SYSTEMATICS OF THE CONOESUCIDAE, HELICOPHIDAE, CALOCIDAE
AND ANTIPODOECIIDAE (INSECTA:TRICHOPTERA), WITH EMPHASIS ON
THE IMMATURE STAGES.

by

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This thesis contains no material which has been accepted for the award of any other higher degree or diploma in any tertiary institution, and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text.

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ABSTRACT

The systematics of the trichopteran families Conoesucidae, Helicophidae, Calocidae and Antipodoeciidae was investigated, with particular emphasis on immature stages (larvae and pupae). Study of Antipodoeciidae was limited to its inclusion in phylogenetic analysis, due to lack of material.

Collecting was carried out throughout Tasmania to establish the species to be included in these families and their distribution. Immatures were associated with adults by rearing for all the conoesucid species, 3 of the 6 helicophids and 2 of the 5 calocids known from Tasmania. Larvae and pupae are described and keys to species given.

Two new species of *Conoesucus* are described. Univariate morphometric analysis of male genitalia of *Lingora vesca* and *L. aurata* showed that *L. vesca* is a variant of *L. aurata*, and is therefore synonymised with it. Electrophoretic data showed *Conoesucus adiastolus* sp. n. to be distinct from the morphologically similar *C. brontensis*. Morphometric analysis of wing venation enabled adults of *Conoesucus brontensis*, *C. nepotulus* and *C. adiastolus* to be separated, but with some overlap; measurement of male maxillary palps showed that males could be reliably identified by their structure.

Species distribution within Tasmania falls into two categories: those restricted to the west, and those species which are widespread. The 12 western species are all endemics; of the ten widespread species, at least six are shared with the mainland. More detailed study of mainland species is required before detailed biogeographic hypotheses explaining the entire Australian distribution of these families can be proposed.

Chromosomes were counted in all the species for which immatures were identified. Chromosome number varied between families: for Conoesucidae n=25, Calocidae (*Caenota* and *Tamasia*) n=22, Helicophidae (*Alloecella*) n=32-40. Although the number for *Alloecella* could not be determined precisely, it is the second highest so far recorded for Trichoptera. Chromosomes were too small and uniform for other characteristics to be studied with the method used. These results are discussed in relation to placement of the families within Trichoptera, and chromosome evolution in Trichoptera and the sister order Lepidoptera.

Phylogenetic analysis based on larval and pupal characters (including case characters) was carried out for a) the 22 Tasmanian taxa studied in detail and b) the Tasmanian species plus *Antipodoecia* and species of Conoesucidae, Calocidae and Helicophidae from New Zealand and South America. Analysis of Tasmanian taxa resulted in groups generally in agreement with the existing classification. Monophyly was demonstrated for the Tasmanian Conoesucidae, Helicophidae (*Alloecella*) and the Calocidae studied. The genera *Lingora*, *Hampa* and *Matasia* were shown to constitute a monophyletic group, providing evidence in support of congeneric status, although this conflicts with some characters of adults. In analysis of all taxa, New Zealand species were grouped with Australian confamilials. Groups outside the Conoesucidae were not shown to be monophyletic and thus their status remains uncertain.

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CHAPTER 1. GENERAL INTRODUCTION AND METHODS

1.1 GENERAL INTRODUCTION.

The order Trichoptera (caddis flies) is an ecologically important group of holometabolous insects, showing greater diversity in various habitats than any other insect order with wholly aquatic larvae (Mackay & Wiggins 1979). They inhabit almost every type of freshwater habitat, and also include several species with terrestrial larvae, e.g. the Tasmanian endemic *Caloca saneva* (Mosely) (Neboiss 1979), and marine species in Australia and New Zealand. Larvae are involved in all the trophic processes of freshwater ecosystems (Cummins 1973, Cummins & Klug 1979, Mackay & Wiggins 1979) and are important as food for various fish species (Jackson 1978, Hortle & White 1980, Otto & Svensson 1980) and other aquatic animals, including the platypus (Faragher *et al.* 1979) and crayfish (Hamr 1990). Trichoptera are also important in terrestrial systems because of the vast numbers of adults which may emerge, providing food for birds, spiders and insects.

The order is relatively small, with at least 10,000 species worldwide (Wiggins 1977) (cf. Lepidoptera with about 160,000 species (Common 1990)). So far, 169 species have been recorded from Tasmania and 369 from mainland Australia, in 26 families; numerous undescribed species have been collected. Major taxonomic studies on Australian Trichoptera include those of Cartwright (e.g. 1990), Dean (e.g. 1984, Dean & Bunn 1989), Neboiss (e.g.1986), St Clair (1991) and Wells (e.g. 1985). Other studies published   are on life histories (Towns 1983, Dean & Cartwright 1987), diet (Chessman 1986) and macroinvertebrate ecology (Lake *et al.* 1985, Marchant *et al.* 1985). Australian species are poorly known biologically and ecologically, compared with northern hemisphere species (e.g. Beam & Wiggins 1987, Lamberti *et al.* 1987).

The sister order to Trichoptera is Lepidoptera (Hennig 1981, Kristensen 1981), from which adult Trichoptera are most readily distinguished by the form of the mouthparts (which lack functional mandibles and are never developed into a coiled proboscis), and the hairy vesture of the wings (although scale-like hairs are found in some species). Larvae can be distinguished by the lack of abdominal prolegs on segments 1-8, the single-segmented antennae (Weaver 1984) and the largely aquatic habitat.

The problem.

A great deal of systematic work remains to be done on Trichoptera: the higher classification is somewhat unstable, and several groups require revision.

The families Conoesucidae, Helicophidae, Calocidae, and Antipodoeciidae were chosen for the present detailed systematic study, with the aim of developing a sound classification. The existing classification is based on intuitive analysis of adults: monophyly of these families and their genera has not been demonstrated, and the taxa should be regarded with caution (Weaver 1983). The validity of family separation is uncertain, as is the status of some genera (particularly *Lingora, Hampa* and

Matasia). Relationships of these families with others are unresolved (Weaver 1983, Weaver & Morse 1986), and the status of the monospecific Antipodoeciidae is also unclear: it's family status may be unjustified. Additional families involved in the confusion are the Beraeidae from South America and the northern hemisphere, and Anomalopsychidae from South America (Flint pers. comm.). Past confusion in the classification of taxa currently included in these families is evident from their taxonomic history (see section 1.1.2). These taxa, and additional closely allied species included in the phylogenetic analysis, are listed in Table 1.1.

Resolution of these problems is important, as the Conoesucidae are the second most diverse of the case-making families in Australia, after Leptoceridae, which have recently been studied by St Clair (1990). Larvae of Australian conoesucids have not been described and therefore cannot be identified, although they are abundant in most lotic habitats. Therefore, description of immatures is a priority. Many of the New Zealand immatures in these families, and others, have been described by Cowley (1975, 1976b, 1978).

In addition, further knowledge of this group of families is essential for elucidation of the phylogeny of the order. They are included as part of the leptocerid branch in the phylogenies of Ross (1967, 1978) and Schmid (1980) (Figs1.1 and 1.2), and are placed by Weaver (1983, Weaver & Morse 1986) in the superfamily Sericostomatoidea, within which family relationships are unresolved (Fig.1.3). Monophyly of the superfamily is based on the shared derived characters of an adult tibial spur formula of 2:2:4, and the reduction of larval abdominal tergite 9.

The four families under investigation constitute the exclusively southern hemisphere component of this superfamily, except for the marine family Chathamiidae and the South American Anomalopsychidae. Their disjunct southern hemisphere distribution raises interesting zoogeographical questions, which are discussed in this study.

Tasmania is the ideal base for a study of these taxa, being the centre of diversity of Conoesucidae and Helicophidae in Australia, and with many calocids recorded. Due to the constraints of time, several undescribed species (and possibly genera) known from the Australian mainland and referred to this group of families (pers. obs.) were omitted from the study. However, this study of the majority of presently known species (i.e. the Tasmanian ones) will provide a framework for classification of additional taxa.

