until the soft tissues were dissolved. It was washed in water and further dissected in 75% alcohol. Only the abdominal terga were removed and mounted in xylene-free balsam. For SEM study, the whole nymph was first cleansed in 75% alcohol with a fine camel hair brush and further cleansed with an ultrasonic cleaner for 30 minutes. The nymph was then air-dried and coated with approximately 100Å of Au-Pd. The specimen was then studied under a Cambridge Stereoscan with an operating voltage of 5 KV.

The publication of Matsuda (1970) has necessitated several changes in the thorax terminology used in our earlier work (Tsui and Peters, 1972). In the propleuron of the nymph and imago, the former term 'katepisternum' is now called 'trochantin'. However, contrary to Matsuda (1970), this sclerite is rather common among mayflies although it may undergo various forms of reduction. In the mesopleuron of the nymph and imago, the former terms 'prescutal suture' and 'precoxal suture' are now called 'prescutoscutal suture' and 'paracoxal suture' respectively. In the mesonotum and metanotum of the imago the suture formerly identified as 'scutoscutellar suture' is now called 'posterolateral scutal suture'. Matsuda (1970) considered that the typical scutoscutellar suture in the Pterygota arises from the area anterior to the axillary cord on each side. Such a suture is absent in the mayfly and hence the Ephemeropteran notum is not divided into a distinct scutum and scutellum.

The following is a list of abbreviations used in the figures. Pro-, meso-, and metathoracic structures are distinguished from each other by the Arabic numerals 1, 2, and 3 after the abbreviations.

AB	Abdominal segment
ANEP	Anepimeron
ANP	Anterior notal wing process
ANST	Anepisternum
AP	Apodeme
AStS	Anterior sternal suture
ATA	Anterior tentorial arm
ATG	Acrotergite
AX	Axillary sclerite
BA	Basalar sclerite (Basalare)
BS	Basisternum
CV	Cervical sclerite
CX	Coxa
DA	Dorsal arm
EPM	Epimeron
EPS	Episternum
FS	Furcasternum
FWP	Fore wing pad
HP	Humeral plate
HWP	Hind wing pad
KEPM	Katepimeron
KEPS	Katepisternum
MEPSAp	Mesoepisternal apodeme
MNS	Median notal suture
MP	Median plate
OF	Occipital foramen
PAL	Postalar bridge
PAR1	Parapsidal suture, inner
PAR2	Parapsidal suture, outer
PCAp	Procoxal apodeme
PCB	Postcoxal bridge
PCS	Paracoxal suture
PL	Pleuron
PLS	Pleural suture
PLSS	Posterolateral scutal suture
PNP	Posterior notal wing process
PrAl	Prealar bridge
PrScS	Prescutoscutellar suture
PrStS	Presternal suture
PSC	Prescutum
PST	Presternite
PStS	Posterior sternal suture
PTA	Posterior tentorial arm
PWP	Pleural wing process
RSSS	Recurrent scutoscutellar suture
SA	Subalar sclerite (Subalare)
SC	Scutoscutellum
SP	Spiracle
ST	Sternum
StAp	Sternal apophysis
StApP	Sternal apophyseal pit
StS	Sternacostal suture
T	Tergum
TG	Tegula
TB	Tentorial body
Tr	Trochanter
TR	Trochantin
W	Wing

Table 1 lists all species used in this study.

MORPHOLOGY OF THE TAXONOMIC CHARACTERS

This section is a detailed morphological study of the thoracic exoskeleton of the nymph and imagos, the nymphal tentorium and abdominal terga. *Kirrara amenia* Harker was chosen for this study as it is readily available, and as it has all the morphological features necessary to establish an anatomical terminology applicable to the Gondwanian Leptophlebiidae discussed in this paper. Tsui and Peters (1972) made a similar study of *Leptophlebia pacifica* (McDunnough) which represents a typical member of the Palearctic Leptophlebiidae.

(1) Nymphal Tentorium of *Kirrara amenia* (Fig. 1)

The tentorium is an endoskeletal structure in the cranium which functions as an internal support and for muscle attachments. It consists of the tentorial body, a pair of anterior tentorial arms, a pair of dorsal arms, and a pair of posterior tentorial arms. The tentorial body is slightly rectangular and is centrally placed in the head capsule. A longitudinal chitinous outgrowth occurs mid-ventrally on the tentorial body. The anterior tentorial arms are broad invaginations from the cranium near the antennal pits. The dorsal arms are small outgrowths of the anterior tentorial arms and are attached apically near the lateral ocelli. The posterior tentorial arms are shorter and are invaginations of the posterior tentorial pits in the postoccipital suture.

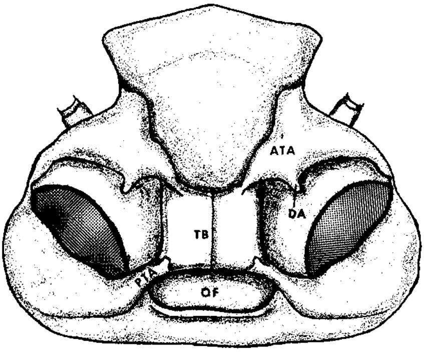
(2) External Thoracic Morphology of *Kirrara amenia* Nymph

The Tergum (Fig. 4)

Pronotum (Fig. 4). — The pronotum is a rectangular plate bisected by a median notal suture. Anteriorly the antecostal suture divides a narrow acrotergite from the pronotum. The anterolateral margins are without spines. Posteriorly the pronotum is fused with the mesonotum.

Mesonotum (Fig. 4). — Anteriorly the antecostal suture sets off a narrow acrotergite which is fused with the posterior margin of the pronotum. Internally, the antecostal suture forms the anterior phragmata. Posterolaterally the mesonotum is evaginated to form the fore wing buds. A median notal suture traverses the entire notum.

FIGURES 1-3. — Posteroventral view of the nymphal tentorium: 1, *Kirrara amenia*, Type 2; 2, *Atalophlebia australis*, Type 1; 3, *Jappa* sp., Type 3.



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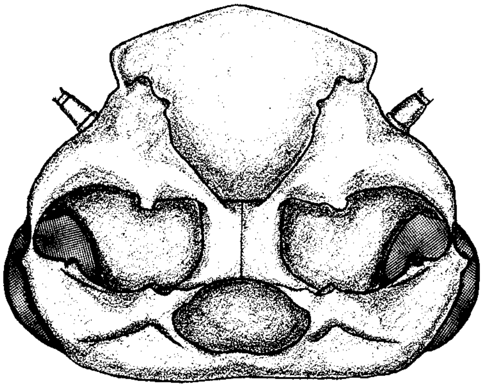

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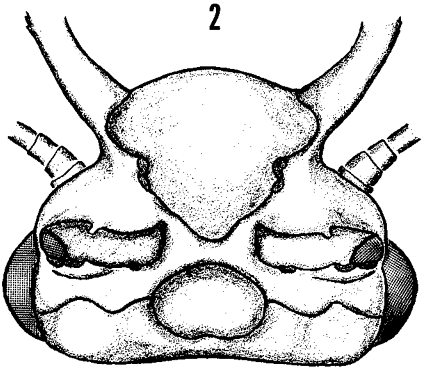

3

Metanotum (Fig. 4). — The anterior margin of the metanotum is bordered by the antecostal suture which fuses with the median notal suture to form a Y-shaped structure. Internally, the antecostal suture forms the posterior phragmata. The median notal suture does not reach the posterior margin of the metanotum.

The Pleuron (Fig. 7)

Propleuron (Fig. 7). — A distinct pleural suture extends from the coxal process obliquely upward; it divides the pleural plate into the episternum and the epimeron. The episternum extends anteriorly into the cervical region and articulates with the posterior end of the cervical sclerite. Dorsal to the pleural suture is the propleural apodeme. Procoxal apodemes are absent.

Mesopleuron (Fig. 7). — The mesopleuron is divided by the pleural suture into the episternum and epimeron. The paracoxal suture is absent. Dorsally the pleural plate fuses with the posterolateral margin of the tergum, but ventrally it is not fused with the mesosternum. Ventral to the episternum is an apodeme called the mesoepisternal apodeme (Fig. 6). Anterior to the episterna in the membranous area are the closed mesothoracic spiracles; Ephemeroptera have an apneustic tracheal system (Imms, 1964). Internally, they are joined to the tracheal system. These spiracles occur also in each abdominal segment (Figs. 15, 16).

Metapleuron (Fig. 7). — The metapleuron is divided by a distinct pleural suture into the episternum and epimeron. The paracoxal suture is absent. Posterodorsally the metapleuron fuses with the metanotum and posteriorly fuses with the first abdominal tergum.

The Sternum (Fig. 5)

Prosternum (Fig. 5). — The prosternal plate is a truncated triangle. Between the two sternal furcal pits is a distinct sternacostal suture dividing the prosternum into the basisternum anteriorly and the furcasternum posteriorly. The anterior sternal sutures consist of two sublateral sutures joined anteriorly by

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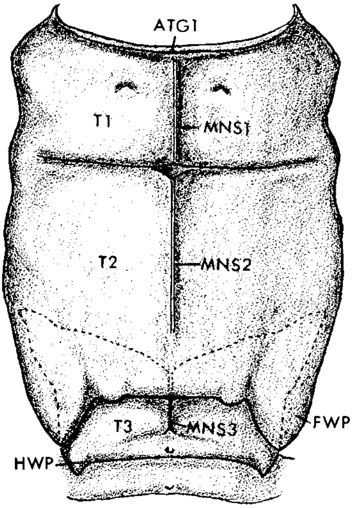
FIGURES 4-5. — Nymph of *Kirrara amenia:* 4, dorsal view of the thoracic terga; 5, ventral view of the thoracic sterna.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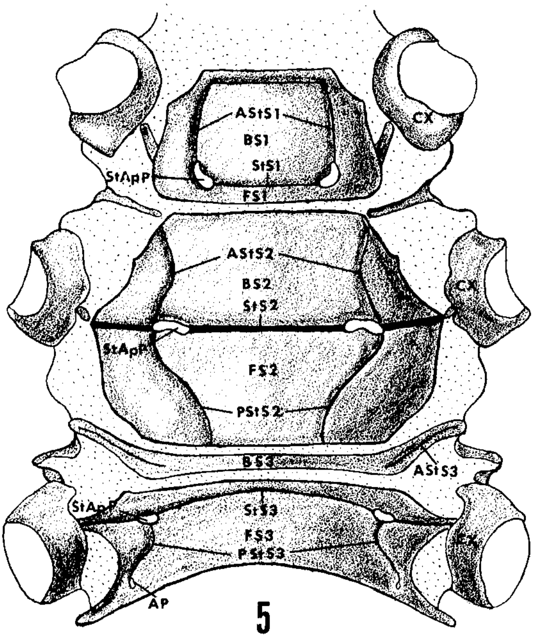
MNS1
T2
MNS2
T3
MNS3
FWP
HWP

4


AStS1
BS1
CX
StS1
StApP
FS1
AStS2
BS2
StS2
CX
StApP
FS2
PStS2
BS3
AStS3
StApP
StS3
FS3
PStS3
CX
AP

5

a horizontal submarginal suture. Posterior width of the prosternum is equal to the anterior width of the mesobasisternum. On each posterolateral margin is a cuticular process which articulates with the posteroventral surface of a fore coxa. Thus, *Kirrara* has a tricondylic coxal articulation, consisting of the pleural articulation, the trochantin, and the sternal articulation. Such an arrangement of coxal articulations will probably limit the movement of the fore legs to an anterotransverse plane.

Mesosternum (Fig. 5). — The mesosternum is a broad hexagonal plate divided by a strong sternacostal suture into the basisternum and furcasternum. The sternacostal suture is divided into three sections, the two lateral sections and the median section bounded by the sternal furcal pits. The width of each lateral section is more than one third width of the median section. Length of the basisternum is about equal to length of the furcasternum. Both the anterior and posterior sternal sutures are present and distinct.

Metasternum (Fig. 5). — The basisternum is a narrow sclerite of about equal width to and separated from the furcasternum. Anteriorly the presternal suture forms a narrow presternum and a pair of long anterior sternal sutures occur laterally. The furcasternum is bordered anteriorly by the sternacostal suture and the posterior sternal sutures curve inward mesally. At the posterior end of each suture is an apodeme which is probably of abdominal origin since they occur segmentally up to the ninth abdominal sternum. Therefore, the furcasternum is probably a compound structure and the posterior part corresponds to the true first abdominal sternum.

(3) Abdominal Terga of *Kirrara amenia* Nymph (Figs. 44, 50)

Under the SEM, the abdominal terga of *Kirrara amenia* are seen to be covered with small cuticular spikes interspersed with hairs about 80-100 μm long and 5 μm thick in diameter (Fig. 50). The

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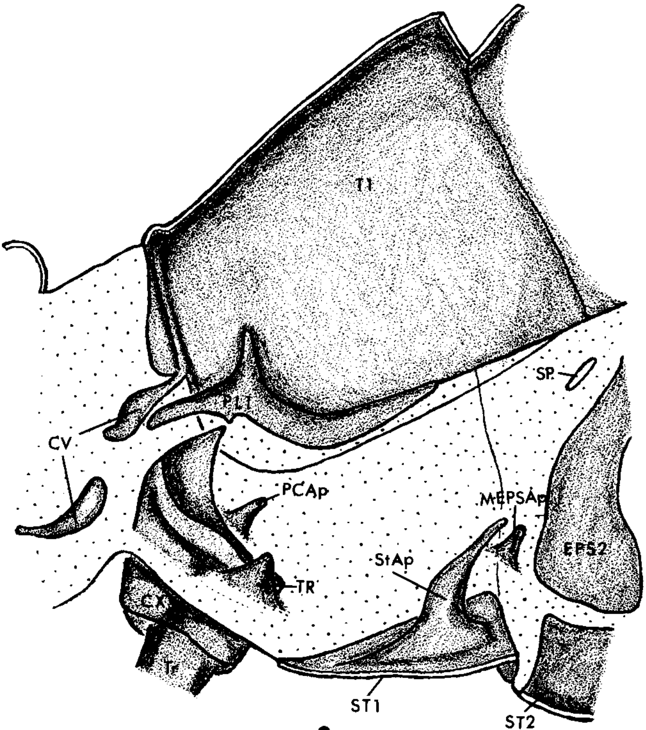
FIGURES 6-7. — 6. — Diagram of the nymphal pleura (internal view), showing the positions of the procoxal apodeme (PCAp) and the mesoepisternal apodeme (MEPSAp); 7. — Lateral view of the thoracic pleura of *Kirrara amenia* nymph.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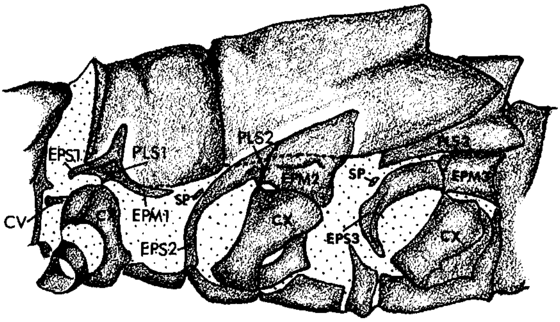
6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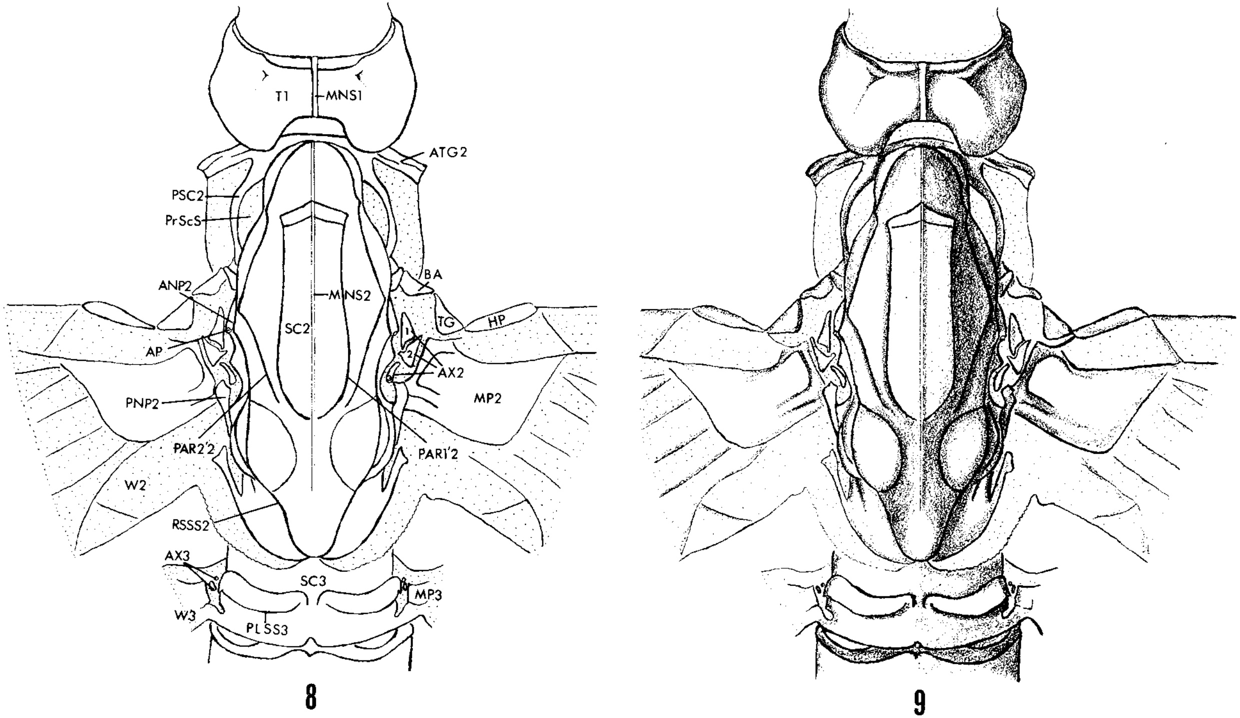
7



FIGURES 8-9. — Dorsal view of the thoracic terga of *Kirrara amenia:* 8, abbreviations of terminology; 9, male imago.

posterior margin consists of small spines in groups of three or four (Fig. 44). They are of a similar size and shape (uniordinal type), about 7.5 μm in length.

(4) External Thoracic Morphology of *Kirrara amenia* Imago

The Tergum (Figs. 8, 9)

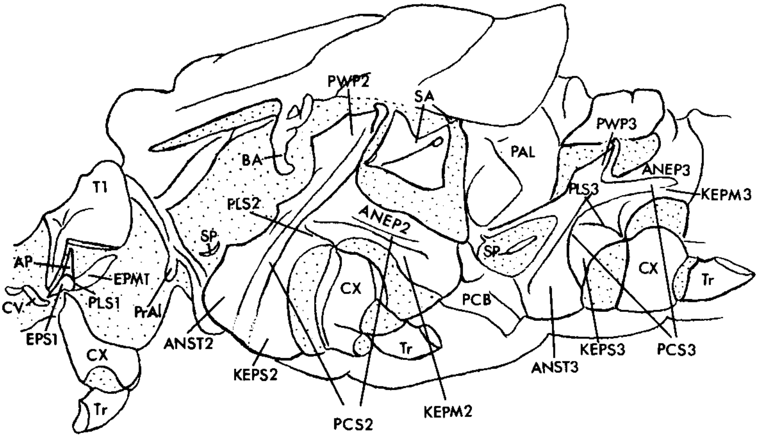
Pronotum (Figs. 8, 9). — The pronotum is an H-shaped sclerite bisected medially by the median notal suture. The antecostal suture forms a narrow acrotergite anteriorly. Near the anteromedian margin is a pair of depressions where several prothoracic muscles are attached internally. The pro- and mesonotum are connected by a membranous area.

Mesonotum (Figs. 8, 9). — The mesonotum consists of the acrotergite, the prescutum, the scutoscutellum, and the postnotum. The acrotergite is a narrow region separated from the scutoscutellum by the antecostal suture. Internally this suture forms the anterior phragmata. The acrotergite fuses lateroventrally with the mesopresternite forming the prealar bridge at the anterior end of the mesothorax. The prescutum is separated from the scutoscutellum by a membranous prescutoscutellar suture. Anteriorly the prescutum is fused with the acrotergite and posteriorly it articulates with the basalar sclerite. Anterolaterally the scutoscutellar shield is bound by a deep notal furrow on each side (Matsuda's anterolateral scutal suture). Posterior to the notal furrow is the anterior notal wing process, bearing an internal apodeme at the point where the first axillary sclerite articulates with it. The scutoscutellar surface is bisected by the median notal suture. Lateral to this are the paired inner and outer parapsidal sutures. According to Matsuda (1970), the scutoscutellar suture is absent in Ephemeroptera; only the recurrent scutoscutellar suture is present as in some Apterygota and in the Plecoptera. Therefore, the separation of the scutum and scutellum is indistinct in the Ephemeroptera. The recurrent scutoscutellar sutures occur laterally on the notal shield dorsal to the notal furrows. Each fore wing axillary region has three axillary sclerites. The first axillary sclerite articulates anteriorly with the basalar sclerite and the anterior notal wing process. The inner posterolateral margin of the first axillary sclerite has a projection which fits into a notch formed on the anterior margin of the second axillary sclerite. Laterally, the second axillary sclerite articulates with the median plate on one side and the third axillary sclerite on the other. The third axillary sclerite is fused to the side of the notal shield in a notch formed between the anterior and posterior notal wing processes. Laterally, the notal shield bears the posterior notal wing processes with the posterolateral scutal suture running from each posterior notal wing process backward along the notal shield. The posterior margin of the notal shield bears the corrugated hind margins of the fore wings. The postnotum consists of the precosta and antecosta. The precosta is a transverse sclerite beneath the scutoscutellum and ventral to it is the antecosta which fuses with the anterior part of the metascutoscutellum forming the posterior phragmata. Laterally the antecosta is fused with the postalar bridges of the mesopleura.

Metanotum (Figs. 8, 9). — The acrotergite and prescutum are absent in the metanotum. Anteriorly, the notum fuses with the antecosta of the mesothorax forming the posterior phragmata of the thorax. As in the mesonotum, the scutoscutellar suture is absent (Matsuda, 1970). Therefore, the metanotum is not divided into a scutum and scutellum. A mid-lateral apodeme marks the position of the anterior notal wing process. The posterolateral scutal sutures transverse the notal surface and mark the positions of the posterior notal wing processes. There are two axillary sclerites in each hind wing base. Anteriorly the first axillary sclerite articulates with the anterior notal wing process and posteriorly with the second axillary sclerite. The second axillary sclerite in turn articulates with the median plate and the posterior notal wing process. Posterior margin of the scutoscutellum bears the posterior margin of the hind wings. The postnotum is divided by a transverse suture into the precosta anteriorly, and the antecosta posteriorly. Laterally they are fused to the metapleuron.

The Pleuron (Figs. 10, 11)

Propleuron (Figs. 10, 11). — Each propleuron is divided by the pleural suture into the anterior episternum and the posterior epimeron. Dorsal to the pleural suture is the propleural apodeme.



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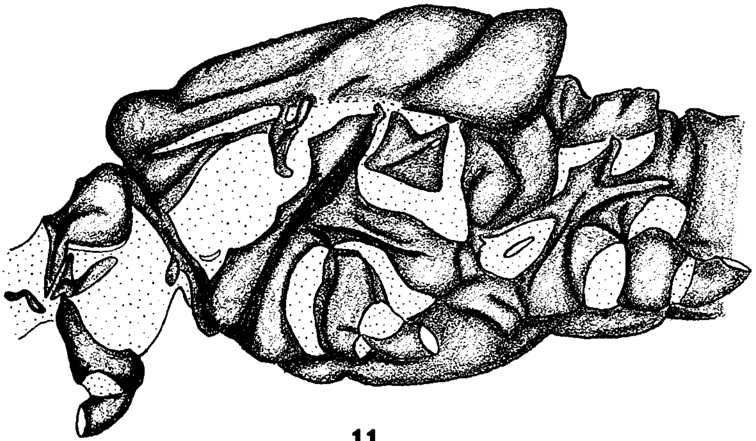

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Figures 10-11. — Lateral view of the thoracic pleura of *Kirrara amenia:* 10, abbreviations of terminology; 11, male imago.