The approach.

The emphasis of this study is on immatures (larvae and pupae), as they are considered the best source of new data for resolution of existing problems. Previous work on the families in Australia has been restricted to adults (e.g. Neboiss 1977), with the exception of descriptions of larvae of two species by Neboiss (1979) and Drecktrah (1984). Therefore, adults are considered to be relatively well known and likely to provide little new information. The value of larvae in systematic study of Trichoptera has been demonstrated by Wiggins (1981), who gives examples of systematic problems where immature stages have provided information critical in

Table 1.1. Species currently assigned to families Conoesucidae, Helicophidae, Calocidae and Antipodoeciidae, and other sericostomatoid taxa included in phylogenetic analysis (ch. 6).

1= immatures described in this study

2= included in phylogenetic analysis

TA=Tasmania; AUse=south eastern Australia; AUne=north eastern Australia; AU= Australia not incl. Tasmania; NZ=New Zealand; SAm=South America.

	SPECIES	AUTHOR	DISTRIBUTION
	Conoesucidae		
1,2	*Conoesucus adiastolus* sp.n.	this study	TA
1,2	*C. brontensis*	Neboiss,1977	"
1,2	*C. digitiferus*	Jacquemart,1965	"
1,2	*C. fromus*	Mosely,1936	"
1,2	*C. nepotulus*	Neboiss,1977	"
1,2	*C. norelus*	Mosely,1953	"
1,2	*C. notialis* sp. n.	this study	"
	C. semiauratus	Mosely,1953	AUse
1,2	*Costora delora*	Mosely,1953	TA, AUse
1,2	*C. ebenina*	Neboiss,1977	"
1,2	*C. krene*	Neboiss,1977	TA
1,2	*C. luxata*	Neboiss,1977	"
1,2	*C. ramosa*	Jacquemart,1965	"
1,2	*C. rotosca*	Mosely,1953	"
1,2	*C. seposita*	Neboiss,1977	"
	C. iena	Mosely,1936	"
1,2	*Lingora aurata*	Mosely,1936	"
	L. vesca	Neboiss,1977	"
	L. coomata	Mosely,1953	AUse
	L. plicata	Banks,1939	"
1,2	*Matasia satana*	Mosely,1936	TA
1,2	*Hampa patona*	Mosely,1953	TA, AUse
	Coenoria boera	Mosely,1953	AUne, AUse
	Pycnocentrodes aureola	(McLachlan,1868)	NZ
	P. modesta(?)syn. of *aureola*?	Cowley,1976	NZ
2	*P. aeris*	Wise,1958	"
2	*Confluens hamiltoni*	(Tillyard,1924)	"
	C. olingoides	(Tillyard,1924)	"
2	*Beraeoptera roria*	Mosely,1953	"
2	*Pycnocentria evecta*	McLachlan,1868	"
	P. forcipata	Mosely,1953	"
2	*P. sylvestris*	McFarlane,1973	"
2	*P. funerea*	McLachlan,1866	"
	P. hawdonia	McFarlane,1956	"
2	*Conuxia gunni*	(McFarlane,1956)	"
2	*Periwinkla childi*	McFarlane,1973	"
2	*Olinga feredayi*	(McLachlan,1868)	"
2	*O. jeanae*	McFarlane,1966	"
	O. fumosa(?)syn. of *feredayi*?	Wise,1958	"
	Helicophidae		
1,2	*Alloecella grisea*	Banks,1939	TA, AU se

cont.......

1,2	*A. longispina*	Jacquemart,1965	TA
1,2	*A. pilosa*	Neboiss,1977	"
	Helicopha astia	Mosely,1953	"
	H. delamarei	Jacquemart,1965	"
	H. hortena	Mosely,1953	"
2	*Zelolessica cheira*	McFarlane,1956	NZ
	Z. meizon	McFarlane,1981	"
2	*Alloecentrella magnicornis*	Wise,1958	"
	Alloecentrellodes obliquus	Flint,1979	SAm
	A. elongatus	Flint,1979	"
2	*Austocentrus griseus*	Schmid,1964	"
	Microthremma caudatum	Flint,1969	"
	M. crassifimbriata	Schmid,1955	"
	M. griseum	Schmid,1957	"
	M. villosum	Schmid,1957	"
	M. bipartitum	Flint,1979	"
	Eosericostoma aequispina	Schmid,1955	"
2	*E. inaequispina*	Schmid,1955	"
	Pseudosericostoma simplississimum	Schmid,1957	"

Calocidae

	Caloca straminea	Mosely,1953	AU
	C. ascita	Neboiss,1977	TA
	C. tertia	Mosely,1953	"
	C. fallia	Mosely,1953	AUse
2	*C. saneva*	(Mosely,1953)	TA
	C. eba	Mosely,1953	AUse
1,2	*Tamasia variegata*	Mosely,1936	TA, AUse
	T. acuta	Neboiss,1984	AUse
	T. furcilla	Neboiss,1984	"
	Calocoides aquilona	Neboiss,1984	AUne
	Pliocaloca mucronata	Neboiss,1984	"
	P. dasodes	Neboiss,1984	"
	P. fastigiata	Neboiss,1984	"
1,2	*Caenota plicata*	Mosely,1953	TA, AUse
	C. simulans	Mosely,1953	AUne
	C. nemorosa	Neboiss,1984	"
	C. monteithi	Neboiss,1984	"
	C. galeata	Neboiss,1984	"
2	*Pycnocentrella eruensis*	Mosely,1953	NZ

Sericostomatidae

2	*Parasericostoma laterale*	Schmid,1964	SAm
2	*P. cristatum*	Flint,1983	"
2	*Notidobiella chacayana*	Schmid,1957	"
2	*N.* sp.		"
	Myotrichia murina	Schmid,1955	"

Anomalopsychidae

2	*Anomalopsyche minuta*	(Schmid,1957)	SAm

Antipodoeciidae

2	*Antipodoecia turneri*	Mosely,1934	AUse, TA?

References: Neboiss (1977, 1983, 1986)
         Flint (1974, 1979, 1983, pers. comm.)

Figure 1.1. Phylogeny of Trichoptera proposed by Ross (1967).

Figure 1.2. Phylogeny of Trichoptera proposed by Schmid (1980).

Family

Suborder | Infraorder | Superfamily

Order — Trichoptera

Annulipalpia

Curvipalpia
- Hydropsychoidea
  - Ecnomidae
  - Hydropsychidae
  - Polycentropodidae
  - Dipseudopsidae
  - Psychomyiidae
  - Xiphocentronidae
- Philopotamoidea
  - Philopotamidae
  - Stenopsychidae

Spicipalpia
- Hydroptiloidea
  - Glossosomatidae
  - Hydroptilidae
- Rhyacophiloidea
  - Hydrobiosidae
  - Rhyacophilidae

Integripalpia

Plenitentoria
- Limnephiloidea
  - Goeridae
  - Limnephilidae
  - Oeconesidae
  - Thremmatidae
  - Uenoidae
  - Brachycentridae
  - Lepidostomatidae
- Phryganeoidea
  - Phryganeidae
  - Phryganopsychidae