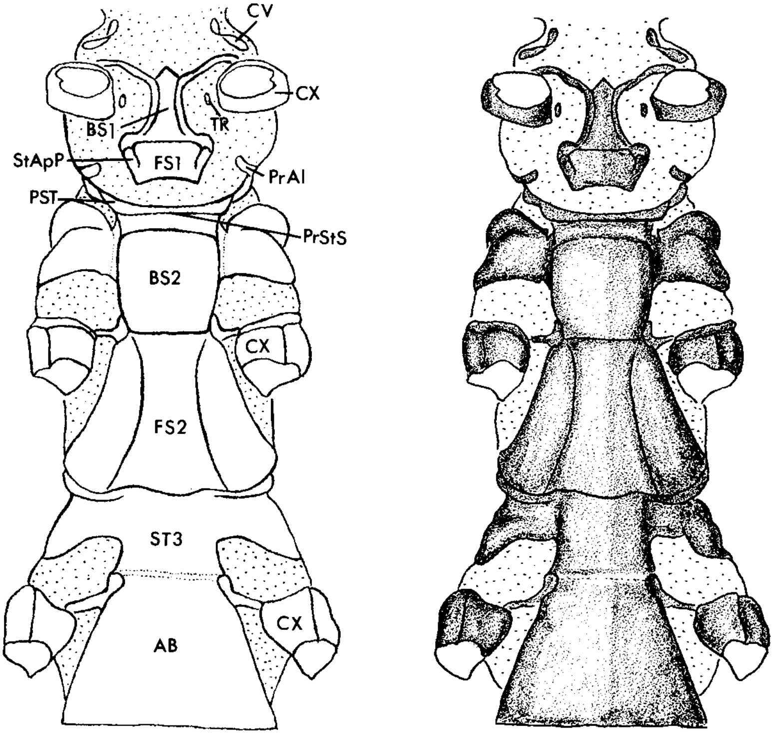
Because of its dorsal position, it is not a typical pleural apophysis as found in most Pterygota. Ventral to the pleural suture is the coxal process which articulates with a fore coxa. Anteriorly, the episternum articulates with the anterolateral arm of the probasisternum and with the cervical sclerite.

Mesopleuron (Figs. 10, 11). — In the anterior membranous area are the basalar sclerite and the mesothoracic spiracle. Dorsally, the basalar sclerite articulates with the prescutum and the tegula. The mesopleuron is divided by the pleural suture into the anterior episternum and the posterior epimeron. The pleural suture extends into the pleural arm and the paracoxal suture divides the episternum into the anepisternum and the katepisternum. Basally, the episternum is fused with the mesobasisternum. In the epimeron, the paracoxal suture is long and delimits an anepimeron and a katepimeron. Ventrally, the katepimeron fuses with the postcoxal bridge which is fused with the mesofurcasternum. Posteriorly, the epimeron fuses with postalar bridge. In the posterodorsal membranous area of the mesopleuron are the anterior and posterior subalar sclerites. The larger anterior subalar sclerite is rectangular and is cut diagonally by a suture. The posterior subalar apodeme is situated at the posterodorsal end of this suture. The anterior margin of the anterior subalar sclerite is folded ventrally to form the anterior subalar apodeme. The smaller posterior subalar sclerite is posterodorsal in position to the larger anterior subalar sclerite. It rests partly on the anterior subalar sclerite and partly on the postalar bridge when the fore wings extend horizontally.

Metapleuron (Figs. 10, 11). — The pleural suture does not extend directly into the pleural wing process. The paracoxal suture is distinct and extends into the episternum and epimeron, delimiting an approximate anapleural and katapleural area. Dorsally, a notal pleural suture separates the metapleuron from the metapostnotum and ventrally, the episternum fuses with the metabasisternum. The basalar and subalar sclerites are absent and the metathoracic spiracle is anterior to the episternum.

The Sternum (Figs. 12, 13)

Prosternum (Figs. 12, 13). — It consists of the basisternum and the furcasternum. Anteriorly, lateral arms of the basisternum articulate with the cervical sclerites and the episterna of the propleura. Laterally, the basisternum is bordered by a longitudinal carina on each side; they are widely separated. The furcasternum is separated from the basisternum by a sternacostal suture. The



12

13

FIGURES 12-13. — Ventral view of the thoracic sterna of *Kirrara amenia:* 12, abbreviations of terminology; 13, male imago.

two sternal apophyseal pits are located on the lateral margins of the furcasternum. In the membranous area between the coxae and the basisternum the trochantins are greatly reduced. At the junctions of the prealar bridge and the presternite of the mesothorax, a process extends from each side to hold the sternal apophyses of the prothorax.

Mesosternum (Figs. 12, 13). — It consists of the presternite, the basisternum, and the furcasternum. The presternite is marked off from the basisternum by the presternal suture. Laterally the presternite fuses with the prealar bridge, forming a small apodeme on each side. The basisternum is elevated with the lateral margins slightly expanded. The length of the basisternum is slightly greater than its width. The posterior margin of the basisternum is truncated. Lateral to the junction of the basisternum and furcasternum are the sternal apophyseal pits together with the ventral processes which act as sternal articulations with the coxae. Thus, with the coxal process of the mesopleuron, the mesocoxal articulation is dicondylic. The furcasternum is divided by a wide median longitudinal invagination with the lateral margins of the invagination being almost parallel. The posterior margin of the furcasternum is convex and fused with the metasternum.

Metasternum (Figs. 12, 13). — The basisternum is fused anterolaterally with the episterna of the metapleura. A distinct sternacostal suture separates the basisternum from the furcasternum. The two sternal apophyseal pits are located on both ends of the sternacostal suture together with the ventral processes. Posteriorly, the furcasternum is fused with the first abdominal sternum.

TAXONOMIC CRITERIA AND CHARACTERS

Taxonomic Criteria

The imaginal taxonomic characters employed in this study have been previously used by Tsui and Peters (1972) in studying the phylogeny of the Leptophlebiidae. Taxonomic characters used in this study were carefully evaluated before they were selected as phylogenetic markers. The selection was based on the following criteria: **1.** Since this study is concerned with phylogenetic relationships among the genera, it is important that characters chosen are not of individual or population variances, or specific characters. To ensure this, individuals of a species collected at the same and at different localities were studied, and for each genus several species were studied. Initially, certain morphological features were chosen when they occurred consistently in a group of species, or certain species groups. They were further selected for low variabilities and high consistencies. Other mormphological features were eliminated because they were consistent in all forms. **2.** The characters were also chosen on the basis of their anatomical complexities. Certain characters were rejected because of their simple morphology, e.g., those of the metasternum in the imago. Complex structures are more reliable indicators of relationships since the probability of parallel or convergent evolution is lower for such structures. **3.** Analysis was made to ensure that characters chosen were not correlated with any special function or habitat. For example, Hudson (1951) demonstrated that the shape of the nymphal tentorium was not correlated with the habitat of the nymph but they appeared to be phylogenetically correlated. In spite of the difference in their ecological requirements the tentoria of the two closely related species *Adenophlebia auriculata* (Eaton) (swift-water form) and *Aprionyx tricuspidatus* Crass (slow-water form) are very similar. Another example was found in the nymphal mesosternum. Nymphs are known to differ in either the presence or absence of the median sternacostal suture. This suture was thought to be correlated with the swift-water habitat of the nymph since it can function as a better attachment for the sternacoxal muscles of the legs. However, this hypothesis was rejected since this suture was absent in such swift-water forms as *Adenophlebia auriculata* but present in slow-water and lake-forms like certain *Atalophlebia* species.

Taxonomic Characters

Nymphal Tentorium. — The value of the tentorium as a phylogenetic marker was established by Hudson (1951). The shape of the tentorial body appears to indicate relationships. It varies two dimensionally from a square to a rectangle with several intermediate grades in between. Basically, three groups were distinguished (Figs. 1-3); **Type 1** — length and width of tentorial body is more or less equal (Fig. 2); **Type 2** — width of tentorial body is greater than its length (Fig. 1); **Type 3** — width of tentorial body is decidedly greater than its length (Fig. 3).

Nymphal Terga.

Pronotum. — Characters chosen were: presence or absence of spines on the anterolateral margins; presence or absence of setae on the lateral margins; and whether or not the pronotum is fused to the mesonotum.

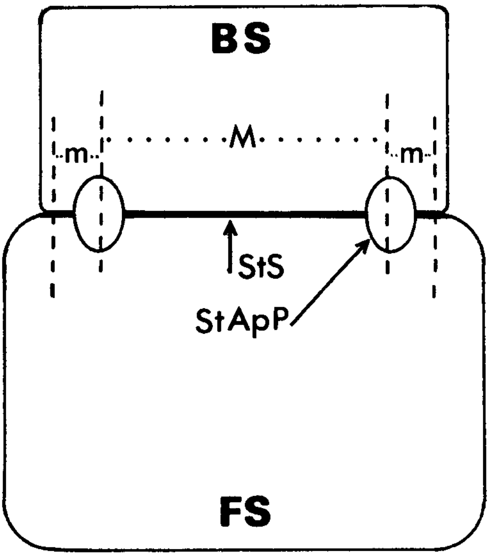


FIGURE 14. — Schematic diagram of the nymphal mesosternum.

Nymphal Pleura.

Propleuron. — The procoxal apodeme, which is located on the dorsal margin of the basicoxite, can be present or absent. This seems to be a good character in separating the major phyletic groups of genera.

Mesopleuron. — The presence or absence of the mesoepisternal apodeme is strongly correlated with the procoxal apodeme, and is useful in separating the major lines of evolution.

Nymphal Sterna.

Prosternum. — Characters chosen were: shape of the prosternum; width of the posterior margin; presence or absence of the sternal costal suture; and the shape of the anterior sternal sutures. The shape of the prosternum is a good character of the genus or higher categories. It can be triangular, or triangular but with the apical portion truncated, or extended, or a square with the anteromedian margin notched. The posterior width of the prosternum varies considerably with the anterior width of the mesosternum. It can be wider, narrower, or equal to the anterior width of the mesosternum. The sternacostal suture can be present or absent. The anterior sternal sutures are variously developed. They are either convergent, with or without being joined apically, or the sutures are parallel, with or without being joined anteriorly by a horizontal suture, or the sutures are absent.

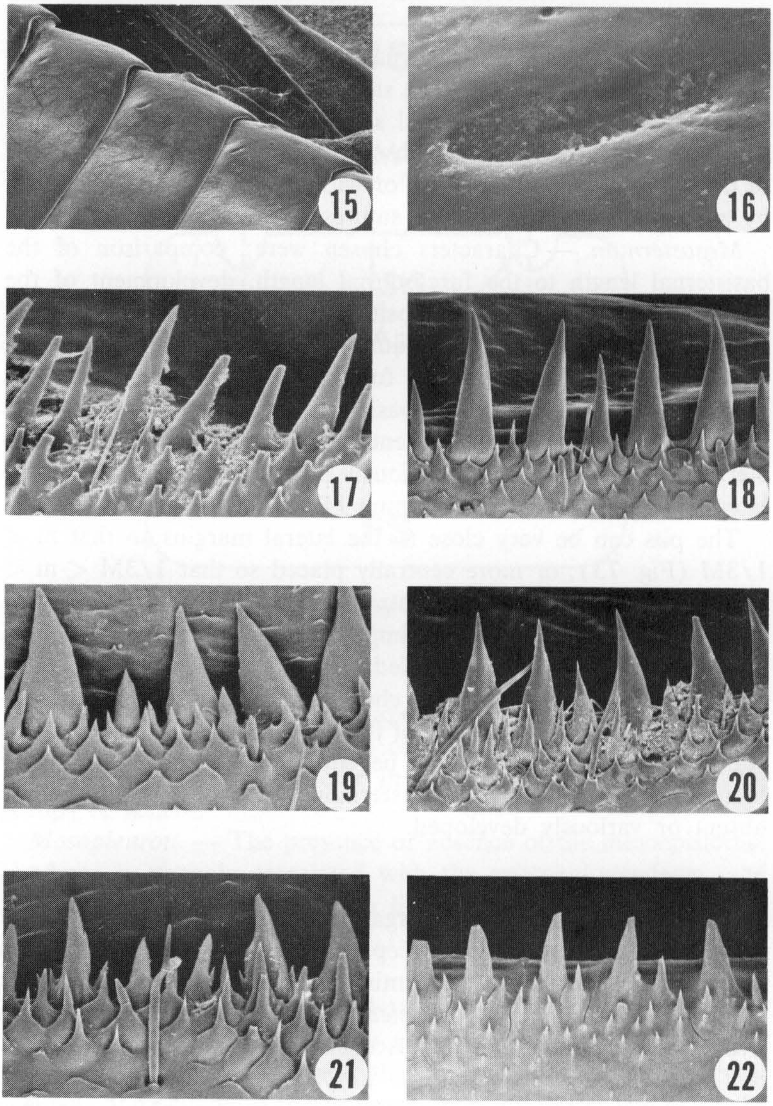
Mesosternum. — Characters chosen were: comparison of the basisternal length to the furcasternal length, development of the sternacostal suture, and the positions of the sternal apophyseal pits. The length of the basisternum can be greater than, equal to, or less than the length of the furcasternum. These differences seem to correspond with the basic types of mesosternum. The sternacostal suture can be absent or variously developed. The sternal apophyseal pits are variously positioned in relation to the lateral margins of the mesosternum (Fig. 14).

The pits can be very close to the lateral margins so that $m < 1/3M$ (Fig. 73); or more centrally placed so that $1/3M < m < 1/2M$ (Fig. 92); or most centrally placed so that $m \geqq 1/2M$ (Fig. 5). This character is important in separating the main lineages among the genera studied.

Metasternum. — Characters chosen were: width of the basisternum, and the development of the anterior sternal sutures. The width of the metasternum can be equal to, less than, or greater than the width of the mesofurcasternum. The anterior sutures are absent or variously developed.

Nymphal Abdominal Terga.

The nymphal abdominal terga have been seldom used as a taxonomic character of the Leptophlebiidae. This required a series of observations to determine the taxonomic value of this structure. Nymphs of *Leptophlebia cupida* (Say) collected from five different river systems in Wisconsin were studied for individual and population variance (Figs. 17-21). Two other species of *Leptophlebia* (Figs. 22, 23), *L. intermedius* (Traver), *L. pacifica* (McDunnough); 1 species of *Habrophlebia, H. vibrans* Needham (Fig. 24); three species of *Paraleptophlebia* (Figs. 25-27), *P. bicornuta* (McDunnough), *P. debilis* (Walker), *P. packii* (Needham) were studied for specific and generic variations. In addition,



FIGURES 15-22. — Figs. 15-16. — Nymph of *Kimminsula* sp.: 15, SEM micrograph of abdominal sterna, showing positions of spiracles (52X); 16, a higher magnification of a single spiracle (1050X). Figs. 17-22. — SEM micrographs of posterior margin of nymphal abdominal terga: 17, *Leptophlebia cupida,* from Wisconsin, Sawyer Co., Weigor Creek (1500X); 18,

nymphs representing each genus of the Southern Hemisphere Leptophlebiidae were studied (Figs. 28-49).

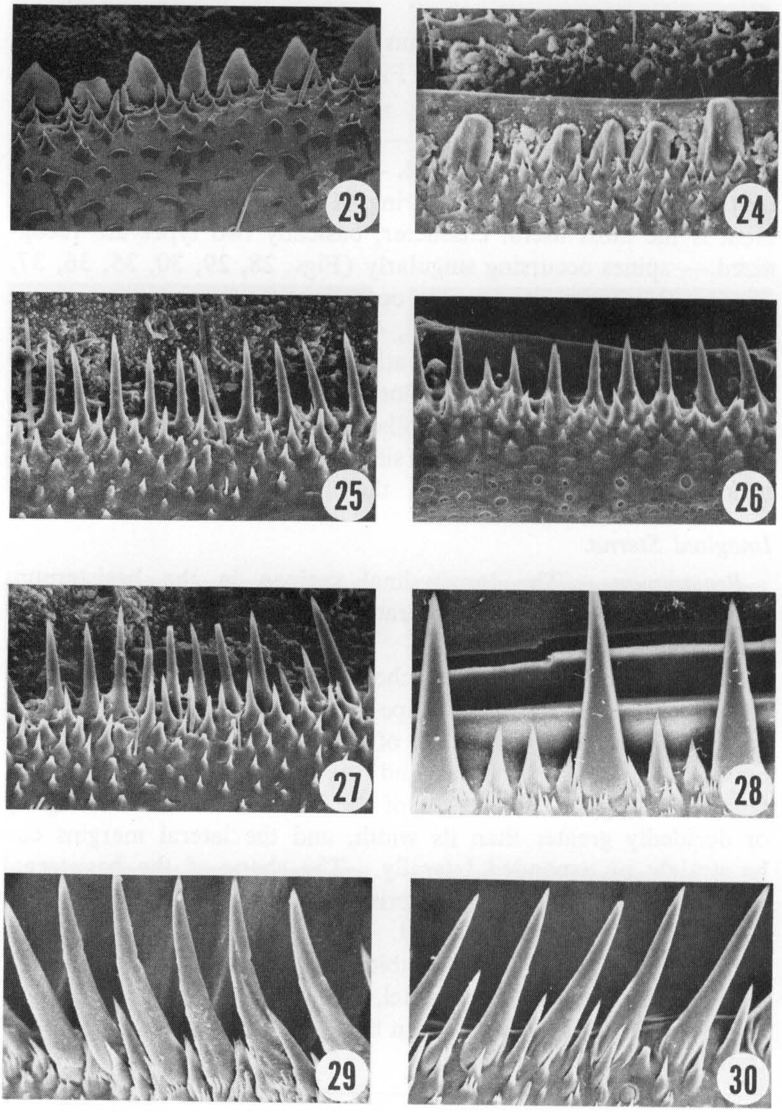
Based on this study, certain structures were found to be of taxonomic value, namely: **1.** — arrangement of spines at the posterior margin of the terga; **2.** — types of cuticular outgrowths on the terga and; **3.** — sculpturing of the terga. Spine arrangement is the most useful character; basically two types are recognized — spines occurring singularly (Figs. 28, 29, 30, 35, 36, 37, 38, 41, 42, 43, 46), and spines occurring in groups (Figs. 31, 32, 33, 34, 39, 40, 44, 45, 47, 48, 49). Cuticular outgrowths can be hair-like (Figs. 50, 51), feather-like (Fig. 52), or rod-like. They are useful in separating closely related genera. Sculpturing on the terga is probably a familial character since almost all the Leptophlebiidae studied have a similar scale-like pattern of sculpturing (Fig. 53) except for the genus *Kirrara* (Fig. 50).

Imaginal Sterna.

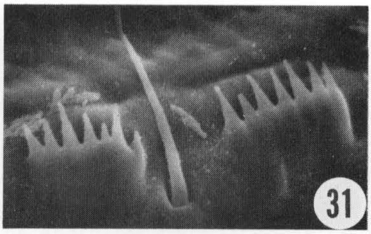
Prosternum. — The longitudinal carinae in the basisternum vary from fused to widely separated. This character is useful in delimiting genera.

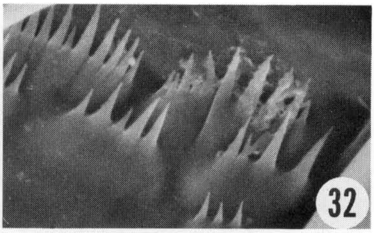
Mesosternum. — Characters chosen were: the relative length and width of the basisternum, shape of the basisternal lateral and posterior margins, development of the median longitudinal invagination in the furcasternum, and the shape of the furcasternal posterior margin. The length of the basisternum can be slightly or decidedly greater than its width, and the lateral margins can be straight or expanded laterally. The shape of the basisternal posterior margin is also characteristic of a genus. It can be acute, rounded, truncated, or concaved. The median longitudinal invagination in the furcasternum exhibits several structural patterns; its lateral margins can be parallel, or variously divergent. The furcasternal posterior margin can be smoothly or acutely concaved, truncated, or convex.

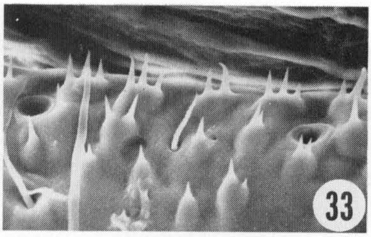
L. cupida, from Wisconsin, Juneau Co., Little Yellow River (1000X); 19, *L. cupida,* from Wisconsin, Dunn Co., Chippewa River (1500X); 20, *L. cupida,* from Wisconsin, Portage Co., Buena Vista Creek (1000X); 21, *L. cupida,* from Wisconsin, Wood Co., Yellow River (1500X); 22, *L. pacifica* (1000X).

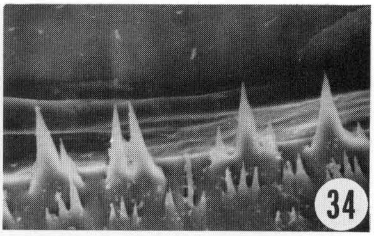


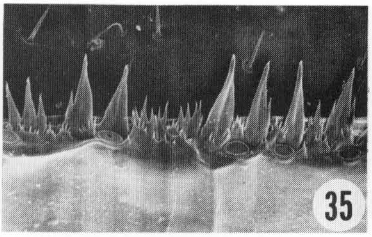
FIGURES 23-30. — SEM micrographs of posterior margins of nymphal abdominal terga: 23, *Leptophlebia intermedia* (1000X); 24, *Habrophlebia vibrans* (950X); 25, *Paraleptophlebia bicornuta* (1000X); 26, *P. debilis* (1000X); 27, *P. packii* (1000X); 28, *Adenophlebia auriculata* (1400X); 29, *A. peringueyella* (1200X); 30, *Aprionyx intermedius* (1000X).

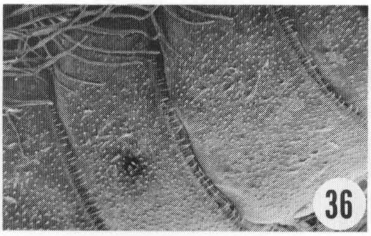


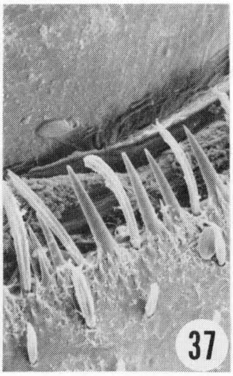




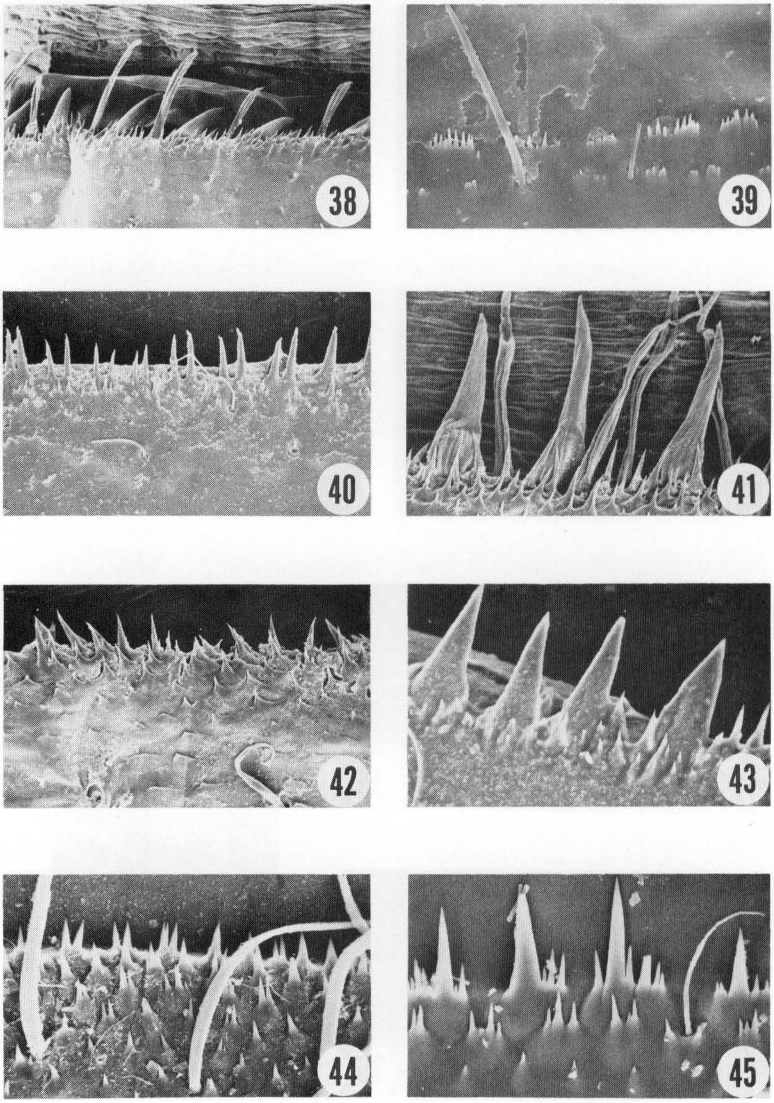








FIGURES 31-37. — SEM micrographs of posterior margins of nymphal abdominal terga: 31, *Ulmerophlebia* sp. (Australia) (5000X); 32, *Jappa* sp. (5000X); 33, *Atalomicria* sp. (2200X); 34, *Atalonella* sp. (Australasian) (2150X); 35, *Atalonella* sp. (South American) (1050X); 36, *Atalophlebia* sp. (50X); 37, *Atalophlebia* sp. (500X).



FIGURES 38-45. — SEM micrographs of posterior margins of nymphal abdominal terga: 38, *Massartella* sp. (580X); 39, *Zephlebia* (*Neozephlebia*) sp. (2000X); 40, *Zephlebia* s.s. sp. (1050X); 41, *Penaphlebia* sp. (1050X); 42, *Hapsiphlebia* sp. (1100X); 43, *Kimminsula* sp. (1000X); 44, *Kirrara amenia* (1500X); 45, *Atalophlebioides* sp. (Australasian) (2200X).

The following is a list of the taxonomic characters, and their character states, used in the phylogenetic analysis of this study. The ancestral state of each character will be indicated but the evolution of the character states will be discussed in a later section.

Our decision concerning the ancestral condition of a character or character state is based on the following criteria: **1.** A character or character state is considered to be ancestral when it is also found in other primitive groups of mayflies, or other primitive insect orders. **2.** A character or character state is considered to be ancestral when it is distributed irregularly or commonly over a wide spectrum of related genera. This is based on the assumption that the earlier a character state is acquired the more commonly it will be integrated into the genetic systems of the progenies and the greater will be the possibility of their appearance. **3.** The ancestral character state is more generalized and from which other specialized conditions can be most easily derived (Mayr, 1969).

Nymphal Tentorium

1. Relative length and width of the tentorial body.
    a. Length and width about equal, Type 1 (ancestral).
    b. Width greater than length, Type 2.
    c. Width decidedly greater than length, Type 3.

Nymphal Terga:

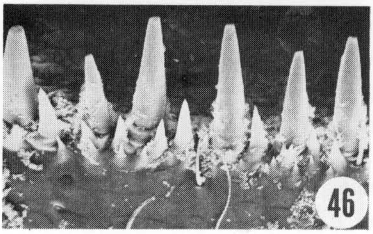
Pronotum

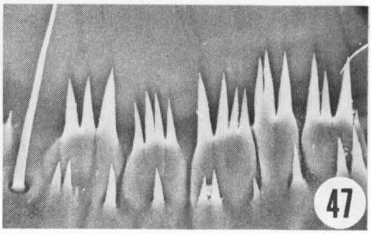
2. Spines on anterolateral margins.
    a. Present (ancestral).
    b. Absent.
3. Setae on lateral margins.
    a. Absent (ancestral).
    b. Present.
4. Fusion of pronotum with mesonotum.
    a. Not fused (ancestral).
    b. Partially or completely fused.

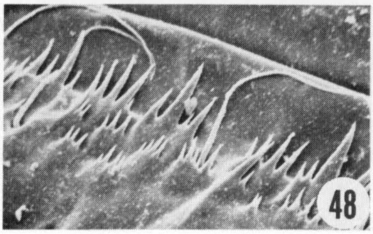
Nymphal Pleura:

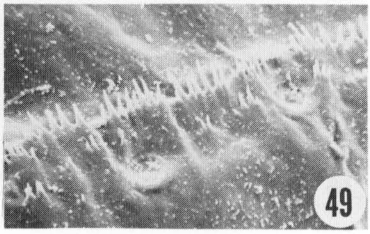
Propleuron

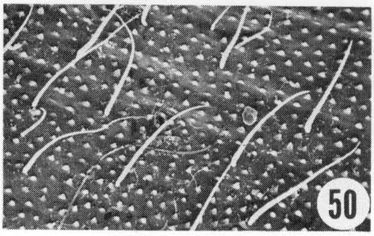
5. Procoxal apodeme.
    a. Present (ancestral).
    b. Absent.

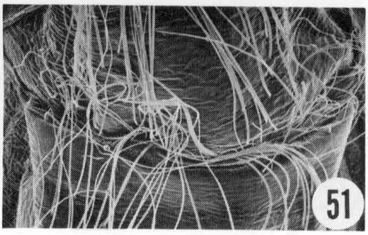


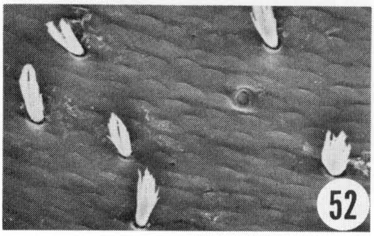


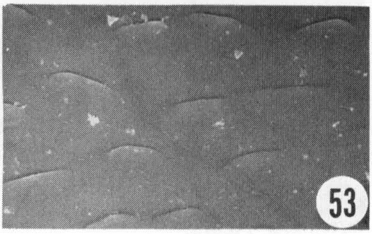












FIGURES 46-53. — Figs. 46-49. — SEM micrographs of posterior margins of nymphal abdominal terga: 46, *Atalophlebioides* sp. (New Zealand) (1000X); 47, *Deleatidium* sp. (2100X); 48, *Massartellopsis* sp. (2100X); 49, *Meridialaris* sp. (2100X). Figs. 50-53. — SEM micrographs of nymphal

Mesopleuron

6. Mesoepisternal apodeme.
    - a. Absent (ancestral).
    - b. Present.

Nymphal Sterna:

Prosternum

7. Shape of prosternum.
    - a. Triangular (ancestral).
    - b. Triangular, with apex truncated.
    - c. Triangular, with apex extended.
    - d. Square, with anteromedian margin notched.
8. Posterior width of prosternum compared to anterior width of mesosternum.
    - a. Wider (ancestral).
    - b. Equal.
    - c. Narrower.
9. Sternacostal suture.
    - a. Present (ancestral).
    - b. Absent.
10. Anterior sternal sutures.
    - a. Convergent, fused apically (ancestral).
    - b. Convergent, without fusing apically.
    - c. Parallel, joined anteriorly by a horizontal suture.
    - d. Parallel.

Mesosternum

11. Mesobasisternal length compared to mesofurcasternal length.
    - a. Longer (ancestral).
    - b. Equal.
    - c. Shorter.
12. Sternacostal suture.
    - a. Absent, or weakly developed (ancestral).
    - b. Present, normally developed.
    - c. Present, strongly developed.
13. Positions of the sternal apophyseal pits.
    - a. $m < 1/3M$ (ancestral).
    - b. $1/3M < m < 1/2M$.
    - c. $m \geqq 1/2M$.

Metasternum

14. Metabasisternal width compared to mesofurcasternal width.
    - a. Narrower or equal (ancestral).

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abdominal terga: 50, *Kirrara amenia* (525X); 51, *Jappa* sp. (200X); 52, *Atalophlebia* sp. (1050X); 53, *Paraleptophlebia memoralis* (3000X).

b. Wider.

15. Anterior sternal sutures.
    a. Absent (ancestral).
    b. Present, i) long, ii) short.

Nymphal Abdominal Terga:

16. Spine arrangement at the posterior margin.
    a. Occur singularly (ancestral).
    b. Occur in groups.

Imaginal Sterna:

Prosternum

17. Development of the longitudinal carinae in the basisternum.
    a. Carinae fused.
        i. Caudal halves fused (ancestral).
        ii. Fused mesally.
        iii. Fused subanteriorly.
    b. Carinae separated.
        i. Slightly separated mesally.
        ii. Widely separated.

Mesosternum

18. Relative length and width of the basisternum.
    a. Length decidedly greater than width (ancestral).
    b. Slightly greater.
19. Lateral margins of basisternum.
    a. Straight to only slightly expanded ventrally (ancestral).
    b. Expanded mesally.
20. Shape of basisternal posterior margin.
    a. Acute.
    b. Rounded.
    c. Truncated.
    d. Concaved.
    (Ancestral state undetermined).
21. Lateral margins of the furcasternal median longitudinal invagination.
    a. Parallel.
    b. Divergent, i) margins slightly separated, ii) margins widely separated.
22. Shape of furcasternal posterior margin.
    a. Smoothly concaved (ancestral).
    b. Acutely concaved.
    c. Convex.
    d. Truncated.

SYSTEMATIC ACCOUNT

This section gives a systematic account of the distribution, habitat, and comparative morphology of the selected genera. Many thoracic characters of the selected genera are similar to those of *Kirrara amenia;* therefore, in this chapter we will discuss only those character states that are different from *K. amenia* and those that differ among genera. The genera are grouped according to their positions on the phylogenetic tree and are discussed in a later section.

Genus ADENOPHLEBIA Eaton, 1881

Distribution. — Africa, south of the Sahara Desert.

Habitats. — Nymphs are found under stones and rocks in pools, small shaded streams or larger rivers; usually at high altitudes 700-1800 m (Crass, 1947; Schoonbee, 1973).

Nymph (Figs. 28, 29, 74). Tentorium. — Tentorial body width slightly greater than length (Type 1). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterolateral margins fused with mesonotum. Propleuron: procoxal apodeme absent. Prosternum: Fig. 74. Triangular, posterior width wider than anterior width of mesosternum. Sternacostal suture present, anterior sternal sutures convergent, without fusing apically. Mesopleuron: mesoepisternal apodeme absent. Mesosternum: Fig. 74. Basisternal length longer than furcasternum. Sternacostal suture absent; $m < 1/3M$. Metasternum: Fig. 74. Basisternum narrower than mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Figs. 28, 29. With scale-like sculpturings; spines at posterior margin occur singularly.

Imago (Fig. 55). Thorax. — Prosternum: Fig. 55. Caudal halves of longitudinal carinae fused. Mesosternum: Fig. 55. Basisternum — length slightly greater than width, lateral margins straight, posterior margin truncated. Furcasternum — lateral margins of median longitudinal invagination parallel, posterior margin smoothly concaved.

Genus APRIONYX Barnard, 1932

Distribution. — Africa, south of Sahara Desert.

Habitats. — Nymphs are found under stones, or marginal vegetation, in slow current (Harrison and Agnew, 1962; Schoonbee, 1973); restricted to montane or semimontane regions (Harrison, 1965).

Nymph (Figs. 30, 73). Tentorium. — Tentorial body width greater than length (Type 2). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme absent. Prosternum: Fig. 73. Triangular, posterior width wider than anterior width of mesosternum. Sternacostal suture present, anterior sternal sutures convergent, without fusing apically. Mesopleuron: mesoepisternal apodeme absent. Mesosternum: Fig. 73. Basisternal length shorter than furcasternum. Sternacostal suture absent; m < 1/3M. Metasternum: Fig. 73. Basisternum wider than mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Fig. 30. With scale-like sculpturings; spines at posterior margin occur singularly.

Imago (Fig. 54). Thorax. — Prosternum: Fig. 54. Caudal halves of longitudinal carinae fused. Mesosternum: Fig. 54. Basisternum — length slightly greater than width, lateral margins straight, posterior margin rounded. Furcastenum — lateral margins of median longitudinal invagination parallel, posterior margin smoothly concaved.

Genus ADENOPHLEBIODES Ulmer, 1924

Distribution. — Africa, south of Sahara Desert.

Habitats. — Nymphs are found under stones in pools and quiet sections of permanent streams (Agnew, 1961, 1962); usually found in montane or semimontane regions, 590-685 m (Harrison, 1965).

Nymph (Fig. 75). Tentorium. — Tentorial body length slightly greater than width (Type 1). Thorax. — Pronotum: anterolateral margins with spines, lateral margins without setae. Posterolateral margins fused with mesonotum. Propleuron: procoxal apodeme absent. Prosternum: Fig. 75. Triangular, posterior width equal to anterior width of mesosternum. Sternacostal suture present, anterior sternal sutures convergent, fused apically. Mesopleuron: Mesoepisternal apodeme absent. Mesosternum: Fig. 75. Basisternal length longer than furcasternum. Sternacostal suture present only in *A.* (*Hyalophlebia*); m < 1/3M. Metasternum: Fig. 75. Basisternum wider than mesofurcasternum. Anterior sternal sutures present but weakly formed. Abdominal Terga. — With scale-like sculpturings; spines at posterior margin occur singularly. (Data from phase contrast microscopy only).

Imago (Fig. 56). Thorax. — Prosternum: Fig. 56. Caudal halves of longitudinal carinae fused. Length of carinae shorter in *A.* (*Hyalophlebia*). Mesosternum: Fig. 56. Basisternum — length slightly greater than width,

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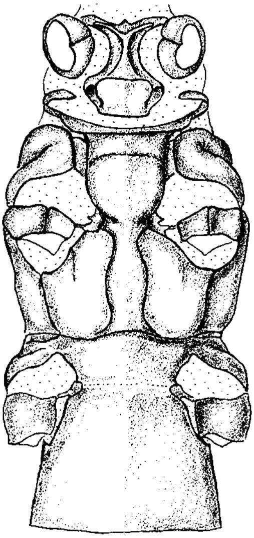
FIGURES 54-57. — Ventral view of thoracic sterna of male imago: 54, *Aprionyx tricuspidatus;* 55, *Adenophlebia auriculata;* 56, *Adenophlebiodes* (*Adenophlebiodes*) *bicolor;* 57, *Hapsiphlebia anastomosis.*



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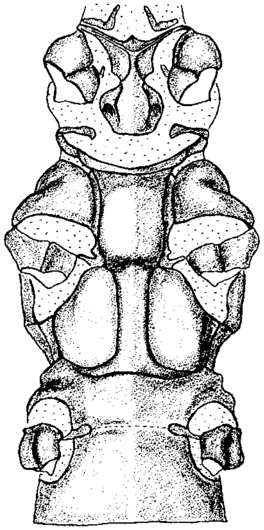

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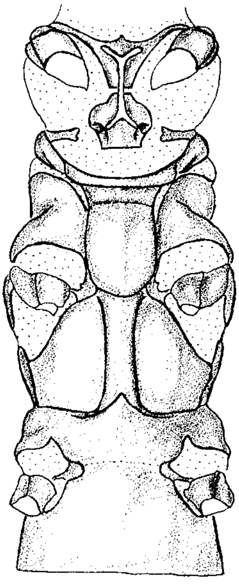

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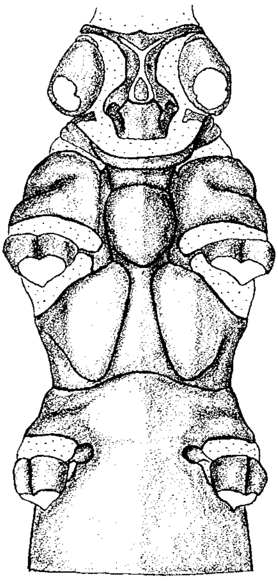

57

lateral margins straight, posterior margin rounded. Furcasternum — lateral margins of median longitudinal invagination parallel, posterior margin acutely concaved.

Genus ULMEROPHLEBIA Demoulin, 1955

Distribution. — Australia, eastern states.

Habitats. — Nymphs are found burrowing beneath rocks in streams with slow flow (Riek, 1970).

Nymph (Figs. 31, 86). Tentorium. — Tentorial body decidedly greater than length (Type 3). Thorax. — Pronotum: anterolateral margins with spines; lateral margin with long setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 86. Triangular, posterior width wider than anterior width of mesosternum. Sternacostal suture absent; anterior sternal sutures convergent, fused apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 86. Basisternal length longer than furcasternum. Sternacostal suture only partially formed; $m < 1/3M$. Metasternum: Fig. 86. Basisternum wider than mesofurcasternum; anterior sternal sutures present. Abdominal Terga. — Fig. 31. With scale-like sculpturings, spines at posterior margin in groups.

Imago. Thorax. — Prosternum: (As in Fig. 65). Longitudinal carinae fused mesally. Mesosternum: (As in Fig. 65). Basisternum — length decidedly greater than width; lateral margins slightly expanded, posterior margin acute. Furcasternum — lateral margins of median longitudinal invagination divergent and slightly separated, posterior margin smoothly concaved.

Genus JAPPA Harker, 1954

Distribution. — Australia, eastern states.

Habitats. — Nymphs are found burrowing beneath rocks in streams with slow flow (Riek, 1970).

Nymph (Figs. 32, 87). Tentorium. — Tentorial body decidedly greater than length (Type 3). Thorax. — Pronotum: anterolateral margins with spines, lateral margin with long setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 87. Triangular, with apex truncated, posterior width equal to anterior width of mesosternum. Sternacostal suture absent; anterior sternal sutures convergent without fusing apically. Mesopleuron: mesoepisternal apodeme

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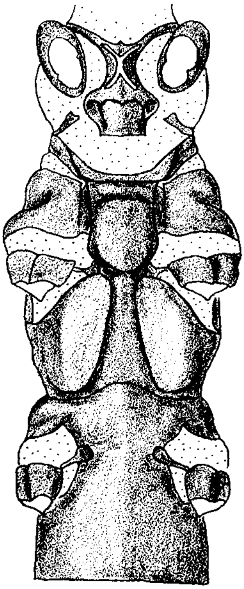
FIGURES 58-61. — Ventral view of thoracic sterna of male imago: 58, *Penaphlebia chilensis;* 59, *Zephlebia* s.s sp.; 60, *Zephlebia* (*Neozephlebia*) *nodularis;* 61, *Atalonella* sp. (Australasian).



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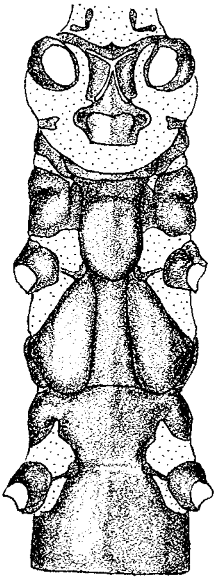

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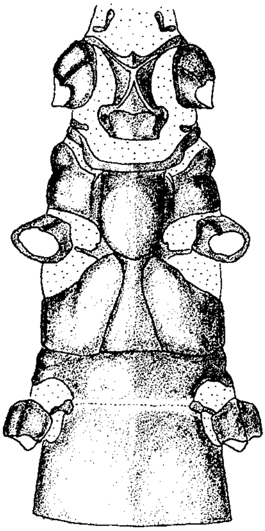

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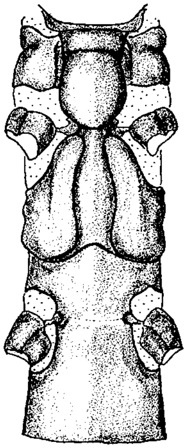

61

present. Mesosternum: Fig. 87. Basisternal length equal to furcasternum. Sternacostal suture only partially formed; m < 1/3M. Metasternum: Fig. 87. Basisternum wider than mesofurcasternum; anterior sternal sutures absent. Abdominal Terga. — Fig. 32. With scale-like sculpturings, spines at posterior margin in groups.

Imago (Fig. 65). Thorax. — Prosternum: Fig. 65. Longitudinal carinae slightly separated. Mesosternum: Fig. 65. Basisternum — length greater than width, lateral margins expanded mesally, posterior margin acute. Furcasternum — lateral margins of median longitudinal invagination divergent, and slightly separated, posterior margin smoothly concaved.

Genus ATALOMICRIA Harker, 1957

Distribution. — Australia, Queensland to southern New South Wales.

Habitats. — Nymphs are restricted to small, moderately flowing, cool mountain streams in heavily forested areas (Riek, 1970).

Nymph (Figs. 33, 88). Tentorium. — Tentorial body width decidedly greater than length (Type 3). Thorax. — Pronotum: anterolateral margins with spines, lateral margins with setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme absent. Prosternum: Fig. 88. Triangular, with apex extended; posterior width equal to anterior width of mesosternum. Sternacostal suture absent, anterior sternal sutures convergent and fused apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 88. Basisternal length equal to furcasternum. Sternacostal suture present; m < 1/3M. Metasternum: Fig. 88. Basisternal width about equal to mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Fig. 33. Spines at posterior margin occur in groups.

Imago (Fig. 66). Thorax. — Prosternum: Fig. 66. Longitudinal carinae fused mesally. Mesosternum: Fig. 66. Basisternum — length decidedly greater than width, lateral margins expanded mesally, posterior margin acute. Furcasternum — lateral margins of median longitudinal invagination parallel, posterior margin acutely concaved.

Genus ATALONELLA Needham and Murphy, 1924

Distribution. — Australia, eastern; Tasmania; South America, Chile and Argentina.

Habitats. — Australasian nymphs occur in fast cold riffles (Riek, 1970); South American nymphs occur in smaller mountain

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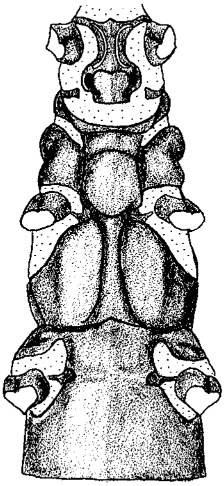
FIGURES 62-65. — Ventral view of thoracic sterna of male imago: 62, *Atalonella* sp. (South American); 63, *Atalophlebia australis;* 64, *Massartella* sp.; 65, *Jappa* sp.



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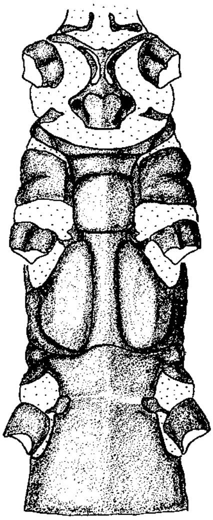

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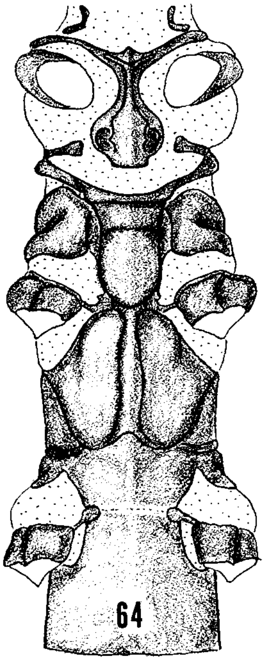

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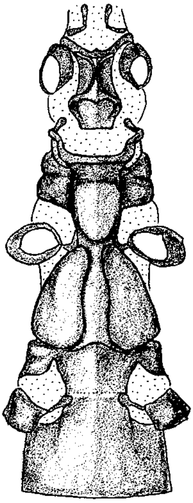


65

streams that may dry up in middle to late summer (Peters and Edmunds, 1972).

Nymph (Figs. 34, 35, 81, 82). Tentorium. — Tentorial body width slightly greater than length (Type 1). Thorax. — Pronotum: Second cervical sclerites detached. Anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Figs. 81, 82. Triangular, with apex truncated; posterior width narrower than anterior width of mesosternum. Sternacostal suture present, anterior sternal sutures convergent, without fusing apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Figs. 81, 82. Basisternal length longer than furcasternum in South American species but equal in Australasian species. Sternacostal suture absent in South American species but present in Australasian species; $m < 1/3M$. Metasternum: Figs. 81, 82. Basisternum wider than mesofurcasternum in South American species but narrower in Australasian species. Anterior sternal sutures absent. Abdominal Terga. — Figs. 34, 35. With scale-like sculpturings; spines at posterior margin occur singularly.