Brevitentoria
- Leptoceroidea
  - Atriplectididae
  - Odontoceridae
  - Philorheithridae
  - Plectrotarsidae
  - Limnocentropodidae
  - Calamoceratidae
  - Leptoceridae
  - Molannidae
  - Tasimiidae
- Sericostomatoidea
  - Anomalopsychidae
  - Beraeidae
  - Calocidae
  - Chathamiidae
  - Conoesucidae
  - Helicophidae
  - Helicopsychidae
  - Sericostomatidae
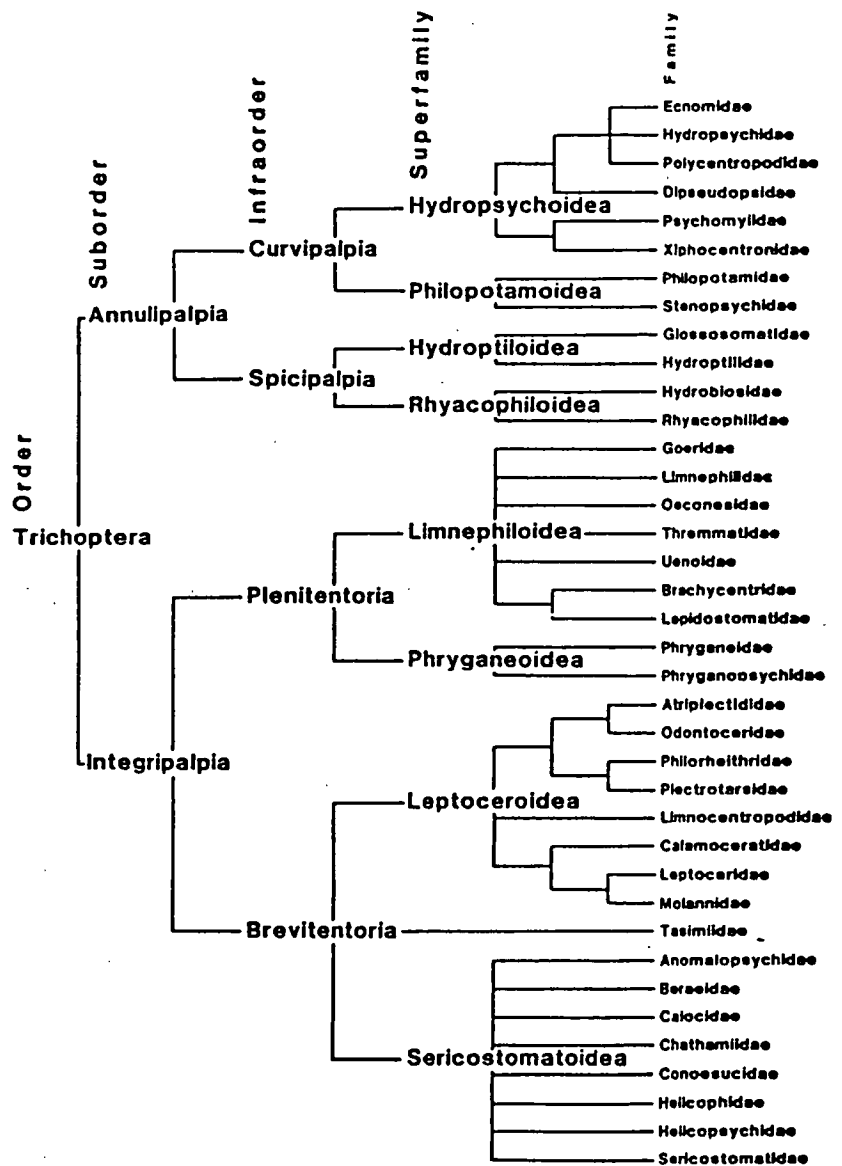
Figure 1.3. Phylogeny of Trichoptera proposed by Weaver & Morse (1986), modified from that of Weaver (1983).

revealing relationships. Inclusion of immatures in the systematic database can provide insights into ecological factors influencing evolution, and diagnosis of larvae enables information on larval behaviour (e.g. case making) and habitat to be used in systematics.

Thus in the present study, immatures provide an independent source of data with which to test the existing classification, which is based on adults. In a sound classification larval data will corroborate data from adults.

Characteristics of immatures are important in the delineation of the order, and in its phylogeny: larval characters constitute 8 of 11 autapomorphies of the order listed by Weaver (1984), and Ross (1967) deduced that much of the phylogenetic development of Trichoptera is reflected in the mode of life and morphology of larvae.

The initial step of surveying and delimiting species requires definition of a species concept, to provide a theoretical basis for practical work. Species concepts have been the subject of much debate (e.g. Ghiselin 1975, Paterson 1981, Coyne *et al.* 1988, Hengeveld 1988, Chandler & Gromko 1989, Masters & Spencer 1989, Nixon & Wheeler 1990, de Queiroz & Donoghue 1990b, Wheeler & Nixon 1990). Scudder (1974) concludes that there is no single species definition which is universally acceptable or applicable, and rather than searching for more definitions, it is preferable to recognise different sorts of species in relation to different inherent characteristics and different mechanisms of evolution.

Explicitly stated concepts include the biological species concept of Mayr (1963): "a group of actually or potentially interbreeding natural populations reproductively isolated from other such groups", and the evolutionary species concept of Simpson (1961), modified by Wiley (1978): "a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate".

More recently, "phylogenetic" species have been defined as "the smallest detected samples of self-perpetuating organisms that have unique sets of characters" (Nelson & Platnick 1981, p.12), or "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)" (Nixon & Wheeler 1990). Nixon & Wheeler (1990) claim that their definition eliminates dependence of the species concept on processes (including reproductive isolation), by definition on the basis of pattern (character state distribution). However, the concept of a "population" in this context implies processes of interbreeding; other phylogentic species concepts use the term "cluster" or "sample" instead.

The definition chosen as most appropriate will depend on the purpose of the study, e.g. the concept adopted in a biogeographical study will influence perception of how species originate (Wiley 1981). A phylogenetic concept may be appropriate when the goal is to identify the "smallest lineages identifiable by cladistic methods" (Nixon & Wheeler 1990), and the biological species concept may be applied in cases where it is possible to obtain direct evidence of reproductive isolation.

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The most applicable concept for this study is the evolutionary concept, which views species as biological entities (and thus allows biological interpretation of the pattern observed), and includes the biological concept but has advantages over it in dealing with hybridisation and the problem that there is likely to be no direct evidence of reproductive isolation. Although different species concepts may lead to different interpretation of the processes resulting in the observed pattern, any of these concepts will have the same practical application: that species are delimited by demonstrating discontinuities in ranges of variation in the organisms.

Many types of characters can provide evidence of species boundaries. In this study, morphological examination and description of immatures is essential for initial identification of taxa, and will provide a basis for more detailed work. Additional character sets derived from chromosome study, allozyme electrophoresis and morphometric analysis will test and enable refinement of the initial framework. These methods have not previously been applied to trichopteran systematics, although they are commonly used with other insects, so this study will investigate their value in studies of Trichoptera.

Karyological data (i.e. structural characteristics of the chromosome set including number, size, shape, chiasmata, sex chromosome characteristics) are important in any systematic study, as evolution is basically a cytogenetic process (White 1973). Karyological information, like other types of genetic information such as allozyme patterns, constitutes a data set additional to, and is assumed independent of, the morphological character set. Such data can be applied to problems at two levels: for confirming species designations (e.g. Halliday 1981), and for elucidating phylogenetic relationships. Although karyological data are available for some other Trichoptera, they are scattered, and have not been used systematically. The karyology of the families under study has not previously been investigated

Allozyme electrophoresis and morphometric analysis will be used to help resolve problems of species delimitation which remain after morphological and karyological study.

Gel electrophoresis of proteins is the most widely used molecular technique in insect systematics, and has proved useful for species discrimination, species identification, and hierarchical classification (Berlocher 1984). Allozymes are different forms of an enzyme produced by different alleles at a single locus (Lincoln *et al.* 1982), which can be separated by their different mobility in an electric field. Allozyme electrophoresis can provide information useful for delimiting species (Avise 1974), particularly for taxa which cannot be distinguished easily by other means, as it has been shown that different but closely related species typically show fixed differences at least for some loci (Ayala 1975), and that the level of genetic divergence between species is much greater than between conspecific populations (e.g. Avise 1974, Gorman & Renzi 1979, Ward 1980b). There are no data available on interspecific patterns of variation in Trichoptera for comparison with this study, as the only published study of electrophoresis of Trichoptera (Ingold *et al.* 1988) examines the variation within each of four species and makes no interspecific comparisons.