Imago (Figs. 61, 62). Thorax. — Prosternum: Figs. 61, 62. Longitudinal carinae widely separated. Mesosternum: Figs. 61, 62. Basisternum — length slightly greater than width, lateral margins slightly expanded ventrally, posterior margin rounded. Furcasternum — lateral margins of median longitudinal invagination divergent and widely separated in South American species, but parallel in Australasian species; posterior margin smoothly concaved in Australasian species, slightly acute in South American species.

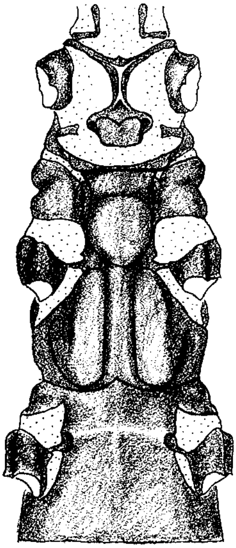
Remark. — The differences in the thoracic structures between the Australasian and South American *Atalonella* show the heterogeneity of this genus. These results support the contentions of M. L. Pescador (pers. comm.) and E. F. Riek (pers. comm.) that the genus *Atalonella* is polyphyletic and can be further subdivided taxonomically in both South America and Australia.

Genus ATALOPHLEBIA Eaton, 1881

Distribution. — Australia, Tasmania.

Habitats. — Nymphs are found in a wide variety of habitats, from lakes, stagnant pools to wide and swift streams (Harker, 1954).

FIGURES 66-69. — Ventral view of thoracic sterna male imago: 66, *Atalomicria* sp.; 67, *Kimminsula* sp. (female subimago); 68, *Atalophlebioides* sp. (Australasian); 69, *Atalophlebioides cromwelli.*



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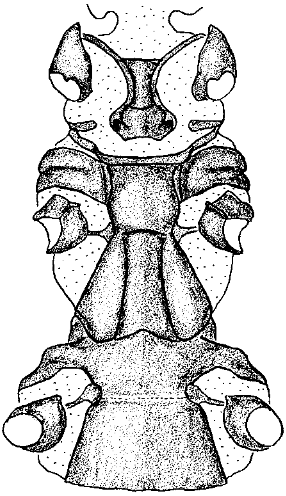

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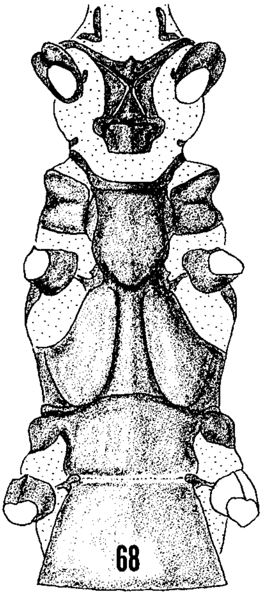

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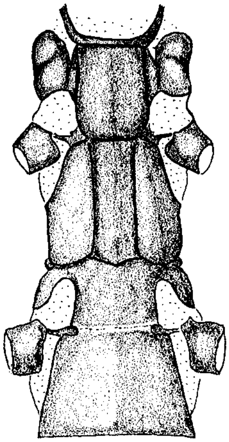


69

Nymph (Figs. 36, 37, 83, 84). Tentorium. — Tentorial body width slightly greater than length (Type 1). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 83. Triangular, posterior width equal to anterior width of mesosternum. Sternacostal suture absent, anterior sternal suture convergent, fused apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 83. Basisternal length equal to furcasternum. Sternacostal suture present; $m < 1/3M$. Metasternum: Fig. 83. Basisternal width equal to mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Figs. 36, 37, 38. With scale-like sculpturings, feather-like setae present. Spines at posterior margin occur singularly and can be mixed with long feather-like spines (biordinal).

Imago (Fig. 63). Thorax. — Prosternum: Fig. 63. Longitudinal carinae slightly separated mesally. Mesosternum: Fig. 63. Basisternum — length slightly greater than width, lateral margins slightly expanded ventrally, posterior margin truncated. Furcasternum — lateral margins of median longitudinal invagination parallel, posterior margin smoothly concaved.

Genus MASSARTELLA Lestage, 1930

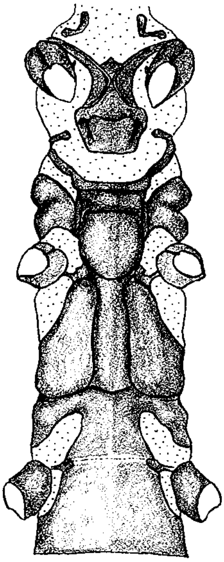
Distribution. — South America, Brazil.

Habitats. — Nymphs are found on rocks in swifter portions of small mountain streams or larger rivers (Peters and Edmunds, 1972).

Nymph (Figs. 38, 85). Tentorium. — Tentorial body width about equal to length (Type 1). Thorax. — Pronotum: anterolateral margins with spines, lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 85. Triangular, with apex extended; posterior width about equal to anterior width of mesosternum. Sternacostal suture absent; anterior sternal sutures convergent, fused apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 85. Basisternal length longer than furcasternum. Sternacostal suture present; $m < 1/3M$. Metasternum: Fig. 85. Basisternal width about equal to mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Fig. 38. With scale-like sculpturings and rod-like setae; spines at posterior margin occur singularly, mixed with feather-like spines (biordinal).

Imago (Fig. 64). Thorax. — Prosternum: Fig. 64. Caudal halves of longitudinal carinae fused. Mesosternum: Fig. 64. Basisternum — length decidedly greater than width, lateral margins straight, posterior margin

FIGURES 70-72. — Ventral view of thoracic sterna of male imago: 70, *Deleatidium* sp.; 71, *Massartellopsis* sp.; 72, *Meridialaris* sp.



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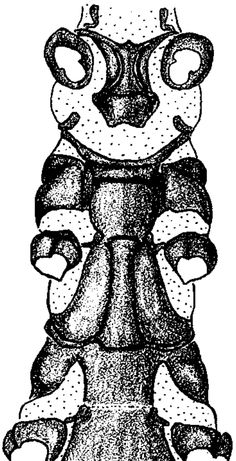

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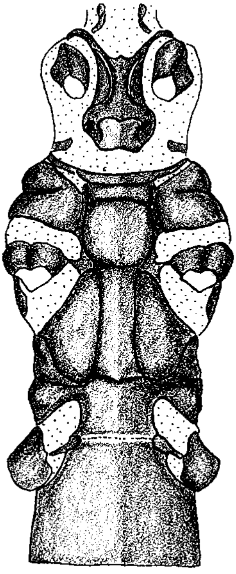


72

rounded. Furcasternum — lateral margins of median longitudinal invagination divergent, slightly separated; posterior margin smoothly concaved.

Genus ZEPHLEBIA Penniket, 1961

Subgenus ZEPHLEBIA s.s.

Distribution. — New Zealand.

Habitats. — Nymphs are found clinging to stones and submerged timbers (Penniket, 1961).

Nymph (Figs. 40, 78). Tentorium. — Tentorial body width decidedly greater than length (Type 3). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 78. Triangular, posterior width wider than anterior width of mesosternum. Sternacostal sutures absent, anterior sternal sutures convergent, without fusing apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 78. Basisternal length about equal to furcasternum. Sternacostal suture only partially formed; $1/3M < m < 1/2M$. Metasternum: Fig. 78. Basisternum wider than mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Fig. 40. With scale-like sculpturings, spines at posterior margin occur singularly.

Imago (Fig. 59). Thorax. — Prosternum: Fig. 59. Longitudinal carinae fused mesally. Mesosternum: Fig. 59. Basisternum — length decidedly greater than width, lateral margins expanded, posterior margin rounded. Furcasternum — lateral margins of median longitudinal invagination divergent, widely separated; posterior margin truncated.

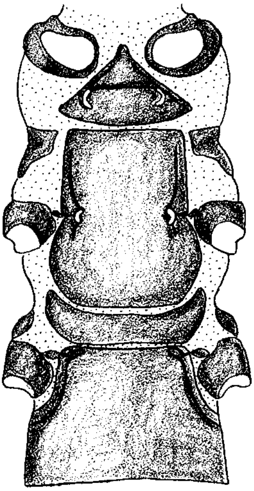
Subgenus NEOZEPHLEBIA

Distribution. — New Zealand.

Habitats. — Nymphs are found clinging among weeds (Penniket, 1961). Diagnostic characters of *Neozephlebia* are similar to *Zephlebia* s.s. except for the following:—

Nymph (Figs. 39, 79, 80). Tentorium. — Tentorial body width greater than length (Type 2). Thorax. — Prosternum: Figs. 79, 80. Posterior width about equal to anterior width of mesosternum. Sternacostal suture present. Mesosternum: Figs. 79, 80. Basisternal length longer than furcasternum. Sternacostal suture normally developed in certain species from the South Island.

FIGURES 73-76. — Ventral view of thoracic sterna of nymph: 73, *Aprionyx peterseni;* 74, *Adenophlebia perinqueyella;* 75, *Adenophlebiodes* (*Hyalophlebia*) *patriciae;* 76, *Hapsiphlebia* sp.



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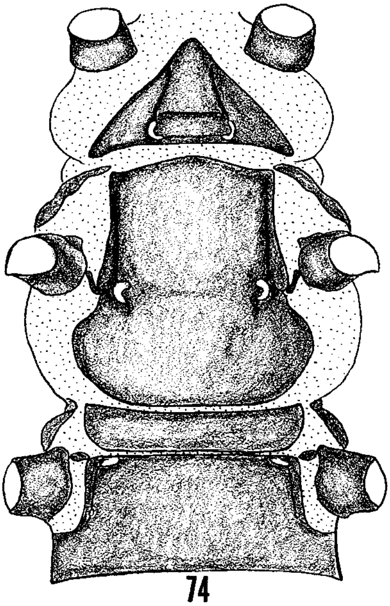

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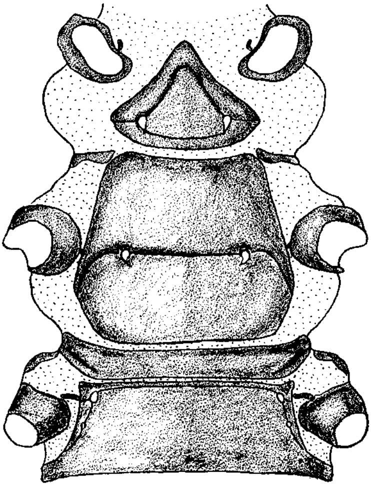

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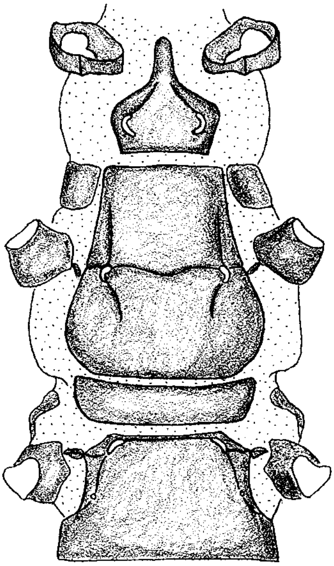

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Imago (Fig. 60). Thorax. — Mesosternum: Fig. 60. Furcasternum — lateral margins of median longitudinal invagination more divergent.

Remark. — *Z.* (*Zephlebia* s.s.) and *Z.* (*Neozephlebia*) have a comparatively low S_J value (0.63) for two subgenera. Preliminary studies indicate that their subgeneric rank is questionable.

Genus PENAPHLEBIA Peters and Edmunds, 1972

Distribution. — South America; Chile, Argentina.

Habitats. — Nymphs occur on rocks in a wide variety of streams, rivers (Peters and Edmunds, 1972), and lakes (M. L. Pescador, pers. comm.).

Nymph (Figs. 41, 77). Tentorium. — Tentorial body length slightly greater than width (Type 1). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 77. Triangular, with apex truncated; posterior width narrower than anterior width of mesosternum. Sternacostal suture absent, anterior sternal sutures convergent, without fusing apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 77. Basisternal length equal to furcasternum. Sternacostal suture present; $m < 1/3M$. Metasternum: Fig. 77. Basisternum wider than mesofurcasternum. Anterior sternal sutures absent. Abdominal Terga. — Fig. 41. With scale-like sculpturings; spines at posterior margin occur singularly.

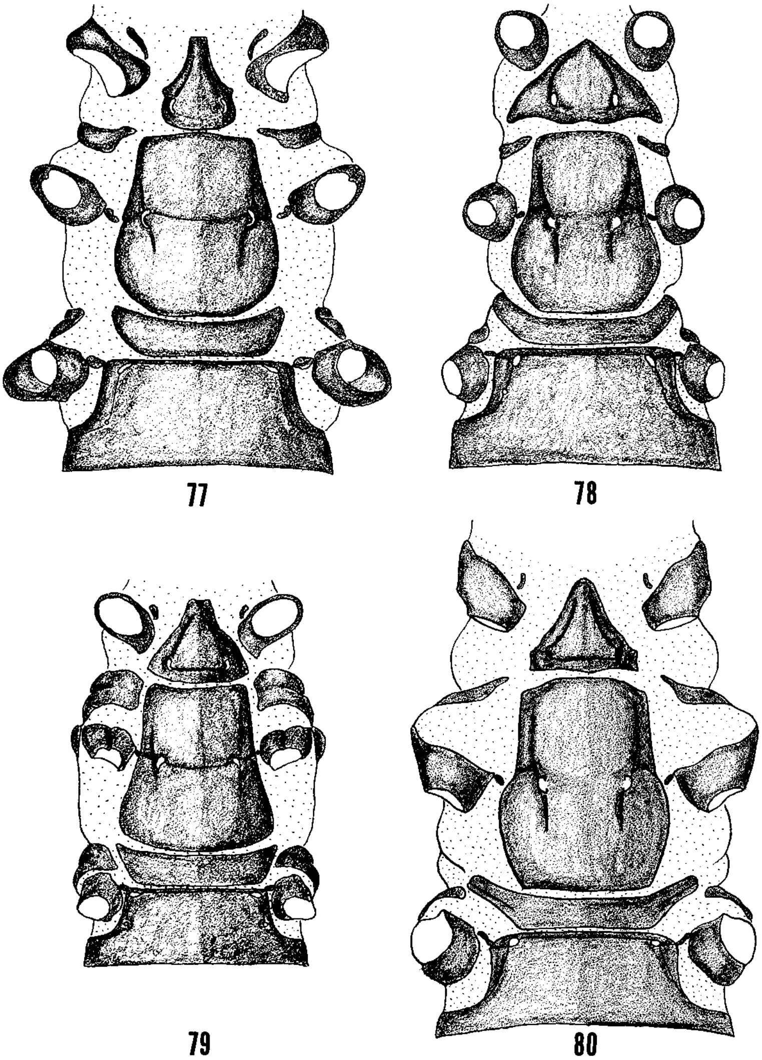
Imago (Fig. 58). Thorax. — Prosternum: Fig. 58. Longitudinal carinae fused mesally. Mesosternum: Fig. 58. Basisternum — length decidedly greater than width, lateral margins slightly expanded, posterior margin acute. Furcasternum — lateral margins of median longitudinal invagination divergent, slightly separated; posterior margin smoothly concaved.

Genus HAPSIPHLEBIA Peters and Edmunds, 1972

Distribution. — South America; Chile, Argentina.

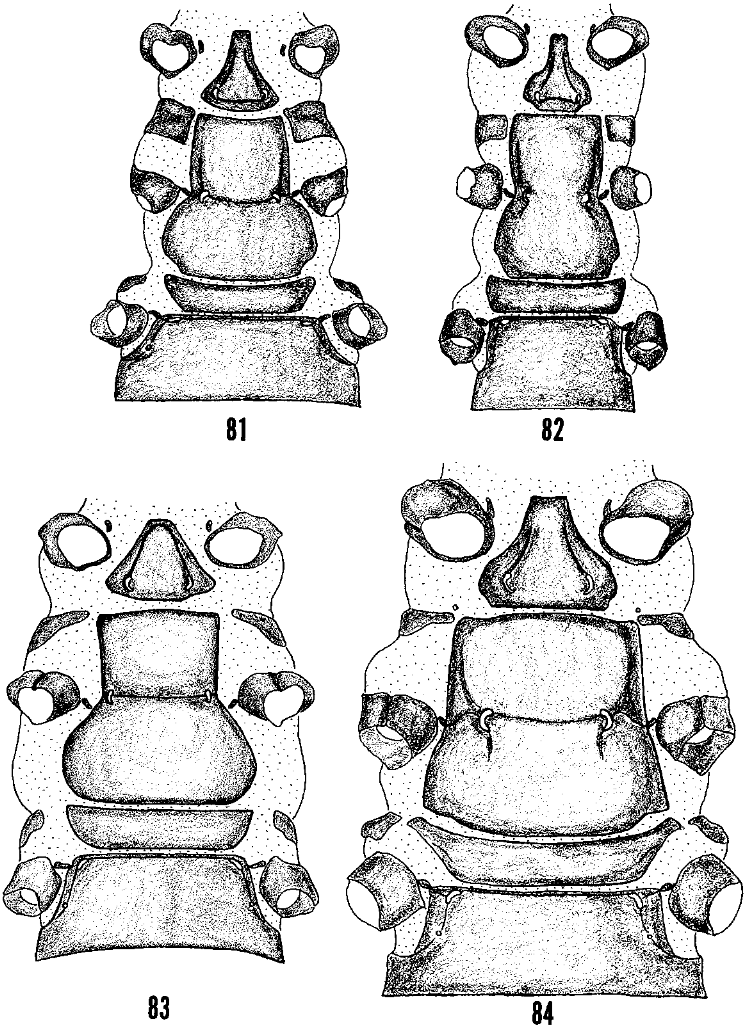
Habitats. — Nymphs occur in small to medium streams with a moderate flow, and lakes (M. L. Pescador, pers. comm.).

Nymph (Figs. 42, 76). Tentorium. — Tentorial body width greater than length (Type 2). Thorax. — Pronotum: anterolateral margins with spines, lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 76. Triangular, with apex extended, posterior width narrower than anterior width of mesosternum. Sternacostal suture absent, anterior sternal sutures convergent without fusing apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig 76. Basisternal length equal to furcasternum. Sterna-



FIGURES 77-80. — Ventral view of thoracic sterna of nymph: 77, *Penaphlebia* sp.; 78, *Zephlebia* (*Zephlebia*) *cruentata;* 79-80, *Zephlebia* (*Neozephlebia*) sp.

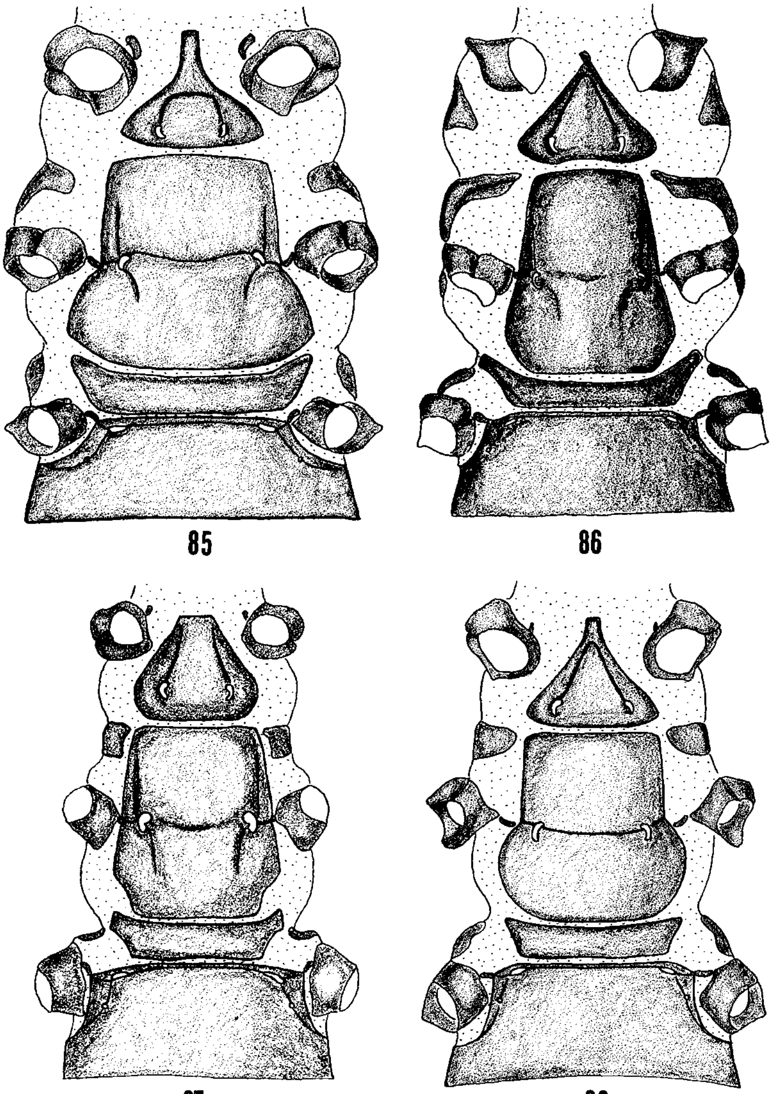
costal suture present; m $<$ 1/3M. Metasternum: Fig. 76. Basisternal width equal to mesofurcasternum. Anterior sternal sutures absent.



FIGURES 81-84. — Ventral view of thoracic sterna of nymph: 81, *Atalonella* sp. (Australasian); 82, *Atalonella* sp. (South American); 83, *Atalophlebia australis;* 84, *Atalophlebia*-ally, undescribed genus (Australia).

Abdominal Terga. — Fig. 42. With scale-like sculpturings, spines at posterior margin occur singularly.

Imago (Fig. 57). Thorax. — Prosternum: Fig. 57. Longitudinal carinae



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FIGURES 85-88. — Ventral view of thoracic sterna of nymph: 85, *Massartella* sp.; 86, *Ulmerophlebia* sp. (Australia); 87, *Jappa* sp.; 88, *Atalomicria* sp.

fused mesally. Mesosternum: Fig. 57. Basisternum — length slightly greater than width, lateral margins expanded mesally, posterior margin acute. Furcasternum — lateral margins of median longitudinal invagination divergent and widely separated, posterior margin smoothly concaved.

Genus KIMMINSULA Peters and Edmunds, 1970

Distribution. — Ceylon.

Habitats. — Nymphs are found under rocks in slow flowing parts of the river (Peters and Edmunds, 1970).

Nymph (Figs. 43, 89). Tentorium. — Tentorial body width decidedly greater than length (Type 3). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin fused with mesonotum, but phragmata not distinct. Propleuron: procoxal apodeme present. Prosternum: Fig. 89. Triangular with apex truncated, posterior width wider than anterior width of mesosternum. Sternacostal suture absent, anterior sternal sutures convergent, fused apically. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 89. Basisternal length shorter than mesofurcasternum. Sternacostal suture strongly developed; $m \geqq 1/2M$. Metasternum: Fig. 89. Basisternum wider than mesofurcasternum. Anterior sternal sutures long and well developed. Second pair of apophyses absent from posterior sternal sutures. Abdominal Terga. — Fig. 43. With scale-like sculpturings, spines at posterior margin occur singularly.

Imago (Fig. 67). Thorax. — Prosternum: Fig. 67. Longitudinal carinae widely separated. Mesosternum: Fig. 67. Basisternum — length about equal to width, lateral margins straight, posterior margin concaved. Furcasternum — lateral margins of median longitudinal invagination parallel to slightly divergent, widely separated; posterior margin smoothy concaved.

Genus KIRRARA Harker, 1954

Distribution. — Australia, eastern states.

Habitats. — Nymphs are found only in very swift and cold streams (Riek, 1970).

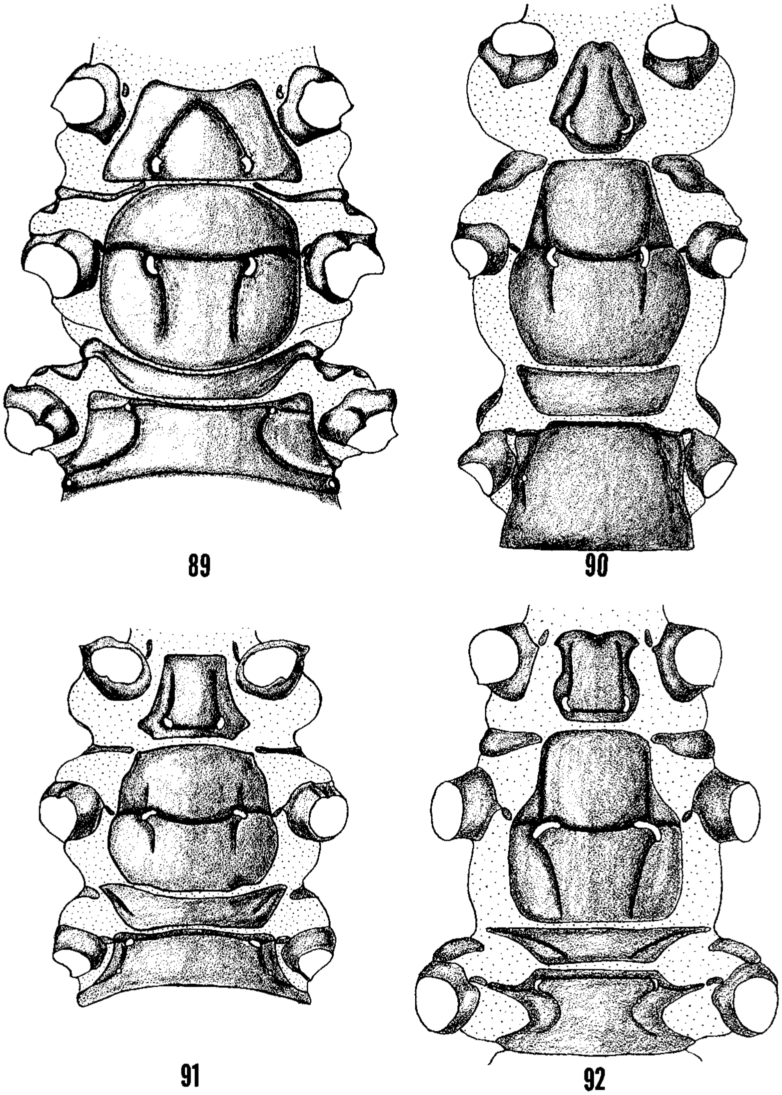
(Morphological characters were discussed earlier.)

Genus ATALOPHLEBIOIDES Phillips, 1930

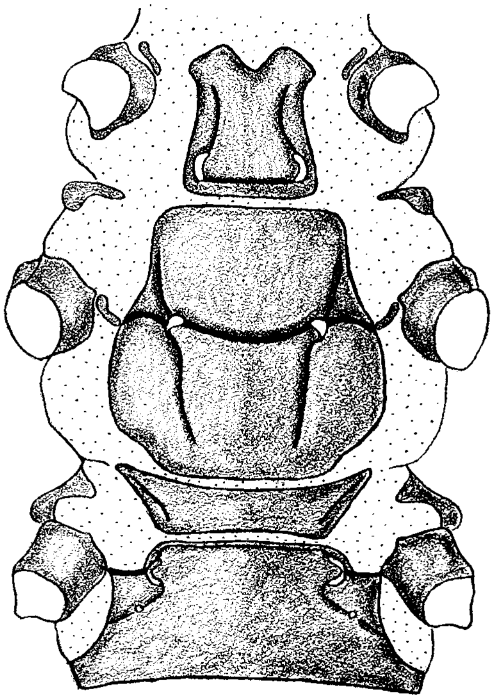
Distribution. — Australia, eastern states; Tasmania; New Zealand; Madagascar.

Habitats. — Nymphs are found in fast, cold riffles (Riek, 1970).

Nymphs (Figs. 45, 46, 90, 91). Tentorium. — Tentorial body width slightly greater than length (Type 1). Thorax. — Pronotum: anterolateral



FIGURES 89-92. — Ventral view of thoracic sterna of nymph: 89, *Kimminsula* sp.; 90, *Atalophlebioides* sp. (Australasian); 91, *Atalophlebioides* sp. (New Zealand); 92, *Deleatidium* sp.



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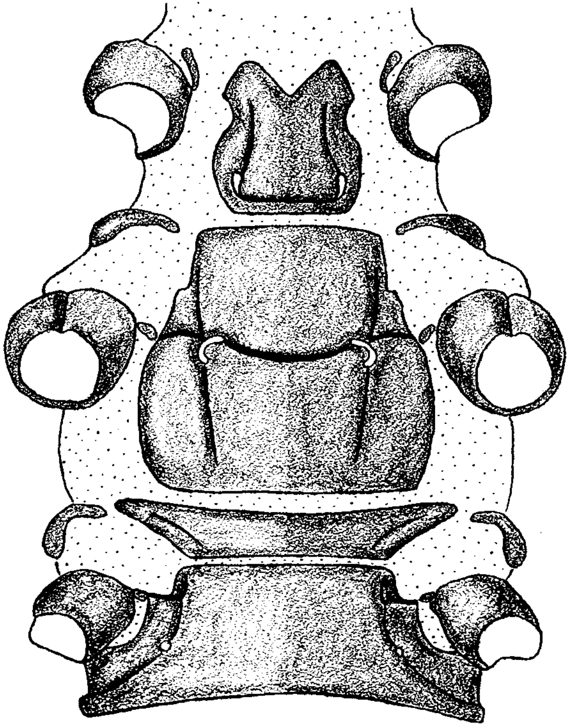

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margins with spines; lateral margins without setae. Posterior margin fused with mesonotum, anterior phragmata present internally. Propleuron: procoxal apodeme present. Prosternum: Figs. 90, 91. Triangular, with apex truncated, posterior width equal to anterior width of mesosternum. Sternacostal suture present, anterior sternal sutures convergent, without fusing apically in the Australasian species, but parallel in New Zealand species. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Figs. 90, 91. Basisternal length equal to furcasternum. Sternacostal suture strongly developed; $1/3M < m < 1/2M$. Metasternum: Figs. 90, 91. Basisternum wider than mesofurcasternum. Anterior sternal sutures absent in Australasian species, but shallowly formed in New Zealand species. Abdominal Terga. — Figs. 45, 46. With scale-like sculpturings; spines at posterior margin occur in groups but occur singularly in certain New Zealand species.

Imago (Figs. 68, 69). Thorax. — Prosternum: Fig. 68. Longitudinal carinae fused subanteriorly. Mesosternum: Figs. 68, 69. Basisternum — length slightly greater than width, lateral margins expanded, but straight in *cromwelli*-group, posterior margin rounded, but truncated in *cromwelli*-group. Furcasternum — lateral margins of median longitudinal invagination divergent and widely separated but parallel in *cromwelli*-group. Posterior margin smoothly concaved in certain Australasian species, and convex in *cromwelli*-and *sepia*-groups in New Zealand.

Remark. — The data obtained here fully support the generic ranking of *Atalophlebioides* as proposed by Peters and Edmunds (1964). However, the thoracic morphology points to certain heterogeneity within the genus. In New Zealand, the nymph of an undescribed species from the South Island has a sternal pattern (Fig. 91) that is different from those of *A. cromwelli* and *A. sepia* which resemble the Australasian species (Fig. 90). In the imago, the sternal pattern of *A. cromwelli* (Fig. 69) is different from that of *A. sepia* whose pattern resembles that of the Australasian species (Fig. 68).

Genus DELEATIDIUM Eaton, 1899

Distribution. — New Zealand.

Habitats. — Nymphs occur in a wide variety of habitats, but usually under stones in running water. Also they are found in marginal vegetation, submerged moss, or buried in sand, particularly during the winter (Phillips, 1931).

FIGURES 93-94. — Ventral view of thoracic sterna of nymph: 93, *Massartellopsis* sp.; 94, *Meridialaris* sp.

Nymph (Figs. 47, 92). Tentorium. — Tentorial body width equal to length (Type 1). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 97. Square, with anterior margin notched medially. Posterior width equal to anterior width of mesosternum. Sternacostal suture present, anterior sternal sutures parallel. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 92. Basisternal length equal to furcasternum. Sternacostal sutures strongly developed; $1/3M < m < 1/2M$. Metasternum: Fig. 92. Basisternum wider than mesofurcasternum. Anterior sternal sutures long and well developed. Abdominal Terga. — Fig. 47. With scale-like sculpturings; spines at posterior margin occur in groups.

Imago (Fig. 70). Thorax. — Prosternum: Fig. 70. Longitudinal carinae fused subanteriorly. Mesosternum: Fig. 70. Basisternum — length greater than width, lateral margins slightly expanded, posterior margin rounded. Furcasternum — lateral margins of median longitudinal invagination parallel, posterior margin convex.

Remark. — In spite of the drastic difference between the nymphal abdominal gills of the *myzobranchia*-group and the *lilli*-group, their thoracic structures are very similar and homogeneous.

Genus MASSARTELLOPSIS Demoulin, 1955

Distribution. — South America; Chile, Argentina.

Habitats. — Nymphs occur in swifter portion of intermediate streams (Peters and Edmunds, 1972).

Nymphs (Figs. 48, 93). Tentorium. — Tentorial body width slightly greater than length (Type 1). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 93. Square, with anterior margin notched medially; posterior margin narrower than anterior width of mesosternum. Sternacostal sutures present, anterior sternal sutures parallel. Mesopleuron: mesoepisternal apodeme present. Metasternum: Fig. 93. Basisternal length about equal to mesofurcasternum. Sternacostal suture strongly developed; $1/3M < m < 1/2M$. Metasternum: Fig. 93. Basisternum wider than mesofurcasternum. Anterior sternal sutures long. Abdominal Terga. — Fig. 48. With scale-like sculpturings, spines at posterior margin in groups.

Imago (Fig. 71). Thorax. — Prosternum: Fig. 71. Longitudinal carinae widely separated. Mesosternum: Fig. 71. Basisternum — length slightly greater than width, lateral margins expanded, posterior margin truncated to slightly concaved. Furcasternum — lateral margins of median longitudinal invagination parallel to slightly divergent, widely separated; posterior margin slightly convex.

Genus MERIDIALARIS Peters and Edmunds, 1972

Distribution. — South America; Chile, Argentina.

Habitats. — Nymphs are found mainly on rocks in a wide variety of streams and rivers (Peters and Edmunds, 1972).

Nymph (Figs. 49, 94). Tentorium. — Tentorial body length slightly greater than width (Type 1). Thorax. — Pronotum: anterolateral margins with spines; lateral margins without setae. Posterior margin not fused with mesonotum. Propleuron: procoxal apodeme present. Prosternum: Fig. 94. Square, with anterior margin notched medially; posterior margin narrower than anterior width of mesosternum. Sternacostal sutures present, anterior sternal sutures parallel. Mesopleuron: mesoepisternal apodeme present. Mesosternum: Fig. 94. Basisternal length about equal to furcasternum. Sternacostal suture strongly developed; $1/3M < m < 1/2M$. Metasternum: Fig. 94. Basisternum wider than mesofurcasternum. Anterior sternal sutures long. Abdominal Terga. — Fig. 50. With scale-like sculpturings, spines at posterior margin in groups.

Imago (Fig. 72). Thorax. — Prosternum: Fig. 72. Longitudinal carinae widely separated. Mesosternum: Fig. 72. Basisternum — length slightly greater than width, lateral margins expanded, posterior margin truncated. Furcasternum — lateral margins of median longitudinal invagination parallel, posterior margin slightly convex.

Remark. — *Massartellopsis* and *Meridialaris* have a high degree of morphological similarity ($S_J = 0.91$). Preliminary studies by M. L. Pescador (per. com.) indicate that these two existing genera may be placed as subgenera.

The foregoing taxonomic descriptions are summarised in the following table (Table 2). The code for the characters and their character states are given in the previous chapter.

EVOLUTION OF THE TAXONOMIC CHARACTERS

Phylogeny of the Southern Hemisphere Leptophlebiidae can be better understood after the evolutionary developments of the taxonomic characters are examined. Each character is analysed for **1.** — its probable ancestral state, **2.** — its evolutionary states, and their distributions among the Southern Hemisphere Leptophlebiidae, **3.** — its probable evolutionary history, and 4) the extent of parallel evolution.

The ancestral state of a character is deduced by comparing it with the homologous character found in other genera of Leptophlebiidae and related mayfly families. Often it can be recognized since it is more widely and irregularly distributed over a wide range of related groups. This is based on the assumption that since it has an older genetic history it has a greater possibility of becoming established in the genome of the progenies.

For each character, its various character states and their distributions among the genera will be discussed. From this we hope to trace the evolutionary history of each character. The evolutionary histories of individual characters collectively reflect the main evolutionary trends of the Southern Hemisphere Leptophlebiidae.

In a phylogenetic analysis it is important to recognize parallel evolution since it cannot be used in establishing sister-group relationships. However, in a complex of closely related genera like the Southern Hemisphere Leptophlebiidae, extensive parallelism often points to a greater genetic similarity between the genera. Since we equate phylogenetic relationship with genetic relationship and not genealogical relationship, it is therefore necessary to take parallelisms into account in assessing the overall genetic similarities between the genera, but without using such for establishing sister-group relationships. Based on the observation on any single character it will be impossible to differentiate conventional homology from parallel evolution, as there is no objective *a priori* way to do so. Parallelism can only be detected when we bring the character in question into relationship with other characters.

The characters will be discussed in the chronological order as given in the earlier section.

NYMPH

Character 1. — The nymphal tentorium has a rather constant morphology with only the tentorial body showing certain variations in its length and width. Three main types of tentorial bodies have been recognized (Figs. 1-3). Type 1 is most common, and is found in *Adenophlebia, Adenophlebiodes, Atalonella, Atalophlebia, Atalophlebioides, Deleatidium, Massartella, Massartellopsis, Meridialaris,* and *Penaphlebia.* Type 2 is found in *Aprionyx,* *Hapsiphlebia, Kirrara,* and *Z.* (*Neozephlebia*). Type 3 is found in *Atalomicria, Jappa, Kimminsula, Ulmerophlebia* (no data on Madagascan species), and *Zephlebia* s.s. Type 1 is probably the ancestral state since it is more common among the lower Pterygota and occurs widely among the Southern Hemisphere Leptophlebiidae. Types 2 and 3 represent increasingly derived conditions and form a transformation series (Hennig, 1966) with Type 1 as the ancestral condition and Type 3 as the most derived condition. It will be shown later that such an evolutionary trend occurred independently at least twice in the phylogeny of the Southern Hemisphere Leptophlebiidae.

Character 2. — Presence of spines on the anterolateral margins of the pronotum is a common feature. *Kirrara* is the only Southern Hemisphere genus in which they are absent. The presence of spines probably represents the ancestral state and the absence of spines is probably the derived state.

Character 3. — Setae are generally absent on the lateral margins of the pronotum (ancestral state) with the exceptions in *Atalomicria, Jappa,* and *Ulmerophlebia* in which they are present (derived condition). These three genera are closely related, hence this derived condition probably evolved once in the phylogeny of the Southern Hemisphere Leptophlebiidae.

Character 4. — In most of the genera studied the pronotum is joined to the mesonotum by an intersegmental membrane except for several genera where they are variously fused to the mesonotum. In *Adenophlebia* and *Adenophlebiodes* the pronotum is fused posterolaterally to the mesonotum; whereas, in *Atalophlebioides* (all groups), *Kimminsula,* and *Kirrara* the entire posterior margin of the pronotum is fused with the mesonotum. In *Atalophlebioides* and *Kirrara* the acrotergite develops into the anterior phragmata internally. The unfused pro- and mesonotum probably represents the ancestral state since it is commonly found among different phyletic lineages of the Leptophlebiidae. The partially fused and entirely fused conditions probably represent increasingly derived conditions. Fusion of the pro- and mesonota occurred at least twice in the phylogeny of the Southern Hemisphere Leptophlebiidae.

Character 5. — The procoxal apodemes are generally present as insertions for certain protractor muscles of the fore legs in the propleuron. However, they are absent in *Adenophlebia, Adenophlebiodes, Aprionyx, Atalomicria,* and *Kirrara.* Presence of the apodemes is probably the ancestral condition; whereas, their absence is the derived condition. The apodemes were lost in the phyletic line that dispersed to Africa and later gave rise to *Adenophlebia, Adenophlebiodes,* and *Aprionyx.* Loss of the apodemes in *Atalomicria* and *Kirrara* is probably due to parallelism.

Character 6. — The mesoepisternal apodemes are present in all genera except for *Adenophlebia, Adenophlebiodes* and *Aprionyx.* Their absence is probably the ancestral state since they are consistently absent in other primitive genera of the Leptophlebiidae e.g. *Leptophlebia* and *Paraleptophlebia. Adenophlebia, Adenophlebiodes,* and *Aprionyx* are strongly correlated in the absence of both the mesoepisternal and the procoxal apodemes.

Character 7. — Shape of the prosternum is characteristic of the genus or group of genera. It is triangular in *Adenophlebia, Adenophlebiodes, Aprionyx, Atalophlebia* (all groups), *Jappa, Ulmerophlebia, Zephlebia* s.s., and *Z.* (*Neozephlebia*); or triangular, with apex truncated as in *Atalonella* (all groups), *Atalophlebioides* (all groups), *Kimminsula, Kirrara,* and *Penaphlebia;* or triangular, with apex extended as in *Atalomicria, Hapsiphlebia,* and *Massartella;* or square with anterior margin notched medially as in *Deleatidium* (both groups), *Massartellopsis,* and *Meridialaris.* The triangular prosternum is probably the ancestral condition since it is found not only among the primitive leptophlebiids e.g., *Leptophlebia,* but is also common in the primitive family Siphlonuridae.

Character 8. — The posterior width of the prosternum varies in being wider than the anterior width of the mesosternum as in *Adenophlebia, Aprionyx, Jappa, Kimminsula, Kirrara, Ulmerophlebia,* and *Zephlebia* s.s.; or about equal to the anterior width of the mesosternum as in *Adenophlebiodes, Atalophlebia* (all groups), *Atalophlebioides* (all groups), *Deleatidium* (both groups), *Massartella,* and *Z.* (*Neozephlebia*); or narrower than the anterior width of the mesosternum as in *Atalonella* (all groups), *Hapsiphlebia, Massartellopsis, Meridialaris,* and *Penaphlebia.* The first type is probably the ancestral condition since the latter types can be easily derived from it. The last type probably represents the most derived condition. Such an evolutionary trend is well illustrated in the phyletic line that includes *Kimminsula, Kirrara, Atalophlebioides, Deleatidium, Massartellopsis,* and *Meridialaris.*

Character 9. — Absence of the sternacostal suture in the prosternum is an important character in separating the phyletic line that includes *Atalomicria, Atalophlebia* (all groups), *Hapsiphlebia, Jappa, Massartella, Penaphlebia, Ulmerophlebia,* and *Zephlebia* s.s. Other members of this line that retained or secondarily developed the sternacostal suture are *Atalonella* (all groups) and *Z.* (*Neozephlebia*). Secondary loss of the suture had also occurred independently in *Kimminsula.*

Character 10. — The anterior sternal sutures in the prosternum are convergent and fused apically in *Adenophlebiodes, Atalomicria, Atalophlebia* (all groups), *Kimminsula, Kirrara, Massartella,* and *Ulmerophlebia;* they are convergent without fusing apically in *Adenophlebia, Aprionyx, Atalonella* (all groups), *Atalophlebioides* (Australasian species), *Hapsiphlebia, Jappa, Penaphlebia, Zephlebia* s.s., and *Z.* (*Neozephlebia*). *Kirrara* is unique in that the sutures are parallel and anteriorly connected by a horizontal suture. In *Atalophlebioides* (New Zealand species), *Deleatidium* (both groups), *Massartellopsis,* and *Meridialaris* the sutures are parallel. The ancestral condition is probably represented by the convergent sutures that fused apically since this arrangement is present in the primitive leptophlebiids e.g., *Leptophlebia,* and in *Siphlonurus* of the Siphlonuridae. From this state probably evolved the convergent sutures that are not fused apically; whereas, the parallel sutures represent another trend of evolution.

Character 11. — The basisternal length of the mesosternum varies in being longer than its furcasternal length as in *Adenophlebia, Adenophlebiodes, Atalonella* (South American species), *Massartella, Ulmerophlebia,* and *Z.* (*Neozephlebia*); or equal to the furcasternal length as in *Atalomicria, Atalonella* (Australasian species), *Atalophlebia, Atalophlebioides* (all groups), *Deleatidium* (both groups), *Hapsiphlebia, Jappa, Kirrara, Massartellopsis, Meridialaris, Penaphlebia,* and *Zephlebia* s.s.; or shorter than the furcasternal length as in *Aprionyx,* and *Kimminsula.* The longer basisternum seems to be the ancestral state since it is common in the primitive families of mayflies e.g., in Siphlonuridae, Ephemeridae, and Baetiscidae. Except for one phyletic line (*Kirrara, Atalophlebioides, Deleatidium, Massartellopsis,* and *Meridialaris*) the various character states seem to be distributed in a mosaic pattern, indicating extensive parallelism.

Character 12. — In the mesosternum, the sternacostal suture is a very useful character in grouping the genera into primary groups. It is absent in *Adenophlebia, Adenophlebiodes* [secondarily developed in *A.* (*Hyalophlebia*)], *Aprionyx* and certain South American species of *Atalonella;* or normally developed in *Atalomicria, Atalonella* (Australian species), *Atalophlebia* (all groups), *Hapsiphlebia, Massartella, Penaphlebia,* and *Z.* (*Neozephlebia*); or strongly developed in *Atalophlebioides* (all groups), *Deleatidium* (both groups), *Kimminsula, Kirrara, Massartellopsis,* and *Meridialaris;* or partially formed in *Jappa, Ulmerophlebia* and *Zephlebia* s.s. Absence of the suture probably represents the ancestral condition since it is absent in other primitive leptophlebiid genera e.g., *Leptophlebia, Paraleptophlebia,* and also other primitive mayfly families e.g., Baetiscidae, Ephemeridae, and Siphlonuridae. The three character states represent a transformation series and correspond to the major phyletic groups of Southern Hemisphere Leptophlebiidae. Loss of the suture in certain South American species of *Atalonella* probably represents a reversal to the ancestral condition.

Character 13. — Positions of the sternal apophyseal pits on the mesosternum are a useful taxonomic character. Usually they are situated close to the lateral margins ($m < 1/3M$) except for *Atalophlebioides* (all groups), *Deleatidium* (both groups), *Massartellopsis, Meridialaris, Zephlebia* s.s. and *Z.* (*Neozephlebia*) where $1/3M < m < 1/2M$; and *Kimminsula* and *Kirrara* where $m \geqq 1/2M$. The lateral position of the pits is probably the ancestral state since it is not only common among the primitive leptophlebiids but also in such genera as *Baetisca, Isonychia,* *Oniscigaster,* and *Siphlonurus.* The evolutionary trend of this structure is the inward migration of these pits with *Kimminsula* and *Kirrara* representing the most derived condition.