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In insects in particular, taxa may not be clearly identifiable on morphological grounds (Berlocher 1979), and the use of biochemical techniques has enabled confident discrimination between sibling species (e.g. Ayala 1975, Ward 1980a, b).

The advantages of allozyme electrophoresis are that it results in quantifiable, independent characters, a measurable proportion of the genome is sampled (whereas the genetic basis of morphological characters is rarely known), and it is practically simple and relatively cheap. Despite these advantages, the electromorphs detected may not necessarily represent single alleles (e.g. Singh *et al.* 1976). Also, only differences are shown, not similarities, as only those amino acid differences which result in different mobility can be detected, and the degeneracy of the genetic code means that there is more than one code for most amino acids (Stryer 1981). Ferguson (1980) estimates that only about 30% of amino acid substitutions can be detected. Another disadvantage is that the technique is not applicable to preserved specimens.

Morphometrics, the quantitative description, analysis and interpretation of shape and shape variation (Rohlf 1990), enables the description and comparison of shape and structure which is needed in any systematic study based on morphology. In this study, quantitative analysis of patterns of variation is applied in cases where suspected diagnostic characters are variable.

Subsequent to the establishment of a sound taxonomy, the objective of a systematic study is to discover the phylogenetic (genealogical) relationships of taxa. There has been no previous cladistic analysis to demonstrate monophyly of the taxa studied; this analysis aims to determine, on the basis of evidence from immatures, whether established generic and family taxa are monophyletic. The phylogenetic relationships found will be compared with those implicit in the present classification.

Phylogenetic analyses are undertaken using the cladistic approach, following the principles of Hennig's (1966) phylogenetic systematics. Groups of taxa can be shown to be monophyletic (i.e. to include the ancestor and all of its descendants) by demonstrating that component taxa share derived character states (synapomorphies) unique to the group. The few cladistic analyses of Trichoptera below family level (e.g. Parker & Wiggins 1985, Vineyard & Wiggins 1988, Wells 1987) have shown the value of this approach for elucidating interspecific and intergeneric relationships in the order.

The present study, then, reexamines the taxonomy and phylogeny of the families Conoesucidae, Calocidae, Helicophidae and Antipodoeciidae, using new types of data, and with emphasis on study of the immatures.

1.1.2 Taxonomic history of genera included in the group Conoesucidae, Calocidae, Helicophidae, Antipodoeciidae.

Originally, most of the taxa in these families were placed in the Sericostomatidae Stephens, but since establishment of the Sericostomatidae by Stephens in 1836, it has been the repository for genera of case-makers (Integripalpia) that fitted into no other families. McLachlan (1876) referred to it as the "curiosity shop" family of Trichoptera (Ross 1978). Many taxa have now been removed from the Sericostomatidae on the basis of larval and adult characters (Ross 1967, 1978; Neboiss 1977). Table 1.2 summarises the development of the existing classification. It should be noted that larval characters have rarely been used in this development, due to lack of knowledge about them.

Conoesucidae.

Ross (1967) split the Sericostomatidae into the subfamilies Sericostomatinae and Conoesucinae, on the basis of the atrophied scutal warts of the conoesucines compared with possession of small scutal warts of the sericostomatines, although he suggested that knowledge of the larvae of Conoesucinae might reveal that the subfamilies are only distantly related. He described the Conoesucinae distribution as Australasian, but did not name the genera to be included. On the basis of the subfamily name, Neboiss (1977) nominated *Conoesucus* Mosely as the type genus.

Neboiss (1977) raised Conoesucinae to family status, after analysis of the Australian sericostomatid genera (*sensu* Mosely & Kimmins (1953)), which lack mesoscutal warts, revealed other important differences from typical sericostomatids. Malicky (1973, cited by Neboiss 1977) gave absence of mesoscutal warts as the only distinguishing character of the Conoesucinae, and indicated that the distribution included Asia and Africa, but did not name any genera additional to *Conoesucus*. Cowley (1975), on the basis of his study of larvae of New Zealand Trichoptera, concluded that "[t]he differences between these two subfamilies [Sericostomatinae and Conoesucinae] in younger stages appear to be sufficient enough to separate them into diferent families. The adults on the other hand are very similar to each other." He found that conoesucine larvae were distinct in having the metanotum with reduced setation and sclerotization, and anal hooks with a single accessory claw.

Genera included in the Conoesucidae by Neboiss (1977) were *Coenoria* Mosely, *Matasia* Mosely, *Hampa* Mosely, *Costora* Mosely, *Lingora* Mosely, and *Conoesucus* Mosely from Australia; and the New Zealand genera *Pycnocentria* McLachlan, *Olinga* McLachlan and *Conuxia* McFarlane, leaving New Zealand genera *Beraeoptera* Mosely, *Pycnocentrodes* Tillyard and *Confluens* Wise in the Sericostomatidae. However, Neboiss considered that a revision of the entire group was needed to establish the genera to be included. *Periwinklia* was described by McFarlane (1973) in the Sericostomatidae but is not mentioned by Neboiss (1977). Neboiss based the separation of Conoesucidae from Sericostomatidae on adult characters: absence of transverse line on sternite 5 in males; absence of mesoscutal warts; absence of hyaline area along cross vein closing discoidal cell; A_1 ending some

Table 1.2. Summary of the development of the existing classification,
and character states on which changes were based.

Author	Taxonomic change	Characters
Ross (1967)	CONOESUCIDAE: -Sericostomatidae split into subfamilies Sericostomatinae and Conoesucinae	atrophied scutal warts of Conoesucinae
Neboiss (1977)	-Conoesucinae raised to family	absence of transverse line on sternite 5 in males absence of mesoscutal warts absence of hyaline line along cross vein closing dc A1 ending some distance basad from arculus
Cowley (1978)	"	larval metanotum with reduced setation and pigmentation larval anal claw with single accessory hook pupal hookplates on segment 3-6, spinose knobs on sgt 2
Ross (1967)	CALOCIDAE: -Calocidae erected	no diagnosis; tibial spurs 2:2:4
	-Pycnocentrella removed from Beraeidae to form new family	anterior tentorial arms sinuate and spreading anteriorly 2 pairs of pronotal warts
Neboiss (1977)	-Pycnocentrellidae synonymised with Calocidae	sinuate tentorial arms modified male maxillary palps wing venation, hyaline areas similar head and scutal warts similar
	-sericostomatid genera added to Calocidae	as above
Mosely & Kimmins (1953)	HELICOPHIDAE: -Helicophidae erected	ocelli absent maxillary palps 5 segmented wing venation

cont........

Neboiss (1977)	-Alloecella from Beraeidae to Helicophidae	scutellum shorter and more angular
		no mesoscutal warts
		head and pronotal scars
		wing hyaline area position
Cowley (1978)	-Alloecentrella from Calocidae to Helicophidae	pronotum single pair of warts
		male wing venation
		mesoscutellum short
		mesoscutum no warts
		larval case with ventral posterior aperture
		anal claw hooks helicophid-like
		pupal mandibles and hookplates helicophid-like
	ANTIPODOECIIDAE:	
Ross (1967)	-Antipodoecia removed from Sericostomatidae to form new family	3 segmented male maxillary palp
		single pair of pronotal warts
		corporotentorium bridging occipital opening above
Riek (1970)	-Antipodoecia from Sericostomatidae to Beraeidae	adult "leg structure"
Neboiss (1986, 1988)	-considers Antipodoeciidae valid	

distance basad from arculus. Cowley (1978), however, after detailed study of larvae and pupae, concluded that all the New Zealand "sericostomatid" genera were conoesucines.

Conoesucidae are widespread in New Zealand, eastern Australia and Tasmania, with the greatest Australian diversity in Tasmania; the family includes 13 genera and more than 30 species, of which 6 genera and 21 species are recorded from Australia (Neboiss 1988).

Calocidae.

The family Calocidae was erected to include sericostomatid elements by Ross (1967). He gave no diagnosis or indication of genera to be included, stating only that calocids were "little changed from ancestor 15", in which the tibial "spur count dropped to 2:2:4". Concurrently, Ross removed the New Zealand genus *Pycnocentrella* Mosely from the Beraeidae to a new family Pycnocentrellidae, diagnosed on the anterior tentorial arms sinuate and spreading anteriorly, and two pairs of pronotal warts, compared with the Sericostomatidae in which pronotal warts are fused into a collarlike band.

In addition to the presumed type genus *Caloca* Mosely (originally described in the Odontoceridae), Neboiss (1977) included the sericostomatid genera *Caenota* Mosely and *Tamasia* Mosely, and synonymised *Tismana* Mosely with *Caloca*. He found that *Caenota* shares with *Caloca* characters of wing venation, hyaline areas, and head and scutal warts. *Tamasia* also shows close similarities to *Caloca*, but in the structure of tentorial arms and male maxillary palps resembles *Pycnocentrella*. Neboiss (1977) considered differences between *Pycnocentrella* and *Tamasia* to be insufficient for separation at the family level, and he therefore synonymised Pycnocentrellidae with Calocidae.

Recently described genera *Calocoides* and *Pliocaloca* (Neboiss 1984) brings the total of genera in Calocidae to 6, with 19 species from Australia and New Zealand, and 5 genera and 18 species from Australia.

The New Zealand genus *Alloecentrella* Wise, originally described in Beraeidae, is included by Neboiss (1986, 1988) in the Calocidae, however Cowley (1978) gives the following larval, pupal and adult characters to support its placement in Helicophidae: male wing venation; pronotal and other warts; larval case; larval anal hooks and notal plates; pupal mandibles and hookplates.

With this placement of *Alloecentrella* in the Helicophidae, the Calocidae are restricted to Australia and New Zealand. However, Flint (1979) considers that the Chilean genus *Alloecentrellodes* Flint belongs in the same taxon as *Alloecentrella*, so inclusion of *Alloecentrella* in Calocidae would extend the family's distribution to South America.

Helicophidae.

This family was erected by Mosely & Kimmins (1953), including the genus *Helicopha* Mosely. The genus *Alloecella* Banks, originally in Molannidae, then transferred to Beraeidae by Mosely & Kimmins (1953), was placed in the Helicophidae by Neboiss (1977) on the basis of thoracic structure, head and pronotal

7

scars, and wing hyaline areas. The family also includes New Zealand genera *Zelolessica* McFarlane and *Alloecentrella* Wise (Cowley 1978, Winterbourn & Gregson 1981).

Flint (1979, 1983, pers. comm.) has established the presence of the Helicophidae in the New World by placing five Chilean genera in the family: *Alloecentrelloides* Flint, *Austrocentrus* Schmid, *Microthremma* Schmid, *Eosericostoma* Schmid, and *Pseudosericostoma* Schmid. The last four genera were previously included in the Sericostomatidae (Flint 1974). Their removal to Helicophidae was based on adult characters, recognising the close relationship to the Beraeidae, therefore the relationship between the Beraeidae and Helicophidae may have to be reassessed when data on immature stages is available (Flint 1979).

Thus, Helicophidae occur in Australia, New Zealand and South America, with a total of 9 genera and at least 15 species, of which 2 genera and 6 species are described from Australia. Neboiss (1986, 1988) includes *Alloecentrella* in the Calocidae (not considered correct in this thesis, see Calocidae), and does not mention the Chilean records.

Antipodoeciidae.

Antipodoeciidae was proposed as a family by Ross (1967) to include the monospecific genus *Antipodoecia* Mosely, thus removing it from Sericostomatidae. Riek (1970) ignored this arrangement and transferred *Antipodoecia* from Sericostomatidae to Beraeidae "on the basis of its leg structure", where it was retained by Ross (1978). Beraeidae also previously included *Alloecella* (now in the Helicophidae (Neboiss 1977)) and *Pycnocentrella* (now in the Calocidae (Neboiss 1977)). However, Antipodoeciidae is presently considered a family by Neboiss (1986,1988), still including only *Antipodoecia*.

Antipodoecia has been recorded from SE Qld, NSW and Vic. (Neboiss 1988); antipodoeciid-like larvae were collected during this study from SW Tasmania, but no adults were obtained to confirm their identity. Lack of larval material limited the study of Antipodoeciidae to its inclusion in phylogenetic analysis (ch. 6).

1.2 GENERAL METHODS

Specimen collection

Larvae and pupae were collected by hand picking them from various substrates (rocks, wood, aquatic plants) or by sieving of loose substrate. Samples of moss, plants and leaf litter were taken for later sorting. Specimens required for rearing were transported alive on ice; others were preserved in 70% ethanol.

Adults were collected from riparian vegetation with a sweep net during the day; at night adults were collected from a sheet hung behind a mercury vapour lamp, or in automatic UV light traps. They were either preserved immediately in 70% ethanol, or kept on ice if required alive (e.g.for electrophoresis). A small number of specimens were preserved dry to retain wing colouring.

Live adults were anaesthetized with CO_2 for sorting.

Association of larvae with adults

Rearing was the most commonly used method of association of different life stages. Larvae or pupae were reared to adults in small plastic "take-away" food containers (15x10x5cm), with a few centimetres of tap or stream water aerated by compressed air through a pipette, at 10-15 °C. Stones, sand, leaves, wood and/or algae were provided as food and case material, and pupation sites. Transparent perforated lids prevented escape of emerged adults.

Another method for association was the use of metamorphotypes, i.e. pupae with developed genitalia. In all the families studied, larval sclerites are retained within the pupal case, enabling association of larva with adult.

Curation

Specimens preserved in fluid were stored with labels in small glass push-capped vials in large screw-topped jars, to prevent evaporation.

A computer database of specimens, life stage, habitat, collection site, date and collector was maintained using Microsoft File, which enabled searching and sorting of records.

CHAPTER 2. KARYOLOGY

2.1 INTRODUCTION

This study was undertaken to obtain data on the karyotype for each of the previously designated species of Conoesucidae, Calocidae, Helicophidae and Antipodoeciidae, with the aim of determining the following.

a) Which, if any, karyotypic features are taxonomically diagnostic and at which taxonomic level, i.e does karyotypic data support species designations made on a morphological basis, or generic or family delimitations, specifically with respect to the separation of the four families from each other and from the Sericostomatidae; and the generic status of *Lingora*, *Hampa* and *Matasia*?;

b) Whether species in this group conform with the general karyotypic characteristics of the Trichoptera, which are:

-holocentric chromosomes ("chromosomes which do not seem to show any localized or individualized centromeres" White (1973, p 14)) (Suomalainen 1966);

-heterogametic females (females XO, males XX) (Suomalainen 1966);

-achiasmatic oogenesis (Suomalainen 1966, White 1973)

-small size, of lengths less than about 5 μ (e.g. Lankhorst 1970, 1972; Kiauta & Kiauta 1979);

-numbers in the range n=6-30 (Lankhorst 1970, White 1973);

-chromatin elimination at first meiotic division in oogenesis is also a trichopteran characteristic (Suomalainen 1966) although methods to detect this were not used in the present study.

c) What phylogenetic inferences can be made about the position of taxa within the group of families, the families within the order, and in relation to other insect orders. Chromosome data have been valuable in some groups for working out phylogenetic branching sequence (e.g. in ants (Crozier 1975)), [cited in Crozier (1983)] although it cannot be used to infer the temporal dimension (Crozier 1983).

d) Developmental features, such as which tissues and life history stages show cell division.

e) Whether internal characters observed during chromosome preparation, such as gonad structure, are systematically useful.