Character 14. — In the metasternum, a membranous suture separates the basisternum from the furcasternum. This is characteristic of all the Southern Hemisphere genera observed. The basisternum can be of about equal width to that of the mesofurcasternum as in *Adenophlebia, Atalomicria, Atalonella* (certain Australasian species), *Atalophlebia* (all groups), *Hapsiphlebia,* and *Massartella;* or wider than the mesofurcasternum as in the rest of the other genera. The first type of basisternum is probably the ancestral conditon since it is the common form among the Leptophlebiidae. The ancestral state is more common in the phyletic line that includes most of the *Atalophlebia*-like genera; whereas, the derived condition is found in the line that includes *Kimminsula, Kirrara, Atalophlebioides* (all groups), *Deleatidium* (both groups), *Massartellopsis,* and *Meridialaris.* However, parallel development of the derived state also occurred in other phyletic branches e.g., in *Adenophlebiodes* and *Aprionyx.*

Character 15. — The anterior sternal sutures in the metasternum are absent in most of the genera observed except for *Adenophlebiodes, Atalophlebioides* (all groups), *Deleatidium* (both groups), *Ulmerophlebia, Kimminsula, Kirrara,* and *Massartellopsis* where they are long, and shorter in *Meridialaris.* Absence of the sutures is probably the ancestral condition, since it is generally absent in the primitive leptophlebiids and other mayfly families. These sutures developed in the phyletic line that gave rise to *Kimminsula, Kirrara, Atalophlebioides, Deleatidium, Massartellopsis,* and *Meridialaris.* Appearance in *Adenophlebiodes* and *Ulmerophlebia* is probably due to parallel evolution.

Character 16. — The singular arrangement of spines on the posterior margin of the abdominal terga is most common among the genera and is probably the ancestral condition. Grouping of the spines is probably a derived feature, and is found in *Atalophlebioides* (except for one New Zealand species group), *Deleatidium* (both groups), *Massartellopsis, Meridialaris,* and probably independently evolved in *Atalomicria, Jappa,* and *Ulmerophlebia.*

IMAGO

Character 17. — The longitudinal carinae in the prosternum vary among the genera observed, but are relatively constant for each genus. The carinae are fused at the caudal halves as in *Adenophlebia, Adenophlebiodes, Aprionyx,* and *Massartella;* or fused mesally as in *Atalomicria, Hapsiphlebia, Penaphlebia, Ulmerophlebia, Zephlebia* s.s. and *Z.* (*Neozephlebia*); or fused subanteriorly as in *Atalophlebioides* (all groups) and *Deleatidium* (both groups). They are slightly separated, as in *Atalophlebia* (all groups) and *Jappa;* or widely separated as in *Atalonella* (all groups), *Kimminsula, Kirrara, Massartellopsis,* and *Meridialaris.* Presence of the longitudinal carinae is probably a derived condition within the Ephemeroptera since in most primitive mayflies the basisternum is flat e.g., *Siphlonurus, Isonychia, Ameletopsis, Tasmanophlebia, Siphlonella, Nesameletus,* and *Mirawara.* Among the less primitive genera the longitudinal carinae are entirely fused as in *Coloburiscoides, Coloburiscus,* and *Hexagenia.* In the Southern Hemisphere Leptophlebiidae the ancestral condition is probably represented by the carinae with fused caudal halves and the evolutionary tendency was toward the separation of the carinae.

Character 18. — Length of the mesobasisternum varies from decidedly greater than its width, as in *Atalomicria, Jappa, Massartella, Penaphlebia, Ulmerophlebia, Zephlebia* s.s. and *Z.* (*Neozephlebia*); to slightly greater than its width as in *Adenophlebia, Adenophlebiodes, Aprionyx, Atalonella* (all groups), *Atalophlebia* (all groups), *Atalophlebioides* (all groups), *Deleatidium* (both groups), *Hapsiphlebia, Kimminsula, Kirrara, Massartellopsis,* and *Meridialaris.* The first type is probably the ancestral condition since a narrower basisternum is also common among other primitive genera of mayflies e.g., *Siphlonurus, Ephemera, Hexagenia.*

Character 19. — Lateral margins of the mesobasisternum vary from being straight, or slightly expanded ventrally, to being expanded mesally. The first type is observed in most genera studied; whereas, the second type is peculiar to *Atalomicria, Atalophlebioides* (certain Australasian species), *Hapsiphlebia, Jappa, Massartellopsis, Meridialaris, Penaphlebia, Ulmerophlebia,* and *Zephle-*

bia s.s. and *Z.* (*Neozephlebia*). The first type is probably the ancestral condition since most primitive mayflies have this type e.g., Baetiscidae, Siphlonuridae. The expanded lateral margins have independently evolved several times in the phylogeny of the Leptophlebiidae, for example it also occurs in the specialized genus *Isca.*

Character 20. — Shape of the mesobasisternal posterior margin is a good taxonomic character at the generic or subgeneric level. It can be acute as in *Atalomicria, Hapsiphlebia, Jappa, Penaphlebia,* and *Ulmerophlebia;* or rounded as in *Adenophlebiodes, Aprionyx, Atalonella* (all groups), *Atalophlebioides* (certain Australasian species), *Deleatidium* (both groups), *Massartella, Zephlebia* s.s. and *Z.* (*Neozephlebia*); or truncated as in *Adenophlebia, Atalophlebia* (all groups), *Atalophlebioides* (certain New Zealand species), *Kirrara, Massartellopsis,* and *Meridialaris;* or concaved as in *Kimminsula.* In most primitive families of mayflies e.g., Ephemeridae and Siphlonuridae, the mesobasisternum is not distinctly separated from the mesofurcasternum by a suture. Therefore, the condition observed in Leptophlebiidae is a derived condition. However, this character has undergone such diversification in the Leptophlebiidae that it is difficult to speculate on the probable ancestral state.

Character 21. — In the mesosternum, lateral margins of the median longitudinal invagination in the furcasternum is parallel in *Adenophlebia, Adenophlebiodes, Aprionyx, Atalomicria, Atalonella* (certain Australasian species), *Atalophlebioides* (certain New Zealand species), *Deleatidium* (both groups), *Kimminsula, Massartellopsis,* and *Meridialaris;* or divergent but with margins slightly separated in *Jappa, Massartella, Penaphlebia,* and *Ulmerophlebia;* or divergent but with margins widely separated, as in *Atalonella* (certain South American species), *Atalophlebioides* (certain Australasian species), *Hapsiphlebia, Kirrara, and Zephlebia.* The parallel margins probably represent the ancestral condition since it occurs in Baetiscidae, Ephemeridae and Siphlonuridae. Evolution of this structure is toward widening of the invagination. The lateral margins of the invagination is a good generic or subgeneric character; however, because it has undergone

Table 1. —— Species of Southern Hemisphere Leptophlebiidae examined. Type species are indicated by an asterisk.

Geographical Region	Species	Form & Sex
Africa	*Adenophlebia auriculata* (Eaton)	Nymphs (♂♀), Imagos (♂♀)
	Adenophlebia perinqueyella Lestage	Nymphs (♂♀), Imagos (♂♀)
	Adenophlebiodes (*Adenophlebiodes*) *bicolor* (Crass)	Nymphs (♂♀), Imagos (♂)
	Adenophlebiodes (*Adenophlebiodes*) *ornata* (Ulmer)*	Nymphs (♂♀), Imagos (♂)
	Adenophlebiodes (*Hyalophlebia*) *patriciae* Agnew	Nymphs (♂♀), Imagos (♂)
	Aprionyx intermedius Barnard	Nymphs (♂♀), Imagos (♂)
	Aprionyx peterseni (Lestage)	Nymphs (♂♀), Imagos (♂)
	Aprionyx tricuspidatus Crass	Nymphs (♂♀), Imagos (♂)
Madagascar	*Atalophlebioides inaequalis* Demoulin and numerous nymphs of undescribed species and genera of leptophlebiids	Nymphs (♂♀)
Ceylon	*Kimminsula* sp. (several undescribed species)	Nymphs (♂♀), Subimagos (♂♀)
Australia–Tasmania	*Atalophlebia australis* (Walker)*	Nymphs (♂♀), Imagos (♂♀)
	Atalophlebia sp.	Nymphs (♂♀), Imagos (♂♀)
	Atalophlebioides sp.	Nympha (♂♀), Imagos (♂)
	Atalomicria sp.	Nymphs (♂♀), Imagos (♂)
	Atalonella sp.	Nymphs (♂♀), Imagos (♂)
	Jappa kutera Harker*	Nymphs (♂♀), Imagos (♂)
	Jappa sp.	Nymphs (♂♀), Imagos (♂)

Table 1. —— Continued

Australia–Tasmania	*Kirrara amenia* Harker	Nymphs (♂♀), Imagos (♂♀)
	Kirrara sp.	Nymphs (♂♀), Imagos (♂)
	Ulmerophlebia sp.	Nymphs (♂♀), Imagos (♂♀)
New Zealand	*Atalophlebioides aucklandensis* Peters	Nymphs (♂♀), Imagos (♂♀)
	Atalophlebioides cromwelli Phillips*	Imagos (♂♀)
	Atalophlebioides sepia Phillips	Nymphs (♂♀), Imagos (♂)
	Atalophlebioides sp.	Nymphs (♂♀), Imagos (♂♀)
	Deleatidium cerinum Phillips	Imagos (♂♀)
	Deleatidium fumosum Phillips	Imagos (♂♀)
	Deleatidium lilli Eaton*	Imagos (♂♀)
	Deleatidium myzobranchia Phillips	Nymphs (♂♀), Imagos (♂)
	Deleatidium sp.	Nymphs (♂♀), Imagos (♂♀)
	Zephlebia (Neozephlebia) nodularis (Eaton)	Nymphs (♂♀), Imagos (♀)
	Zephlebia (Neozephlebia) sp.	Nymphs (♂♀)
	Zephlebia (Zephlebia) cruentata (Hudson)	Nymphs (♂♀), Imagos (♂♀)
	Zephlebia (Zephlebia) versicolor (Eaton)*	Subimagos (♂♀)
South America	*Atalonella* sp.	Nymphs (♂♀), Imagos (♂♀)
	Hapsiphlebia anastomosis (Demoulin)*	Nymphs (♂♀), Imagos (♂♀)
	Hapsiphlebia sp.	Nymphs (♂♀), Imagos (♂♀)
	Massartella sp.	Nymphs (♂♀), Imagos (♂♀)
	Massartellopsis irrarazavali Demoulin*	Imagos (♂)
	Massartellopsis sp.	Nymphs (♂♀), Imagos (♂♀)
	Meridialaris sp.	Nymphs (♂♀), Imagos (♂♀)
	Penaphlebia chilensis (Eaton)*	Nymphs (♂♀), Imagos (♂♀)
	Penaphlebia sepia (Thew)	Imagos (♂)
	Penaphlebia sp.	Nymphs (♂♀), Imagos (♂♀)

Table 2.—Character states for the Southern Hemisphere Leptophlebiidae genera.

Ancestral Character State	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	ai	a	a	?	a	a	Frequency of Ancestral State
Genus / Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Adenophlebia	a	a	a	b	b	a	a	a	a	b	a	a	a	a	a	a	ai	b	a	c	a	a	17
Adenophlebiodes s.s.	a	a	a	b	b	a	a	b	a	a	a	a	a	b	bi	a	ai	b	a	b	a	b	14
A. (Hyalophlebia)	a	a	a	b	b	a	a	b	a	a	a	b	a	b	bi	a	ai	b	a	b	a	b	13
Aprionyx	b	a	a	a	b	a	a	a	a	b	c	a	a	b	a	a	ai	b	a	b	a	a	15
Atalomicria	c	a	b	a	b	b	c	b	b	a	b	b	a	a	a	b	aii	a	b	a	a	b	8
Atalonella (A)	a	a	a	a	a	b	b	c	a	b	b	b	a	a	a	a	bii	b	a	b	a	a	13
Atalonella (SA)	a	a	a	a	a	b	b	c	a	b	a	a	a	b	a	a	bii	b	a	b	bii	a	13
Atalophlebia	a	a	a	a	a	b	a	b	b	a	b	b	a	a	a	a	bi	b	a	c	a	a	14
Atalophlebioides	a	a	a	b	a	b	b	b	a	bd	b	c	b	b	a	b	aiii	b	ab	bc	abii	ac	8
Deleatidium	a	a	a	a	a	b	d	b	a	d	b	c	b	b	bi	b	aiii	b	a	b	a	c	8
Hapsiphlebia	b	a	a	a	a	b	c	c	b	b	b	b	a	a	a	a	aii	b	b	a	bii	a	9
Jappa	c	a	b	a	a	b	b	a	b	b	b	a	a	b	a	b	bi	a	b	a	bi	a	9
Kimminsula	c	a	a	b	a	b	b	a	b	a	c	c	c	b	bi	a	bii	b	a	d	a	a	9
Kirrara	b	b	a	b	b	b	b	a	a	c	b	c	c	b	bi	b	bii	b	a	c	bii	c	4
Massartella	a	a	a	a	a	b	c	b	b	a	a	b	a	a	a	a	ai	a	a	b	bi	a	15
Massartellopsis	a	a	a	a	a	b	d	c	a	d	b	c	b	b	bi	b	bii	b	b	c	a	c	7
Meridialaris	a	a	a	a	a	b	d	c	a	d	b	c	b	b	bii	b	bii	b	b	c	a	c	7
Penaphlebia	a	a	a	a	a	b	b	c	b	b	b	b	a	b	a	a	aii	a	b	a	bi	a	10
Ulmerophlebia	c	a	b	a	a	b	a	a	b	a	a	a	a	b	bi	b	aii	a	b	a	bi	a	11
Zephlebia s.s.	c	a	a	a	a	b	a	a	b	b	b	a	b	b	a	a	aii	a	b	b	bii	d	10
Z. (Neozephlebia)	b	a	a	a	a	b	a	b	a	b	a	b	b	b	a	a	aii	a	b	b	bii	d	10

extensive parallel evolution it can only be used taxonomically when it is correlated with other characters.

Character 22. — Shape of the mesofurcasternal posterior margin is smoothly concaved in most of the genera observed except for *Adenophlebiodes* and *Atalomicria* where the margin is acutely concaved; or convex as in *Atalophlebioides* (certain New Zealand species), *Deleatidium* (both groups), *Kirrara, Massartellopsis,* and *Meridialaris;* or truncated as in *Zephlebia* s.s. and *Z.* (*Neozephlebia*). The smoothly concaved margin probably represents the ancestral state since it is more common among the Leptophlebiidae; the acutely concaved margin probably arose from it. The convex and truncated margin probably evolved separately from the ancestral type.

It becomes apparent from the foregoing discussion that most characters and their character states used in this study are distributed among the genera in a mosaic pattern. Very few characters are peculiar to a genus; instead, each genus is best characterised by a particular combination of characters. Taxonomically, a particular character state will appear several times independently in different phyletic lines. A genetic explanation was given by Throckmorton (1965) for a similar situation in the evolution of the *Drosophila.* He attributed this phenomenon to the persistent polyallelism and heterozygositic nature of the characters. In phylogeny, persistency of such genetic nature will cause a particular character state to appear many times independently. Mayr (1965b, 1969), however, ascribes true parallelism as a response of a common heritage to similar selection pressures. As a group, the Southern Hemisphere Leptophlebiidae show a high degree of genetic similarities in regard to those characters used in this study. Possibly this is due to a long history of sympatry for the ancestors of the recent genera which allowed extensive gene flow between them. This is not impossible for the Leptophlebiidae since they have an ancient lineage that can be traced back prior to the postulated separation of Gondwanaland. Recent geological data support a gradual separation of the Southern Continents (from mid-Mesozoic to mid-Cenozoic); this also extends the possible gene exchange between gene pools of the

Leptophlebiidae on certain continents. The high similarities among the genera may also be explained if similar selection pressures were encountered by the genera after separation of Gondwanaland. The broad similarity in their present habitats (generally cool mountain streams) suggest that they may have occupied a similar habitat in the past, and thus a similar background for natural selection. Their stenothermal nature may have further preserved their similarities since evolutionary rates are usually slower for cool-adapted species (Rensch, 1960).

PHYLOGENY AND ZOOGEOGRAPHY

Phylogeny of certain Southern Hemisphere Leptophlebiidae has been discussed by Edmunds (1972), Penniket (1961), Peters and Edmunds (1964, 1970, 1972). This present study represents an initial attempt to analyse the phylogenetic relationships of the known Leptophlebiidae with Gondwanian affinities only, and is based primarily on tentorial, thoracic and abdominal tergal characters.

The first operational procedure in a phylogenetic analysis is to discover the primary clusters of genera or the main phyletic lineages. Such clusters are the products of speciation and are usually separated by sizeable gaps of phenotypic differences. Conventionally, this is accomplished by tracing the phylogenies of unit characters, and genera are grouped together when many of their unit characters show strong correlations with each other and exhibit similar evolutionary trends. However, in this study, this approach cannot be applied easily because of the mosaic distributions of the character states for a great majority of the characters. This renders character weighing difficult, since there is no objective *a priori* way to determine whether a particular character state represents conventional homology or parallel evolution. Thus, many groupings of genera are possible when special weight is given to certain unit characters.

In this study we have adopted a numerical approach in aiding the selection of characters that are useful in delineating the genera into primary clusters. Based on the total number of character states common between any pair of genera, a similarity index can be calculated for them using Jaccard's Coefficient of Similarity

(Sneath, 1957; Sokal and Sneath, 1963; Sneath and Sokal, 1973), which is expressed mathematically as follows:

$$S_J = \frac{nAB}{nAB + u}$$

$$\text{where } S_J \longrightarrow 0 \text{ as } \frac{nAB}{u} \longrightarrow 0$$

$$S_J \longrightarrow 1 \text{ as } \frac{u}{nAB} \longrightarrow 0$$

S_J = Jaccard's Coefficient of Similarity
nAB = Number of character states common between genera A and B
u = Number of character states peculiar to genus A + number of character states peculiar to genus B

The operational assumption behind this approach is that in assessing the total phenotypic similarities of the genera we are also indirectly determining their degree of genotypic resemblances. A high S_J value between two genera would indicate a more similar genetic make-up and also a closer phylogenetic relationship. In this context, phylogenetic relationship is equivalent to genetic relationship and not genealogical relationship as maintained by the cladists (Mayr, 1965a).

After the S_J values were computed for any pair of genera, they are arranged into a similarity matrix. Table 3 is the similarity matrix completed for this study.

By comparing the S_J values, the genera can be clustered into three main complexes which probably represent the main phyletic lines within the Southern Hemisphere Leptophlebiidae. Within each complex, the S_J value between any pair of genera is usually greater than 0.50. The following are the three complexes with the genera in each group listed alphabetically.

1. *Adenophlebia, Adenophlebiodes* (*Adenophlebiodes*), *A.* (*Hyalophlebia*), *Aprionyx.*
2. *Atalophlebioides, Deleatidium, Kimminsula, Kirrara, Massartellopsis, Meridialaris.*

	Adenophlebia	*Adenophlebiodes* s.s.	*A. (Hyalophlebia)*	*Aprionyx*	*Atalomicria*	*Atalonella* (A)	*Atalonella* (SA)	*Atalophlebia*	*Atalophlebioides*	*Deleatidium*	*Hapsiphlebia*	*Jappa*	*Ulmerophlebia*	*Kimminsula*	*Kirrara*	*Massartella*	*Massartellopsis*	*Meridialaris*	*Penaphlebia*	*Zephlebia* s s.	*Z. (Neozephlebia)*
Adenophlebia																					
Adenophlebiodes s.s.	57																				
A. (Hyalophlebia)	52	91																			
Aprionyx	63	52	52																		
Atalomicria	16	16	26	16																	
Atalonella (A)	42	29	29	42	26																
Atalonella (SA)	42	38	38	47	13	69															
Atalophlebia	42	33	33	33	38	57	38														
Atalophlebioides	33	33	38	33	26	52	52	42													
Deleatidium	19	33	33	26	19	38	33	33	83												
Hapsiphlebia	26	13	13	26	42	52	42	47	29	19											
Jappa	19	10	10	26	38	29	33	29	33	19	33										
Ulmerophlebia	19	22	22	22	42	16	26	26	19	19	29	63									
Kimminsula	22	26	26	29	16	33	33	33	38	29	22	26	29								
Kirrara	19	19	19	22	10	22	26	16	52	33	16	16	13	38							
Massartella	33	33	29	29	38	47	42	57	26	26	42	29	33	26	07						
Massartellopsis	19	22	22	19	16	38	33	29	57	69	26	22	22	29	38	16					
Meridialaris	19	19	19	19	19	38	33	29	63	63	26	22	19	26	33	16	91				
Penaphlebia	22	16	16	26	38	52	47	42	38	22	63	57	42	26	13	47	29	29			
Zephlebia s.s.	22	19	19	33	29	29	33	29	38	22	42	47	42	26	10	29	26	26	47		
Z. (Neozephlebia)	22	26	26	33	26	33	42	29	42	29	38	26	29	16	16	38	26	26	42	63	

Table 3.—C_J values for the Southern Hemisphere Leptophlebiidae; calculations based on Jaccard's Coefficient of Similarity. All numbers are in decimals.

3. *Atalomicria, Atalonella, Atalophlebia, Hapsiphlebia, Jappa, Massartella, Penaphlebia, Ulmerophlebia, Zephlebia* (*Zephlebia*), *Z.* (*Neozephlebia*).

The next step in the analysis is to return to the character chart (Table 2) and search for characters whose evolutionary histories will best show similar clustering of the genera as shown by the matrix. From this, the main phyletic branches of the genera are determined. However, by using the matrix in conjunction with the character chart we can better weigh characters and deduce subsequent branchings within any particular phyletic line. When

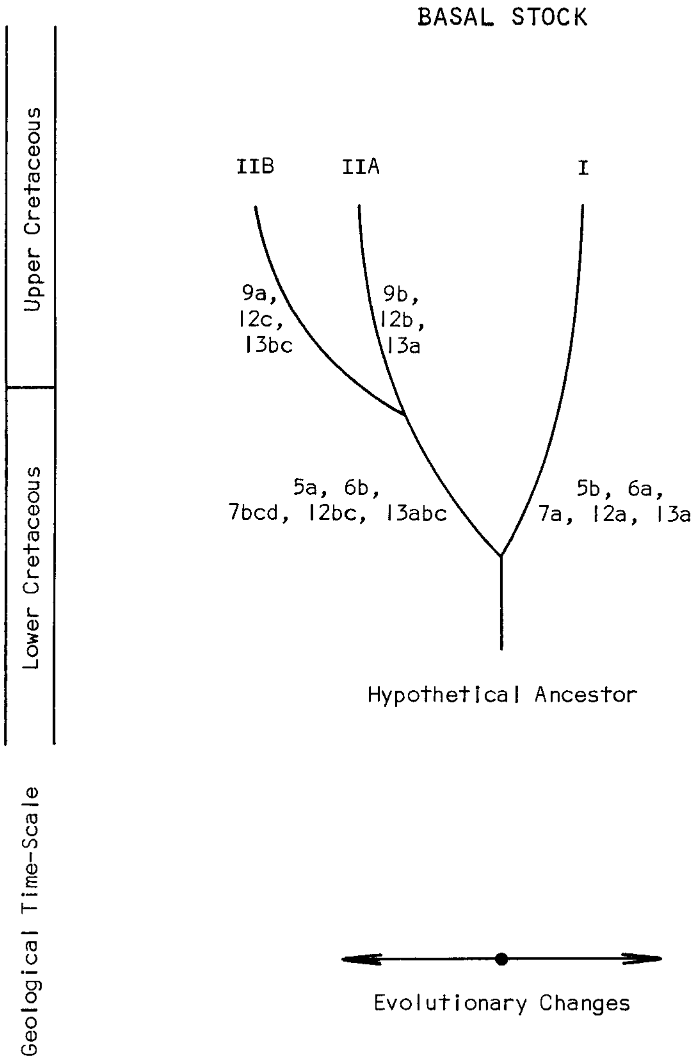

FIGURE 95. — Diagram of main evolutionary lines within Southern Hemisphere Leptophlebiidae. Characteristics of each phyletic line are coded as in Table 2.

all characters are considered simultaneously in this fashion, often similarities due to parallel evolution are recognised. For example, *Atalomicria, Jappa, Kimminsula,* and *Ulmerophlebia* all have an oblong tentorial body; based on this information alone, it is impossible to tell whether this is due to homology or parallel evolution. However, referring to the matrix, *Atalomicria, Jappa,* and *Ulmerophlebia* show a decidedly higher S_J value for each other over that for *Kimminsula.* This indicates a distant relationship of *Kimminsula* to the other three genera and therefore the similarity is most likely due to parallelism. Based on this method, we have arrived at the following hypothesis of the phylogeny of the selected genera.