The present study is the first to examine karyotypes of an entire group of Trichoptera. Systematic and phylogenetic conclusions from previous karyological studies of Trichoptera have been based on scant data, since studies have never examined an entire family or group. Instead, information has accumulated from studies of one or a few often unrelated species (e.g. Lankhorst 1972). The best known family is the Limnephilidae (an extremely diverse family in the cooler regions of the Palearctic and Nearctic, with about 30 genera and more than 1000 species (Neboiss 1986), but represented in Australia by only 3 species), with 20 species in 9 genera studied cytologically (Lankhorst 1970, Kiauta & Kiauta 1979). Limnephilid chromosome number ranges from 6 to 30. In total, at present only 38 species in about 12 families,

out of an estimated 10,000 species (Wiggins 1977) in 38 families (Weaver & Morse 1986), are known karyotypically.

Therefore, since the overall pattern of karyotypic variation within any family or genus is unknown, no prediction of expected variation in chromosome numbers or other characteristics can be made for the group in this study. Although in many groups each species has its own distinctive karyotype, in others, species may share apparently identical karyotypes, for example Hawaiian *Drosophila* (Crozier 1983). Thus, although it is possible that results of this study will not be taxonomically useful due to lack of variation, there are systematic problems at species, genus and family levels within the group studied, so data diagnostic at any of these levels will be valuable. The potential for obtaining data which will increase understanding of the karyology, taxonomy and phylogeny of the family group and of the order make this karyological study essential.

2.2 MATERIALS AND METHODS

Larvae and pupae for chromosome analysis were collected from large populations and maintained alive at 15 $^{\circ}$C with aeration prior to processing. Fresh material was generally used for slide preparation, but a sample of whole animals was preserved in Carnoy's fixative for later preparations if necessary (Carnoy's = 6 parts ethanol: 1 part glacial acetic acid: 3 parts chloroform (Upton & Norris 1980)). It was important to use material at the right developmental stage; information from previous seasons fieldwork enabled collection of the various species at the appropriate time. Adult tissue was not used due to the difficulty of handling live material.

Squash methods (Mahoney 1966, I.C. Murfet pers. comm.; Macgregor & Varley 1983) gave poor results; the following air drying method (after Denton 1973; Imai *et al.* 1977; Macgregor & Varley 1983; A. Wells pers.comm.) resulted in preparations with clear cell divisions. Initially, animals and/or tissue were treated with colchicine (Denton 1973), but as it had no detectable effect on the number or type of divisions, treatment was discontinued.

Various tissue types were examined:

a) larval silk glands (modified salivary glands (Richards & Davies 1978)), which could have polytene chromosomes and large many-branched nuclei as suggested by White (1973);

b) neural ganglia, which have shown good cell divisions for other insect groups (Imai *et al.* 1977; Macgregor & Varley 1983);

c) gonad tissue from both sexes, used in previous cytological studies of Trichoptera (e.g. Lankhorst 1970, 1972; Kiauta & Kiauta 1979) and of many other insects (White 1973, Macgregor & Varley1983).

Slide preparation.

1. Live animals were removed from their cases and dissected in tap water, at room temperature. Dissection took about 5 minutes from opening of the

abdomen until removal of tissue onto a slide, or sometimes up to 10 minutes if dissection was difficult. This dissection in water provided the hypotonic treatment necessary to disperse the chromosomes for clear visualization.

2. Tissue was placed onto a clean, diamond-pencil labelled microscope slide; excess water was carefully blotted away with a twist of lint-free paper tissue (to stick animal tissue to the slide to avoid washing off by addition of fixative); several drops of fixative 1 were added to the slide under a microscope to ensure that the tissue remained in place, then the slide was placed in a petri dish and flooded to the limits of surface tension with fixative 1 (Fixative 1 =3 parts ethanol: 1 part glacial acetic acid, freshly mixed on ice). This was replaced with fresh fixative 1 and left for 30 minutes.

For Carnoy's-preserved material, this fixation with Fixative 1 was omitted.

3. Fixative 1 was carefully drained off and about 15 drops of fixative 2 added, the slide rocked gently for 15-30 seconds, then drained well. (Fixative 2 = 1 ml absolute ethanol: 2 ml glacial acetic acid: 0.5 ml distilled water, freshly mixed.)

4. If necessary, another drop of fixative 2 was added to prevent drying out, then tissue was thoroughly macerated with a fine needle and gently spread to disperse clumps of cells.

5. Two-three drops of glacial acetic acid were added, left 20 seconds, then drained off by tilting the slide.

6. The preparation was air dried for at least 20 minutes.

7. The slide was stained for 15-20 minutes with 15% Giemsa (stock solution in Sorensen's buffer pH 7: 4.54g KH_2PO_4; 5.94g Na_2HPO_4; in 1 litre H_2O). Stain was washed off with gently running tap water, then slides were rinsed in distilled water and allowed to dry thoroughly; they were stored on edge in boxes lined with lint-free tissue.

Slides were scanned at 100x or 200x magnification with a Nikon Labophot or Wild M20 microscope; counts and photographs were made at 1000x (oil immersion objective). Counts of chromosomes were made from at least 5 cells from each of 4 individuals, if possible.

Cells were photographed at 1000x (oil immersion) with a Ziess Axioskop microsope on Kodak Panatomic X film (B & W, 32 ASA) using a green filter for maximum contrast, and printed on Ilfospeed grade 4 paper. Measurements of element length were made from the prints: the largest and smallest elements within each cell were measured.

2.3 RESULTS.

Good preparations were obtained from gonad tissue, particularly larval testes, from late larvae and prepupae. Pupal testes were usually very fragile and

burst when handled resulting in loss of cells, and often only nondividing cells and spermatozoa were observed in preparations from them.

Chromosomes in dividing cells from female gonads (ovarioles) were generally not as clearly visible as those from males, and usually were not countable; however, in these the unpaired X chromosome could often be distinguished. Material preserved in Carnoy's fixative stained more darkly than fresh material and preparations showed clearly visible chromosomes if cells were dividing.

No cell division was observed in neural ganglia.

Silk glands contained large, many branched nuclei but no cell divisions were observed.

Chromosomes could be counted for all 21 species from Conoesucidae, Helicophidae and Calocidae for which preparations were made. Further data could not be obtained as material was unavailable for *Hampa, Helicopha, Caloca* and Antipodoeciidae; male pupae of *Costora ramosa* and *C. krene* could not be obtained and therefore definite specific identification was not possible (larvae are morphologically indistinguishable), so identification of *C. ramosa* was made on the basis of locality. Chromosome numbers for *Alloecella* species are somewhat uncertain, as counting was difficult due to the relatively high number of small chromosomes, and failure to obtain clear preparations. Occasional variation in counts could result from possible loss of chromosomes from nuclei due to excessive hypotonic treatment (Plate 2i), or perhaps unsynchronized pairing of bivalents.

Due to the small number of mitotic metaphases, uniformity in chromosome shape, small variation in size and minute absolute length of elements (ranging from 0.9-3.7 μ), metaphase karyograms could not be prepared.

Comparisons of absolute chromosome size between species were not possible due to the variation between cells in degree of chromosome contraction; only size range data (Table 2.1) was comparable.

No centromeres were detected, *i.e.* chromosomes are holocentric; and no supernumerary chromosomes[1] observed.

No multivalents were seen.

No intraspecific geographic variation in character states was found, although since the study did not aim to examine such variation, material studied was obtained from only a few localities.

Chromosome numbers (n=haploid number), cells counted, and lengths are given in Table 2.1. Photographs of selected cells are shown in Plates 1-6.

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[1]Supernumeraries are chromosomes additional to the normal karyotype and not homologous, or only partly, to members of the regular set; they may be present in some individuals and not others; they can be involved in chromosome rearrangement processes (White 1970, 1973).

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Table 2.1. Chromosome number, mean size of the largest and smallest element per cell, and presence of chiasmata. Length in μ; Y=chiasmata observed, N=no chiasmata observed.

Species	Haploid no.	No. cells counted (no. individuals)	Mean length largest (n)	Mean length smallest (n)	Chiasmata ♂/♀
CONOESUCIDAE					
Conoesucus					
adiastolus sp. n.	25	19(4)	1.6(3)	0.8(3)	N/N
C. brontensis	25	14(3)	1.4(3)	0.7(3)	-/N
C. digitiferus	25	23(5)	1.3(5)	0.5(5)	N/N
C. fromus	25	23(5)	1.3(3)	0.5(2)	N/N
C. nepotulus	25	22(4)	0.9(1)	0.4(1)	N/N
C. norelus	25	22(4)	3.4(4)	1.3(4)	Y/N
C. notialis sp. n.	25	17(3)	1.5(4)	1.1(4)	Y?/N
Costora delora	25	23(4)	1.9(5)	1.6(5)	N/N
C. ebenina	25	23(4)	1.5(5)	0.8(4)	N/N
C. krene/C.ramosa	25	20(4)	2.2(1)	0.9(1)	-/N
C. luxata	25	20(4)	1.5(2)	0.8(2)	Y/N
C. ramosa	25	10(1)	1.4(3)	0.9(3)	N/N
C. rotosca	25	17(4)	1.8(4)	0.7(4)	N/N
C. seposita	25	12(3)	3.7(5)	2.1(5)	Y/N
Lingora aurata	25	24(5)	1.9(3)	1.3(3)	Y?/N
Matasia satana	25	24(5)	2.2(5)	1.3(2)	N/N
CALOCIDAE					
Caenota plicata	22	14(2)	2.5(3)	1.6(3)	Y/N
Tamasia variegata	22	20(4)	1.4(4)	1.3(4)	Y/N
HELICOPHIDAE					
Alloecella grisea	30; 29	12(2); 6	1.7(1)	0.9(1)	Y?/N
A. longispina	32-40	12(3)	1.3(1)	0.9(1)	Y?/N
A. pilosa	26; 27	23(5); 7	1.2(4)	0.7(4)	N/N

Plate 1.

Arrows indicate the X chromosome (univalent in females).

M I= meiotic metaphase I; M II= meiotic metaphase II.

a *Conoesucus adiastolus* sp. n. male; M I; note darker staining largest bivalent;

b *C. adiastolus* sp. n. male; M II;

c *C. adiastolus* sp. n. female; M I; note X pale, diffuse, central, univalent;

d *C. adiastolus* sp. n. female; M I; " " " " " "

e *Conoesucus brontensis* female; M I; X not paler but less condensed, central, univalent;

f *C. brontensis* female; M I; X not distinct; bivalents countable;

g *Conoesucus digitiferus* female; M I; X less condensed, not distinct as pale or univalent;

h *C. digitiferus* male; M I; largest bivalent darker stained;

i *C. digitiferus* male; " " " " "

j *C. digitiferus* male; M II.

10μ
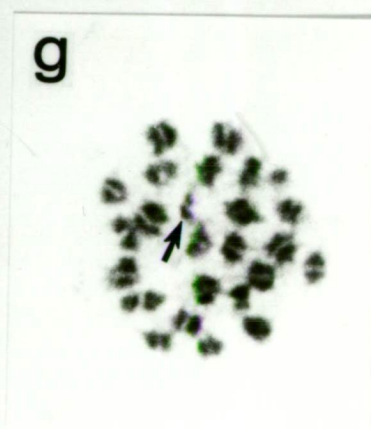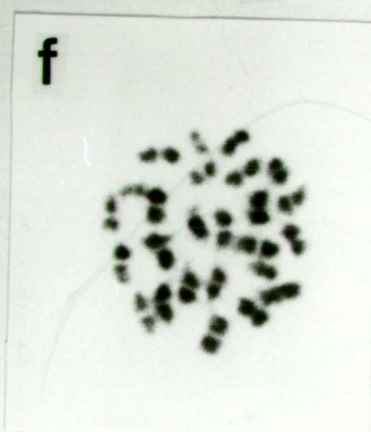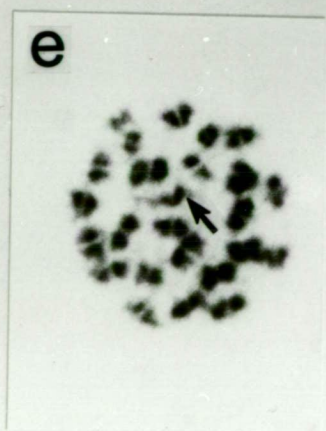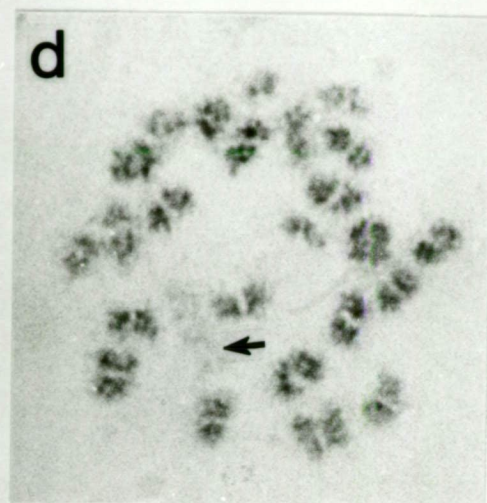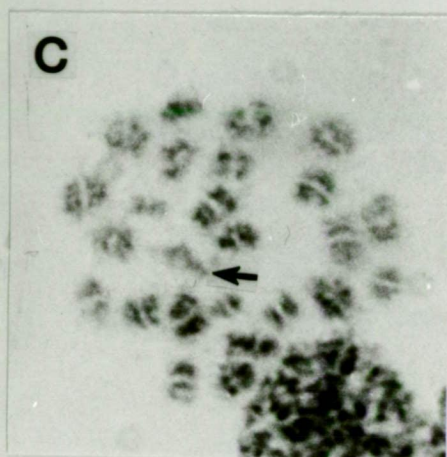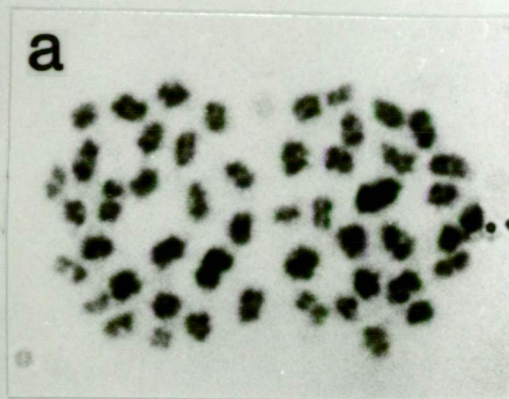
Plate 2.

a *Conoesucus fromus* female; diakinesis; X pale, less condensed, approx. central;

b *C. fromus* female; M I; X (arrowed) not heterochromatic, approx. central, univalent;

c *C. fromus* male; M I;

d *Conoesucus nepotulus* female; mitotic metaphase; 2n =50;

e *C. nepotulus* male; M I;

f *Conoesucus norelus* male; diakinesis; large number of ring bivalents;

g *C. norelus* male; Carnoy's-preserved; diakinesis, later;

h *C. norelus* male;   "   "   ; early anaphase; note chromatin threads between bivalents;

i *C. norelus* male; Carnoy's-preserved; M I well condensed; note loss of element from one nucleus (arrowed).