If the genera were ranked phenetically, *Massartellopsis* and *Meridialaris* would probably receive subgeneric rank ($S_J = 0.91$) with the two present genera combined. Numerically they would be comparable to the S_J value (0.91) for subgenera *Adenophlebiodes* s.s. and *A.* (*Hyalophlebia*). Also, the present subgenera *Zephlebia* s.s. and *Z.* (*Neozephlebia*) would be elevated to full generic rank ($S_J = 0.63$). However, we have not attempted to rearrange the taxonomic ranks of the genera based on their S_J values alone, because the S_J values do not distinguish similarities due to homology and parallel evolution. Moreover, the S_J values were based on a rather limited number of taxonomic characters. A wider range of taxonomic characters would have to be studied before the present taxonomic arrangement of the genera could be justifiably rearranged.

Figure 95 represents the probable evolution of the main phyletic lines among the Southern Hemisphere Leptophlebiidae. The hypothetical ancestral lineage probably existed in the beginning of the Jurassic in the Southern Hemisphere when all the Southern continents were in close proximity (Gondwanaland). The first furcation gave rise to daughter lines I and II.

Daughter line I represents an early African dispersal, and all of the recent genera are characterised by the following: 1) procoxal apodemes are absent; 2) mesoepisternal apodemes are absent; 3) nymphal prosternum is triangular; 4) sternacostal suture is present in the nymphal prosternum; 5) $m < 1/3M$; and 6) sternacostal suture is absent in the nymphal mesosternum.

Subsequent evolution of daughter line I is represented by the following phylogenetic diagram (Fig. 96). The gene pool ancestral to these recent genera probably evolved at a time when

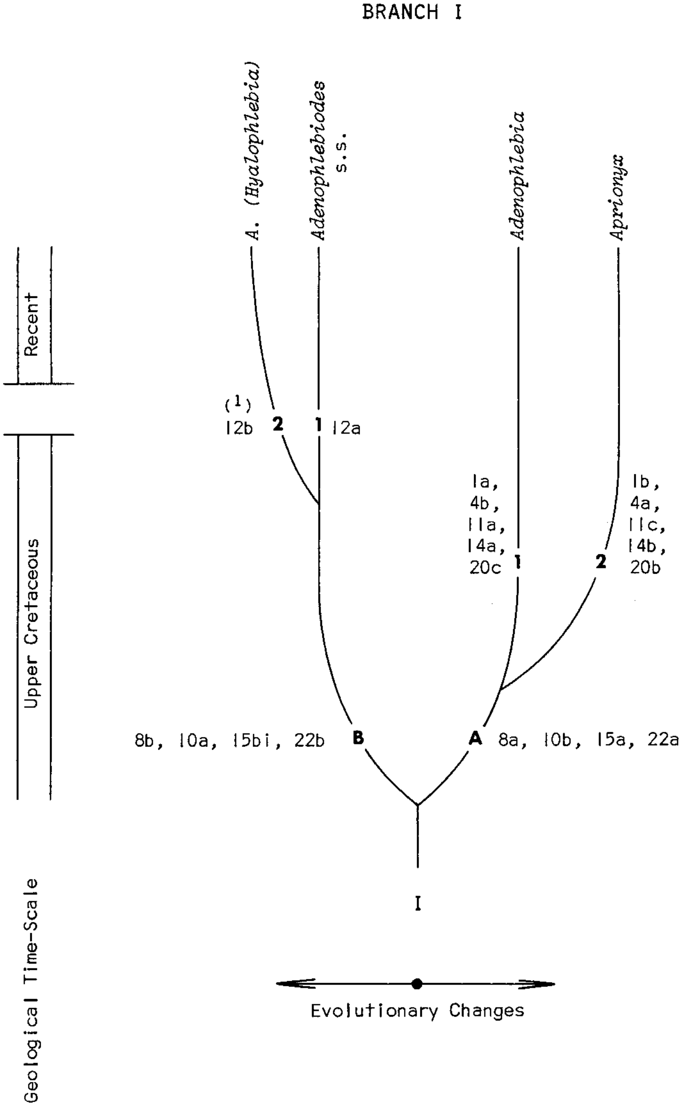

FIGURE 96. — Phylogenetic diagram of daughter line I. (1) Longitudinal carinae in imaginal prosternum reduced.

Africa was sufficiently isolated from the rest of Gondwanaland. The present separation may have been acquired over a period of 50 to 60 million years. Valencio and Vilas (1970) proposed that Africa and South America began to drift apart in the mid-Jurassic. Perhaps the final link between West Africa and Brazil did not break until well into the Cretaceous (Wright, 1968; Reyment, 1969). Some geological data suggest that rifting of the South Atlantic began at the southern end. Le Pichon and Hayes (1971) estimated that the spreading rate was probably three times faster in the south than in the north. This difference alone would produce enough oceanic barrier between southern Africa and South America to prevent effective intercontinental dispersals of the Leptophlebiidae even before any hypothetical final separation. Separation of Africa from the Antarctica probably also happened at about this period, i.e., between mid-Jurassic to mid-Cretaceous (Le Pichon and Heirtzler, 1968; McElhinny, 1970). The time of separation of Africa/Madagascar/India/Antarctica is still unsettled since there are many controversial data over the origin of the Indian Ocean.

The time scale adopted here is that given by McElhinny (1970) in his paper on the formation of the Indian Ocean. Based on paleomagnetic data, McElhinny postulated that the India/Madagascar/Antarctica block broke away from Africa between mid-Jurassic and mid-Cretaceous, thus opening up the Indian Ocean. This estimate is therefore also in accord with the time of separation between Africa from South America, and Antarctica.

After isolation had been attained, ancestral populations of daughter line I gave rise to two lines of evolution; daughter lines IA and IB. The hypothesis that these two phyletic lines arose after Africa was sufficiently isolated from the rest of Gondwanaland is supported by the absence of these paleo-endemic genera or lines outside Africa. Daughter line IA includes the recent genera *Adenophlebia* and *Aprionyx;* they evolved in southern Africa and possess the following features: 1) posterior width of the nymphal prosternum is greater than the anterior width of the mesosternum; 2) in the nymphal prosternum the anterior sternal sutures are convergent but without fusing apically; 3) anterior sternal sutures in the nymphal metasternum are absent; 4) in the mesothorax of the adult, the posterior margin of the furcasternum is smoothly concaved; and 5) penes are fused in the imagos. This phyletic line includes the two most ancestral recent genera among the Southern Hemisphere Leptophlebiidae. From the works of Barnard (1932), Crass (1947), and Schoonbee (1973), it is apparent that the present distributions of these two genera are largely restricted to high altitude areas. The paleoclimate of the African continent probably was temperate throughout Mesozoic (Balinsky, 1962); it is therefore likely that *Adenophlebia* and *Aprionyx* once had a wider distribution. As the continent drifted north, the temperature rose, causing the stenothermal species to retreat into montane and semimontane areas (Harrison, 1965).

Morphologically, the recent genus *Adenophlebiodes* of daughter line IB is more derived than its sister-group (daughter line IA). It is characterised by: 1) nymphal prosternum has a posterior width equal to the anterior width of the mesosternum; 2) anterior sternal sutures of nymphal prosternum are convergent and fused apically; 3) long anterior sternal sutures are present in the nymphal metasternum; 4) in the imaginal mesothorax, posterior margin of furcasternum is acutely concaved; and 5) penes in the imagos are separated. In *A.* (*Hyalophlebia*) a sternacostal suture had independently evolved in the nymphal mesosternum. The recent genus of daughter line IB represents a hardy element that is more eurythermal and specialised to live in silted habitats. Therefore, its species are not confined to the montane or Southern Cape Provinces but have extended northward to the southern boundary of the Sahara Desert. During the Cretaceous, most of northern and western Africa was covered by epicontinental seas (Cracraft, 1973; Cooke, 1968) which retreated in the Paleocene and Eocene. Therefore, the present species-range of *Adenophlebiodes* probably was attained after the Eocene.

Gondwanian leptophlebiids in Africa are more closely related to each other than to those in Madagascar, South America, Australia or New Zealand, thus possibly indicating a longer history of genetic and geographic isolation. This phylogenetic interpretation also seems to support the geological idea of an early separation of Africa from the rest of Gondwanaland.

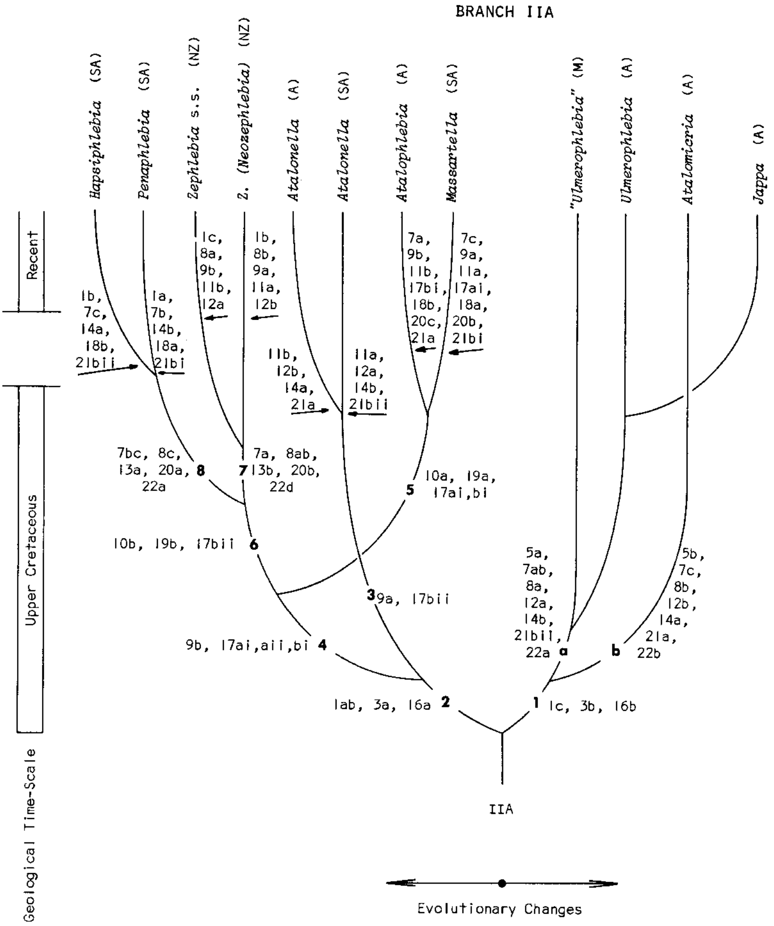

FIGURE 97. — Phylogenetic diagram of daughter line IIA. A = Australia, M = Madagascar, NZ = New Zealand, SA = South America.

Based on wing venation studies, Peters and Edmunds (1970) considered the recent Ethiopian genera *Castanophlebia* and *Fulleta* to be close relatives of *Adenophlebiodes*. Due to the lack of specimens, we have not included these two genera in the present study.

Daughter line II is an ancient phyletic branch that existed in

Gondwanaland; its recent genera are characterised by the following: 1) procoxal apodemes are present; 2) mesoepisternal apodemes are present; 3) prosternum of nymph is usually not triangular; and 4) sternacostal suture is present in the nymphal mesosternum. During the early evolutionary history of daughter line II it further divided into two daughter lines, IIA and IIB (Figs. 97, 98). Based on distributions of the recent genera this probably occurred in very early Lower Cretaceous.

Recent genera of daughter line IIA are characterised by the following: 1) sternacostal suture is absent in the nymphal prosternum; 2) $m < 1/3M$; and 3) sternacostal suture is present in the nymphal mesosternum, but not strongly developed. The phylogenetic relationships between the recent genera of daughter line IIA can be hypothesised by the following diagram (Fig. 97).

Evolution of daughter line IIA gave rise to daughter lines IIA1 and IIA2. Daughter line IIA1 includes the recent genera *Ulmerophlebia, Jappa,* and *Atalomicria;* they all possess: 1) a tentorial body which has a decidedly greater width than its length; 2) long setae may be present on the lateral margins of the nymphal pronotum; and 3) posterior spines of abdominal terga are arranged in groups. Daughter line IIA1 furcated into two evolutionary lines IIA1a and IIA1b. Daughter line IIA1a includes the recent genera *Ulmerophlebia* which occurs in Australia together with a close ally (an undescribed genus) in Madagascar, and its sister-group *Jappa* occurs in Australia.

The distributions of *Ulmerophlebia,* its Madagascan ally, and *Jappa,* together with several other genera of Southern Hemisphere Leptophlebiidae, are important in understanding the paleogeography of Madagascar. Cracraft (1973) recently reviewed the current geological hypotheses on the possible sequence of separation of Madagascar from Gondwanaland; basically there are three schools of thought. Based on paleomagnetic data that suggest a differential movement of Madagascar and Africa prior to mid-Cretaceous, the first hypothesis suggests that India/Madagascar/Antarctica moved as a single plate and became separated from Africa between mid-Jurassic and mid-Cretaceous (McElhinny, 1970; Crawford, 1971). McElhinny's reconstruction of Gondwanaland, based on paleomagnetic pole positions, shows that for mid-Cretaceous the India/Madagascar/Antarctica block was actually farther southeast of Africa rather than northeast of Africa as indicated by sea-floor spreading data for the Indian Ocean (Le Pichon, 1968; Le Pichon and Heirtzler, 1968; Smith and Hallam, 1970). Subsequently, India/Madagascar became separated from the Antarctica by the end of Lower Cretaceous (McElhinny, 1970). Madagascar and India probably drifted northward together and became separated at the end of Upper Cretaceous. This possibility is supported by paleomagnetic data from their Upper Cretaceous lavas (Roche, 1970).

A second hypothesis proposes that India/Madagascar/Africa moved as a block away from Antarctica before the end of Cretaceous. Subsequently, India/Madagascar would have become separated from Africa in late Cretaceous, and finally from each other in late Cretaceous to early Tertiary (Smith and Hallam, 1970; Veevers et al., 1971).

A third hypothesis suggests that the initial break was between Africa/Madagascar and India/Antarctica/Australia in the late Jurassic to early Cretaceous. Madagascar was subsequently separated from Africa but did not have a close contact with India, and India became separated from Antarctica in mid-Cretaceous (Le Pichon and Heirtzler, 1968).

Distributions of *Ulmerophlebia, Ulmerophlebia*-ally and *Jappa* seem to support the first hypothesis since none of these genera or their close relatives presently occur in continental Africa. As will be seen later, similar evidence can be drawn from the present distributions of *Atalophlebioides* (Madagascar-Australia-New Zealand) and from *Kimminsula-Kirrara* complex (Madagascar-Ceylon-Australia). Very possibly, the New Zealand genus *Deleatidium* can be cited as additional evidence since Peters and Edmunds (1970) have examined imagos from Madagascar that resemble those of *Deleatidium*. All of these genera are presently absent or uncollected from continental Africa, and we do not exclude the possibility of their extinctions from Africa. We do not have direct fossil evidence to indicate that they were previously present in Africa. Indirect evidence of extinction can also be drawn from one other family of mayflies, the Siphlonuridae. This family is an ancient one, and most members have retained very ancestral characters. They are cosmopolitan in distribution except for the Ethiopian region and Ceylon. Edmunds (1972) indicated that since the Siphlonuridae were one of the early radiations of the order, their absence in the Ethiopian region and Ceylon is best explained by extinction due to the lack of cool refugia for survival. Since the nymphs of the leptophlebiid genera in question are mostly cool-adapted rheophils (Harrison, 1965; Peters and Edmunds, 1972; Riek, 1970; Schoonbee, 1973), a similar history of extinction is possible.

Based on the data from this study the first hypothesis may be the most probable one, and dispersal between *Ulmerophlebia* in Australia and its ally in Madagascar probably had taken place prior to the Albian (about 100 m.y.), and a transantarctic dispersal route was possible. Paleoclimatology also indicates that Antarctica probably had a temperature climate during the Cretaceous. Fossilized land plants were found together with an abundant marine molluscan fauna (ammonites, cephalopods, gastropods), which indicates a warmer marine climate (Doumani and Long, 1962; Webb, 1968).

If we accept the first hypothesis, questions would probably be raised concerning the similarities of important marine stratigraphy between Madagascar and Africa (Smith and Hallam, 1970). But it should be noted that these similarities are primarily of Jurassic age and therefore it would be too early to contradict the first hypothesis.

Jappa probably evolved from an *Ulmerophlebia*-like ancestor in Australia; the nymphs developed long frontal processes adapted for burrowing beneath rocks. Daughter line IIA1b gave rise to the recent genus *Atalomicria* of Australia. Ecologically, the nymphs are restricted to cool mountain streams bordered by dense vegetation, and they have developed greatly elongated maxillary palpi (Riek, 1970).

Daughter line IIA2 represents a former transantarctic dispersal whose recent genera are distributed in South America-Australia-New Zealand. Recent genera of this phyletic line are characterised by the following: 1) nymph has a square tentorial body; 2) setae are absent on the lateral margins of the nymphal pronotum; and 3) posterior spines of nymphal abdominal terga occur singularly.

Daughter line IIA2 gave rise to two evolutionary branches, line IIA3 and IIA4. Daughter line IIA3 is represented by the recent genus *Atalonella* which occurs in both Australia and South America. It is characterised by the following: 1) sternacostal suture is present in the nymphal prosternum; and 2) longitudinal carinae are widely separated in the imaginal prosternum.

Daughter line IIA4 includes the recent genera *Atalophlebia, Massartella, Hapsiphlebia, Penaphlebia,* and *Zephlebia.* They are characterised by the following: 1) sternacostal suture is absent in the nymphal prosternum; and 2) longitudinal carinae are fused to slightly separated in the imaginal prosternum. From this evolved daughter lines IIA5 and IIA6.

Daughter line IIA5 is represented by *Atalophlebia* in Australia and *Massartella* in South America. They are characterised by the following: 1) anterior sternal sutures in the nymphal prosternum are convergent and fused apically; 2) longitudinal carinae of imaginal prosternum are not fused mesally; 3) lateral margins of the imaginal basisternum are straight; and 4) posterior spines of the nymphal abdominal terga can be biordinal (straight and feather-like spines together).

Peters and Edmunds (1972) believed that *Massartella* was a derivative of the *Penaphlebia* lineage, and probably *Hapsiphlebia* and *Massartella* both arose from a *Penaphlebia*-like ancestor in continental South America. The morphological characters on which the present study is based, are different from those used by Peters and Edmunds (1972); this may account for the disagreement on the phylogenetic position of *Massartella.* Further study is needed to clarify this problem.

Dispersal of daughter lines IIA3 and IIA5 were probably along a similar route across Antarctica. Geological evidences are overwhelming for a South America-Antarctica connection via the Scotia Arc (Adie, 1962, 1963; Barker, 1970), and based on magnetic anomalies and stratigraphic data Barker suggested that the last break between South America and Antarctica probably occurred only about 25 million years ago (Miocene). Australia on the other hand can be fitted on the basis of similarities of the

Adelaide and Ross geosynclines to the eastern Antarctica. Sea-floor spreading data support a post-Cretaceous separation of Australia and Antarctica; and paleomagnetic data suggest that the connection could have existed up to the Paleocene (Tarling, 1971). This late date for the separation of Australia and Antarctica does not contradict the fossil finding of *Atalophlebia* in Australia during the Miocene, although several geologists (Creer, et al., 1969, 1970) have suggested that drifting began in Paleozoic or Triassic-Jurassic.

The possible dispersal route for daughter lines IIA3 and IIA5 could be eastern Australia-eastern Antarctica-Antarctica Peninsula-southern South America, although not necessarily in that direction. Isolation of the two species groups of *Atalonella* and the evolution of the *Atalophlebia* and *Massartella* therefore probably occurred after the Paleocene when Australia became separated from Antarctica. The paleoclimate of Antarctica would probably have allowed for such dispersal, since most of the late-Cretaceous and early-Tertiary climate of Antarctica have been temperate (Cracraft, 1973).

Daughter line IIA6 represents an early transantarctic dispersal between South America and New Zealand. Its recent genera are characterised by the following: 1) anterior sternal sutures of nymphal prosternum are convergent without fusing apically; 2) longitudinal carinae of imaginal prosternum are fused mesally; and 3) lateral margins of imaginal mesobasisternum are expanded. Daughter line IIA6 gave rise to *Zephlebia* s.s. and *Z.* (*Neozephlebia*) (IIA7) in New Zealand and *Hapsiphlebia* and *Penaphlebia* (IIA8) in South America. The rectangular tentorial body in *Zephlebia* s.s. has probably evolved secondarily. One of us (WLP) disagrees with Penniket (1961) in placing *Z.* (*Neozephlebia*) as a subgenus of *Zephlebia,* and places *Z.* (*Neozephlebia*) as a separate phyletic line more closely related to *Atalophlebioides* than to *Zephlebia.* More study is needed concerning this point.

Dispersal between South America and New Zealand probably occurred before New Zealand became severed from Antarctica. Griffith's reconstruction (1971) of the south-west Pacific margin of Gondwanaland, and Griffith's and Varne's model (1972) of the development of Tasman Sea seem to be well accepted by biogeographers (Cracraft, 1973; Gaskin, 1972). Based on this model New Zealand was connected by the Campbell Plateau and Chatham Rise to West Antarctica about 80 m.y. ago. Therefore, a possible New Zealand-South America dispersal route would be South America-Scotia Arc-Antarctic Peninsula-West Antarctica-Campbell Plateau/Chatham Rise-New Zealand. This is supported by strong stratigraphic and tectonic similarities between the younger West Antarctica (compared to East Antarctica) and the South American Andes (Adie, 1963). Marine magnetic profile data suggest that sea-floor spreading between Campbell Plateau and Antarctica began about 80 m.y. ago, and between Australia and Antarctica about 50 m.y. ago. In Griffith's and Varne's (1972) model, the initial stages of sea-floor spreading in the Tasman Sea was a triangular rift, with the Lord Howe Rise rifting from the Antarctica-Australian plate in the north and the Campbell Plateau spreading sinistrally away from the Antarctica-Australian plate in the south. The Endeavour Fracture Zone indicates a faster spreading rate in the south. If this is the case, then, about Paleocene the West Antarctica dispersal route from South America to New Zealand probably no longer existed. However, this does not exclude the possibility of a dispersal route via Antarctica-Australia-Lord Howe Rise to New Zealand at this time. Based on these geological data evolution of daughter lines IIA7 and IIA8 probably occurred at a post-Paleocene time.

Recent genera of daughter line IIB represent a more derived line of evolution (Fig. 98); the major evolutionary development retained by them are the following: 1) sternacostal suture is present in the nymphal prosternum; 2) $m > 1/3M$; and 3) sternacostal suture is strongly developed in the nymphal mesosternum. A primitive furcation of line IIB gave rise to daughter lines IIB1 and IIB2 (Fig. 98).

Daughter line IIB1 is represented by the recent genus *Kimminsula* in Ceylon, and an undescribed group in Madagascar. The morphology of these genera shows a unique combination of ancestral and derived features. As can be seen from Table 3, *Kimminsula* has a comparatively low S_J value with other genera and probably represents an early offshoot from the ancestral

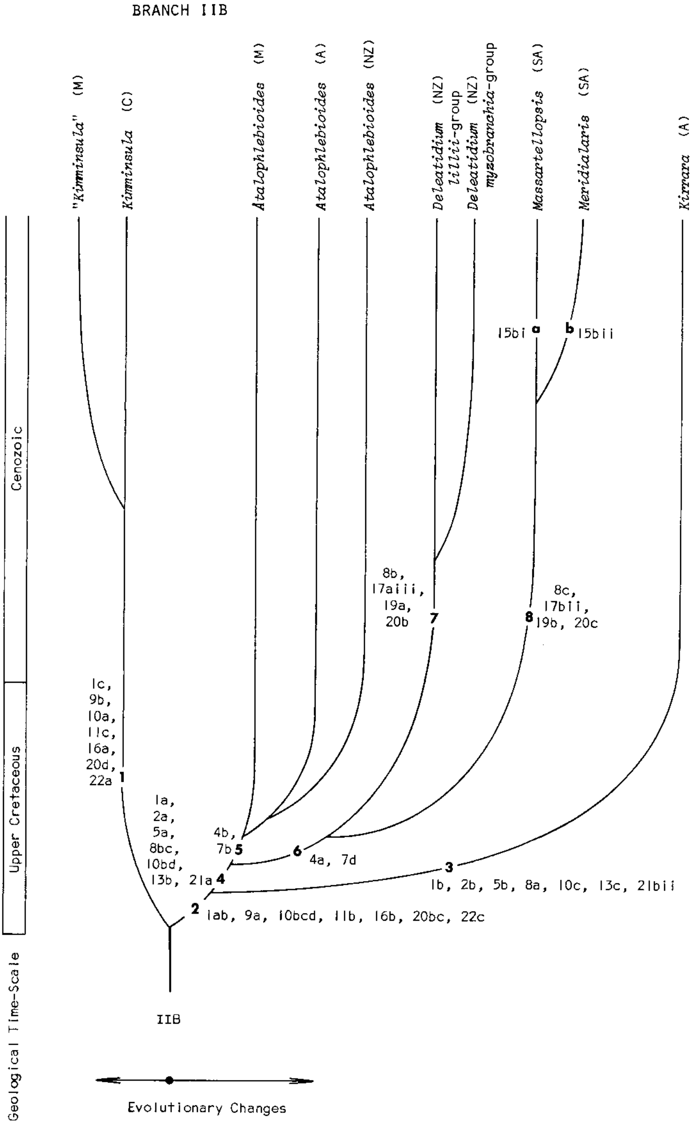

FIGURE 98. — Phylogenetic diagram of daughter line IIB. A = Australia, C = Ceylon, M = Madagascar, NZ = New Zealand, SA = South America.

stock. The developments in this phyletic line are the following: 1) a rectangular tentorial body is present in the nymph; 2) sternacostal suture is absent in the nymphal prosternum; 3) anterior sternal sutures of nymphal prosternum are convergent and fused apically; 4) mesobasisternal length in the nymph is shorter than the mesofurcasternal length; 5) posterior spines of the nymphal abdominal terga occur singularly; 6) posterior margin of the imaginal mesobasisternum is concaved; and 7) posterior margin of the imaginal mesofurcasternum is smoothly concaved. Daughter line IIB1 probably represents an early dispersal to India/Madagascar prior to their separation from the Gondwanaland in the early Upper Cretaceous, but probably after Africa had severed from Gondwanaland. The present distribution of *Kimminsula* and its Madagascar sister-group seems to support the geological hypothesis of an early separation of Africa from Madagascar/India (McElhinny, 1970) since relatives of this line of evolution have not yet been found in continental Africa. However, extinction of this phyletic line in continental Africa could be a possibility.

Recent genera of daughter line IIB2 are characterized by the following: 1) tentorial body in the nymph is more or less square; 2) sternacostal suture is present in the nymphal prosternum; 3) mesobasisternal length is equal to mesofurcasternal length; 4) posterior spines of nymphal abdominal terga occur in groups; and 5) posterior margin of the imaginal mesofurcasternum is convex. This phyletic line gave rise to daughter line IIB3 which probably represents an early Australian dispersal in the Upper Cretaceous. It is represented by the recent genus *Kirrara* whose nymphs are highly adapted to life in torrential mountain streams by developing abdominal gills that function as a suction cup. This phyletic line is characterised by the following: 1) tentorial body has a greater width than length; 2) spines are absent on the anterolateral margins of the nymphal pronotum; 3) procoxal apodemes are absent; 4) posterior width of prosternum is wider than anterior width of mesosternum; 5) anterior sternal sutures in the nymphal prosternum are parallel and joined anteriorly by a horizontal suture; 6) $m \geqq 1/2M$; and 7) lateral margins of the imaginal furcasternal median longitudinal invagination are divergent and widely separated.

Daughter line IIB4 includes the recent genera *Atalophlebioides,* *Deleatidium, Massartellopsis,* and *Meridialaris.* The nymphs of these genera are characterised by a more or less square prosternum in which the anterior sternal sutures are parallel. Daughter line IIB4 gave rise to daughter line IIB5 which includes the three species-groups of *Atalophlebioides,* and are presently distributed in Madagascar, Australia, and New Zealand. Based on this pattern of distribution, the age of this phyletic line can be dated back at least to the mid-Cretaceous, i.e., prior to the separation of Madagascar from Gondwanaland. Based on Griffith's and Varne's model (1972), dispersal between Australia and New Zealand was geologically possible up to the Paleocene via the Lord Howe Rise and Norfolk Ridge. Although it has not been determined exactly how much dry land surface was represented by Lord Howe Rise and Norfolk Ridge, nevertheless they increased the chances of dispersal between Australia and New Zealand. Zoogeography of daughter line IIB5 further suggests an early separation between Africa and India/Madagascar since this phyletic line is yet to be found in Africa; however, extinction remains a possibility.

Daughter line IIB6 represents another transantarctic dispersal between South America and New Zealand. The major evolutionary feature of this line is the variously fused pro- and mesonota of the nymphs. Daughter line IIB7 gave rise to *Deleatidium* in New Zealand. Based on the formation of the nymphal abdominal gills, *Deleatidium* can be divided into two groups, the *myzobranchia*-group, with gills forming a suction cup, and a *lilli*-group in which the gills are not modified as a suction cup. However, the nymphal thoracic structures do not allow for such differentiation.

Daughter line IIB7 can be characterised by the following: 1) posterior width of nymphal prosternum is about equal to anterior width of the mesosternum; 2) longitudinal carinae in imaginal prosternum are fused subanteriorly; 3) lateral margins of imaginal mesobasisternum are straight to slightly expanded ventrally; and 4) shape of the imaginal mesobasisternal posterior margin is rounded.

Daughter line IIB8 includes the recent genera *Massartellopsis* and *Meridialaris* in South America. Their high S_J value suggests that branching of these two genera probably occurred very recently in geological time, and most likely this took place after the other southern continents had drifted away from Antarctica. Daughter line IIB8 can be characterised by the following: 1) posterior width of nymphal prosternum is narrower than the anterior width of the mesosternum; 2) longitudinal carinae in imaginal prosternum are widely separated; 3) lateral margins of imaginal mesobasisternum are expanded mesally; and 4) shape of the imaginal mesobasisternal posterior margin is truncated.

Based on various studies, present day Leptophlebiidae that have evolved from Gondwanian lineages appear to be confined to the Southern Hemisphere, except for several widespread genera in Africa and several endemic genera in Ceylon and southern India. Peters and Edmunds (1970) discussed the phylogeny of the Eastern Hemisphere genera and noted the probable phylogeny of the North American genera. They indicated in Fig. 1 the Gondwanian lineages as phyletic line IIA and showed the relationship of this line to the remaining Eastern Hemisphere Leptophlebiidae. The majority of the Neotropical Leptophlebiidae, except those of the Southern Andes, has not been studied by us and any relationships of these genera to Gondwanian lineages are unknown.

SUMMARY

Peters and Edmunds (1964, 1970, 1972) indicated that the Southern Hemisphere and certain Indian Leptophlebiidae form several distinct phylogenetically related groups. At present one or more of these groups are disjunctly distributed throughout Australia, Tasmania, New Zealand, New Caledonia, southern South America, southern Africa, Madagascar, southern India and Ceylon, thus suggesting one or more Southern Hemisphere dispersal routes in the past. Nominal genera included in this complex are *Atalophlebia, Atalophlebioides, Atalomicria, Atalonella, Deleatidium, Jappa, Kirrara, Ulmerophlebia* and *Zephlebia* from the Australasian region; *Atalonella, Hapsiphlebia, Massartella, Massartellopsis, Meridialaris,* and *Penaphlebia* from the Neotropical region; *Adenophlebia, Adenophlebiodes, Aprionyx, Atalophlebioides,* and *Ulmerophlebia* from the Ethiopian region; and *Kimminsula* from Ceylon.

The objective of this study was to analyse the phylogeny and zoogeography of the above named genera based on the comparative morphology of their nymphal and imaginal thorax, the nymphal tentorium and abdominal terga.

Kirrara amenia was studied in detail as a representative of many Southern Hemisphere Leptophlebiidae and a comparative study was made for all the named genera. Twenty-two taxonomic characters were chosen as phylogenetic markers, and their probable evolutions were discussed. Many characters and their character states have a mosaic distribution among the genera, and, on the whole, these genera show great similarities in their taxonomic characters. Persistent polyalleism was considered as the possible genetic basis; similar selection pressures, and slow evolutionary rate were also possible factors causing their similarities.

Because of the mosaic distribution of the taxonomic characters there were no objective *a priori* methods to group these genera. A numerical approach (Jaccard's Coefficient of Similarity) was used to deduce their overall character similarities. The similarity indices were used to aid in character weighing, and a phylogenetic scheme was proposed.

Three main phyletic lines were hypothesized. Daughter line I represents an ancient African dispersal and includes the recent genera *Adenophlebia, Aprionyx,* and their sitser-group *Adenophlebiodes* s.s. and *A.* (*Hyalophlebia*). These genera probably evolved after Africa was separated from the rest of Gondwanaland sometime between mid-Jurassic and mid-Cretaceous. Daughter line IIA gave rise to the following line of evolution: Line IIA1a includes *Ulmerophlebia* in Australia with a closely related ally in Madagascar, and *Jappa* in Australia. Distributions of these, and several other groups (*Atalophlebioides, Kimminsula, Kirrara,* and possibly *Deleatidium*), seem to support the geological hypothesis that Madagascar/India/Antarctica moved as a single plate away from Africa sometime between mid-Jurassic and mid-Cretaceous. However, based on indirect evidence, we do not exclude the possibility of extinctions of these genera in continental Africa. Daughter line IIA1b is represented by the recent genus *Atalomicria* of

Australia. Daughter line IIA2 includes several phyletic lines whose recent members are distributed in South America, Australia, New Zealand, and thus exhibit transantarctic relationships. Line IIA3 is represented by *Atalonella,* found in Australia and South America; line IIA5, represented by *Atalophlebia* in Australia and *Massartella* in South America; line IIA6 with *Hapsiphlebia, Penaphlebia* in South America and *Zephlebia* s.s., *Z.* (*Neozephlebia*) in New Zealand. Transantarctic dispersal routes were proposed for these genera.

Daughter line IIB gave rise to daughter line IIB1, which includes the recent genus *Kimminsula* of Ceylon with its sister genus in Madagascar, and they represent an early dispersal to Madagascar/India. Daughter line IIB3 is represented by the recent genus *Kirrara* in Australia. Daughter line IIB5 is represented by the recent genus *Atalophlebioides* whose species are found in Madagascar, Australia, and New Zealand. Daughter line IIB6 is represented by *Deleatidium* in New Zealand, and by *Massartellopsis* and *Meridialaris* in South America.

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REFERENCES

ADIE, R. J. 1962. The geology of Antarctica. Am. Geophys. Union Monogr. 7:26-39.

————. 1963. Geological evidence on possible Antarctic land connections. In *Pacific Basin Biogeography,* p. 455-463. Gressitt, J. L. (Ed.) 10th Pac. Sci. Congr. Bishop Mus. Press. Honolulu.

AGNEW, J. D. 1961. New Transvaal Leptophlebiidae (Ephemeroptera). Novos Taxa Entomol. 26:1-9.

————. 1962. New Leptophlebiidae (Ephemeroptera) from the Transvaal. Arch. Hydrobiol. 58:385-386.

BALINSKY, B. I. 1962. Patterns of animal distribution on the African continent. Ann. Cape Prov. Mus. 2:299-310.

BARKER, P. F. 1970. Plate tectonics of Scotia Sea region. Nat. Lond. 228:1293-1296.

BARNARD, K. H. 1932. South African mayflies (Ephemeroptera). Trans. R. Soc. S. Afr. 20:201-259.

————. 1940. Additional records, and descriptions of new species of South African alder-flies (Megaloptera), mayflies (Ephemeroptera), caddis-flies (Trichoptera), stone-flies (Perlaria), and dragon-flies (Odonata). Ann. S. Afr. Mus. 32:609-661.

BRUNDIN, L. 1965. On the real nature of transantarctic relationships. Evol. 19:496-505.

————. 1966. Transantarctic relationships and their significance as evidenced by the chironomid midges, with a monograph of the subfamily Podonominae, Aphroteaeninae and austral Heptagiae. Kgl. Sv. Vetenskapsakad. Handl. (4)11:1-472.

COOKE, H. B. S. 1968. Evolution of mammals on southern continents. II. The fossil mammal fauna of Africa. Q. Rev. Biol. 43:234-264.

CRASS, R. S. 1947. The mayflies (Ephemeroptera) of Natal and the eastern Cape. Ann. Natal Mus. 11:37-110.

CRACRAFT, J. 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. J. Zool. 169:455-545.

CRAWFORD, A. R. 1971. Gondwanaland and the growth of India. J. Geol. Soc. India 12:205-221.

CREER, K. M., B. J. J. EMBLETON, AND D. A. VALENCIO. 1969. Comparison between the Upper Palaeozoic and Mesozoic palaeomagnetic poles for South America, Africa and Australia. Earth Planet Sci. Lett. 7:288-292.

————. 1970. Triassic and Permo-Triassic palaeomagnetic data for South America. Earth Planet Sci. Lett. 8:173-178.

CROWSON, R. A. 1970. Classification and biology. 350 pp. Atherton Press, Inc., New York, and Heinemann Educational Books, Ltd., London.

DARLINGTON, P. J., JR. 1970. A practical criticism of Hennig-Brundin's "phylogenetic systematics" and Antarctic biogeography. Syst. Zool. 19:1-18.

————. 1972. What is cladism? Syst. Zool. 21:128-129.

DEMOULIN, G. 1955. Note sur deux nouveaux genres de Leptophlebiidae d'Australie (Ephemeroptera). Bull. Ann. Soc. R. Entomol. Belg. 91:227-229.

————. 1965. Contribution à la connaissance des Éphéméroptères de l'ambre oligocène de la Baltique. Ent. Medd. 34:143-153.

————. 1968. Deuxieme contribution à la connaissance des Éphéméroptères de l'ambre oligocène de la Baltique. Dt. Ent. Z. (N.F.) 15:233-276.

————. 1970. Ephemeroptera des faunes éthiopienne et malgache. S. Afr. Anim. Life 14:24-170.

DOUMANI, G. A. AND W. E. LONG. 1962. The ancient life of the Antarctic. Sci. Am. Sept.

EDMUNDS, G. F., JR. 1972. Biogeography and evolution of Ephemeroptera. Ann. Rev. Entomol. 17:21-42.

FAIRCHILD, G. B. 1969. Climate and the phylogeny and distribution of Tabanidae. Bull. Entomol. Soc. Am. 15(1):7-11.

GASKIN, D. C. 1970. The origins of the New Zealand fauna and flora: A review. Geogr. Rev. 60:414-434.

————. 1972. Reappraisal of the New Zealand Mesozoic with respect to sea-floor spreading and modern tectonic plate theory. XVII Congress International de Zoologie. Symposium 1, "Biogeographie et liaisons inter-continentales au cours du Mesozoique." Monte Carlo, September, 1972.

GRESITT, J. L. 1961. Problems in the zoogeography of Pacific and Antarctic insects. Pacif. Insects Monogr. 2:1-94.

GRIFFITHS, J. R. 1971. Reconstruction of the south-west Pacific margin of Gondwanaland. Nat. Lond. 234:203-207.

GRIFFITHS, J. R. AND R. VARNE. 1972. Evolution of the Tasman Sea, Macquarie Ridge and Alpine Fault. Nat. (Phys. Sci.) Lond. 235:83-86.

HARKER, J. E. 1950. Australian Ephemeroptera. Part I. Taxonomy of New South Wales species and evaluation of taxonomic characters. Proc. Linn. Soc. N.S.W. 75:1-34.

————. 1954. The Ephemeroptera of eastern Australia. Trans. R. Entomol. Soc. Lond. 105:241-268.

————. 1957. Some new Australian Ephemeroptera. Part II. Proc. R. Entomol. Soc. Lond. (B)26:69-78.

HARRISON, A. D. 1965. Geographical distribution of riverine invertebrates in Southern Africa. Arch. Hydrobiol 61(3):387-394.

HARRISON, A. D. AND J. D. AGNEW. 1962. The distribution of invertebrates endemic to acid streams in the Western and Southern Cape Province. Ann. Cape Prov. Mus. 2:273-291.

HENNIG, W. 1960. Die Dipteren fauna von Neuseeland als systematisches und tiergeographisches Problem. Beitr. Entomol. 10:221-329.

————. 1966. Phylogenetic systematics. 263 pp. The University of Illinois Press, Urbana.

HUDSON, G. B. 1951. Studies in the comparative anatomy and systematic importance of the hexapod tentorium — IV. Ephemeroptera. J. Entomol. Soc. S. Afr. 14:3-23.

ILLIES, J. 1963. Revision die südamerikanischen Gripopterygidae (Plecoptera). Mitt. Schweiz. Entomol. Ges. 36:145-248.

————. 1965. Verbreitungsgeschichte der Gripopterygiden (Plecoptera) in der südlichen Hemisphere. Proc. 12th Int. Congr. Entomol. Lond. 1964:464-468.

IMMS, A. D. 1964. A general textbook of entomology. 9th ed. (revised). x + 886 pp. Methuen and Co. Ltd., London.

LE PICHON, X. 1968. Sea-Floor spreading and continental drift. J. Geophys. Res. 73:3661-3698.

LE PICHON, X. AND D. E. HAYES. 1971. Marginal offsets, fracture zones, and the early opening of the South Atlantic. J. Geophys. Res. 76: 6283-6293.

LE PICHON, X. AND J. R. HEIRTZLER. 1968. Magnetic anomalies in the Indian Ocean and sea-floor spreading. J. Geophys. Res. 73:2101-2117.

LESTAGE, J. A. 1924. Les Ephémères l'Afrique du Sud. Catalogue critique et systematique des espèces connues et description de trois genres nouveaux et de sept espèces nouvelles. Rev. Zool. Afr. 12: 316-352.

————. 1931. Contribution à l'étude des Ephéméroptères. VIII. Les Ephéméroptères du Chili. Bull. et Ann. Soc. Entomol. Blg. 71:41-60.

MACKERRAS, J. M. 1970. Composition and distribution of the fauna. In *The Insects of Australia,* p. 187-203. Melbourne University Press, Melbourne.

MATSUDA, R. 1970. Morphology and evolution of the insect thorax. Mem. Entomol. Soc. Can. No. 76.

MAYR, E. 1965a. Numerical phenetics and taxonomic theory. Syst. Zool. 14:73-97.

————. 1965b. Animal species and evolution. xiv + 797 pp. Harvard University Press, Cambridge, Mass.

————. 1969. Principles of systematic zoology. xi + 428 pp. McGraw-Hill Book Co., New York.

McElhinny, M. W. 1970. Formation of the Indian Ocean. Nat. Lond. 228:977-979.

Needham, J. G. and H. E. Murphy. 1924. Neotropical mayflies. Bull. Lloyd Libr. 24, Entomol. Ser. 4:1-79.

Nelson, G. J. 1972. Comments on Hennig's "Phylogenetic Systematics" and its influence on Ichthyology. Syst. Zool. 21:364-374.

Penniket, J. G. 1961. Notes on New Zealand Ephemeroptera. I. The affinities with Chile and Australia, and remarks on *Atalophlebia* Eaton (Leptophlebiidae). N. Z. Entomol. 2(6):1-11.

Peters, W. L. and G. F. Edmunds, Jr. 1964. A revision of the generic classification of the Ethiopian Leptophlebiidae (Ephemeroptera). Trans. R. Entomol. Soc. Lond. 116:225-253.

————. 1970. A revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). Pacif. Insects 12: 157-240.

————. 1972. A revision of the generic classification of certain Leptophlebiidae from southern South America (Ephemeroptera). Ann. Entomol. Soc. Am. 65:1398-1414.

Phillips, J. S. 1930. A revision of New Zealand Ephemeroptera. Trans. N. Z. Inst. 61:271-390.

————. 1931. Studies of New Zealand mayfly nymphs. Trans. R. Entomol. Soc. Lond. 79:399-422.

Raven, P. H. and D. I. Axelrod. 1972. Plate tectonics and Australasian paleobiogeography. Sci., N.Y. 176:1379-1386.

Rensch, B. 1960. Evolution above the species level. xvii + 419 pp. Columbia University Press, New York.

Reyment, R. A. 1969. Ammonite biostratigraphy, continental drift and oscillatory transgression. Nat. Lond. 224:137-140.

Riek, E. F. 1970. Fossil history; Ephemeroptera (Mayflies). In *The Insects of Australia,* pp. 168-86, 224-40. Melbourne University Press, Melbourne.

Roche, A. 1970. Palaeomagnetic results from Madagascar: contribution to the continental drift theory. In *Palaeogeophysics,* pp. 117-184. Runcorn, S. K. (Ed.), Academic Press, New York.

Ross, H. H. 1956. Evolution and classification of the mountain caddisflies. vi + 213 pp. The University of Illinois Press, Urbana.

Schoonbee, H. J. 1973. The role of ecology in the species evaluation of the genus *Afronurus* Lestage (Heptageniidae) in South Africa. Proc. 1st Int. Conf. Ephemeroptera 1970:88-113.

Schmid, F. 1970. Le genera *Rhyacophila* et la famille des Rycophilidae (Trichoptera). Mem. Entomol. Soc. Can. No. 66.

SMITH, A. G. AND A. HALLAM. 1970. The fit of the southern continents. Nat. Lond. 225:139-144.

SNEATH, P. H. A. 1957. The application of computers to taxonomy. J. Gen. Microbiol. 17:201-226.

SNEATH, P. H. A. AND R. SOKAL. 1973. Numerical taxonomy. xv + 573 pp. W. H. Freeman and Co., San Francisco and London.

SOKAL, R. AND P. H. A. SNEATH. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco and London.

TARLING, D. H. 1971. Gondwanaland, paleomagnetism and continental drift. Nat. Lond. 229:17-21.

THROCKMORTON, L. H. 1965. Similarity versus relationship in *Drosophila*. Syst. Zool. 14:221-236.

TILLYARD, R. J. 1926. Plecoptera. *In Insects of Australia and New Zealand,* pp. 57-64. Angus and Robertson, Sydney.

————. 1935. The trout-food insects of Tasmania. Part II. A monograph of the mayflies of Tasmania. Pap. Proc. R. Soc. Tasmania 1935:23-59.

TRAVER, J. R. 1946. Notes on Neotropical mayflies. Part I. Family Baetidae, sub-family Leptophlebiinae. Rev. Entomol. (Urug.) 17: 418-436.

TSHERNOVA, O. A. 1970. On the classification of the fossil and recent Ephemeroptera. Ent. Obozr. 49:124-145. [In Russian with English summary]

————. 1971. A mayfly (Ephemeroptera, Leptophlebiidae) from fossil resin of Cretaceous deposits in the polar regions of Siberia. Entomol. Obozr. 50:612-618. [In Russian with English summary]

TSUI, P. T. P. AND W. L. PETERS. 1972. The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera). J. Zool. 168:309-367.

VALENCIO, D. A. AND J. F. VILAS. 1969. Age of the separation of South America and Africa. Nat. Lond. 223:1353-1354.

————. 1970. Paleomagnetism of some middle Jurassic lavas from south-east Argentina. Nat. Lond. 225:262-264.

VEEVERS, J. J., J. G. JONES, AND J. A. TALENT. 1971. Indo-Australian stratigraphy and the configuration and dispersal of Gondwanaland. Nat. Lond. 229:383-388.

VINE, F. J. AND D. H. MATTHEWS. 1963. Magnetic anomalies over oceanic ridges. Nat. Lond. 199:947-949.

WEBB, P. 1968. Comments on late Cretaceous marine climates in New Zealand and adjacent areas. Tuatara 16:8-10.

WRIGHT, J. B. 1968. South Atlantic continental drift and the Benue Trough. Tectonophys. 6:301-310.