10 μ
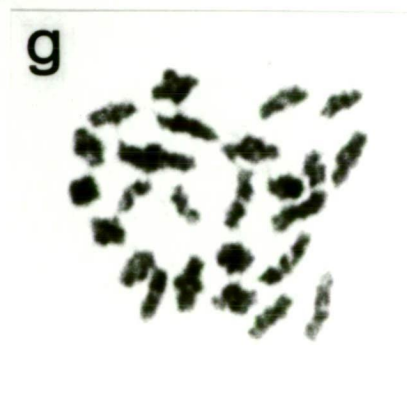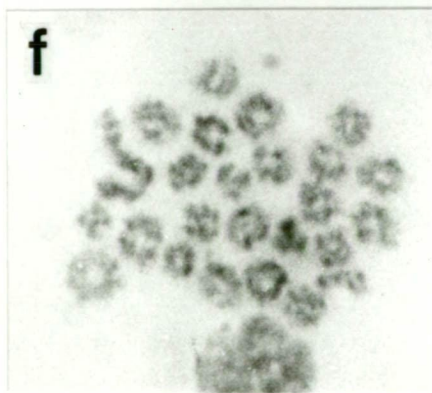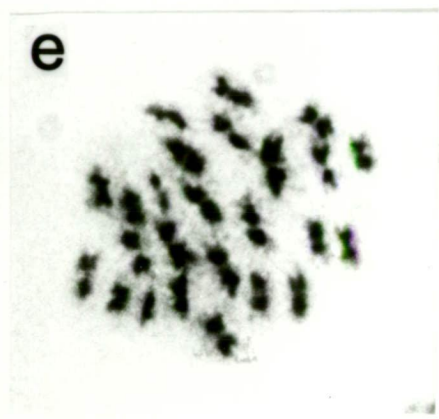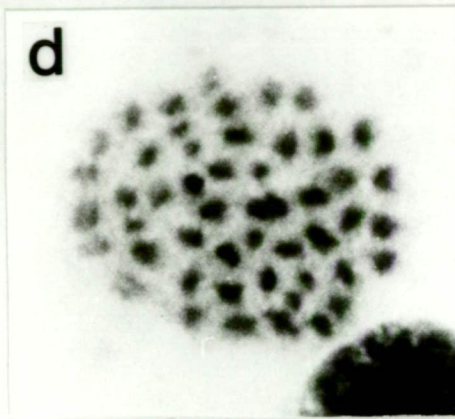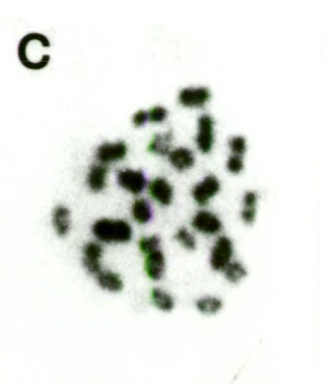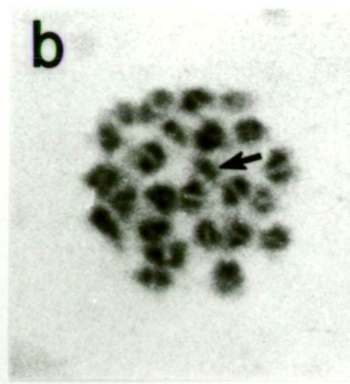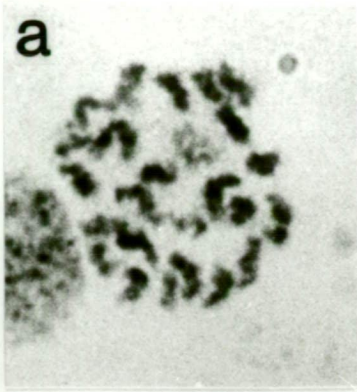
Plate 3.

a *Conoesucus notialis* sp. n.male; M I; darker staining largest bivalent;

b *C. notialis* sp. n. male; possible chiasma;

c *Costora delora* male; M I; largest bivalent darker staining;

d *C. delora* female; Diakinesis/M I; X darker, central, univalent;

e *Costora ebenina* male; M I;

f *C. ebenina* male; anaphase;

g *Costora krene/ramosa* female; M I; X not distinct;

h *Costora ramosa* male; M I; largest bivalent darker staining.

10 μ
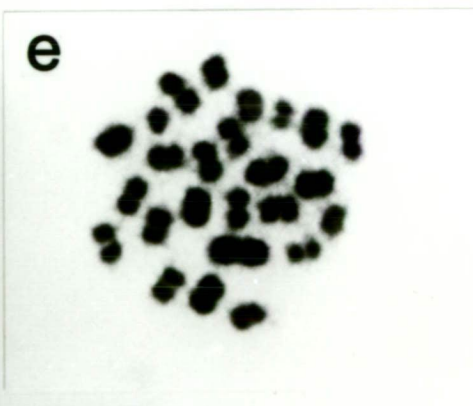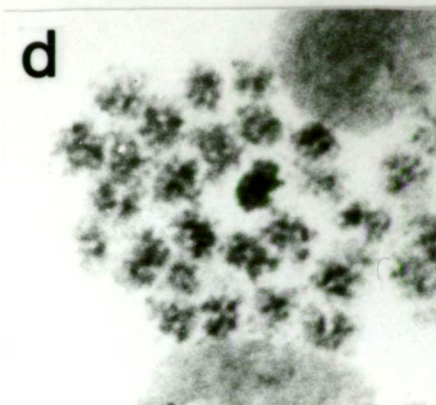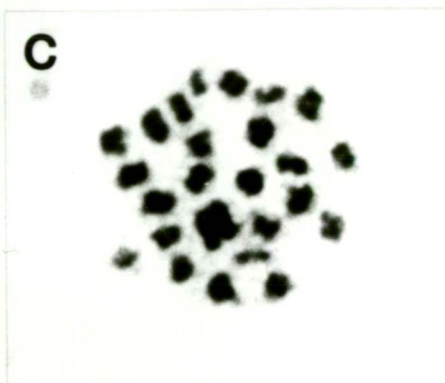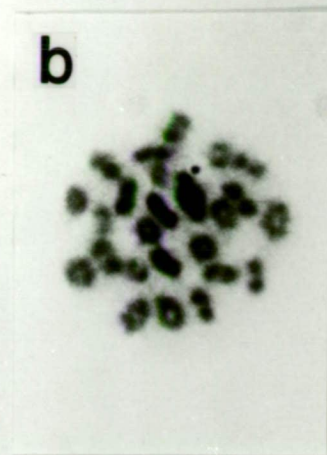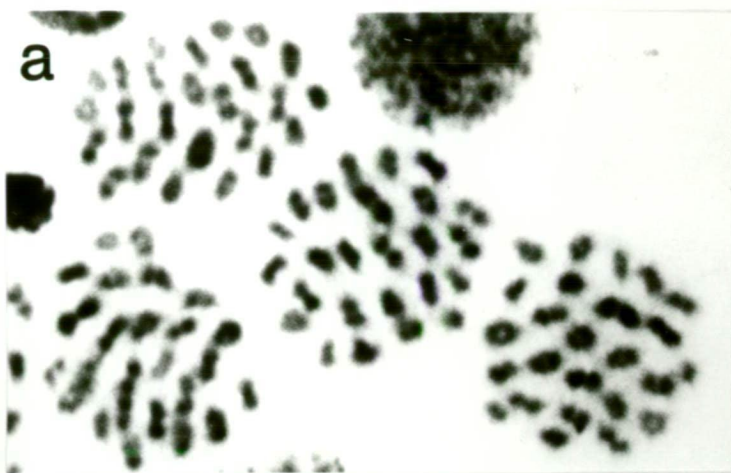
Plate 4.

a *Costora luxata* female; diakinesis/M I; X paler, less condensed, central, univalent;

b *C. luxata* male; M I; largest bivalent darker staining;

c *C. luxata* male; diakinesis; chiasma;

d *Costora seposita* male; diakinesis; ring bivalent;

e *C. seposita* male; later diakinesis;

f *Costora rotosca* male; M II; both nuclei of first meiotic division showing;

g *Lingora aurata* male; M I; largest bivalent darker staining;

h *Matasia satana* female; Carnoy's-preserved; M I; X paler, less condensed, central;

i *M. satana* male; M I; largest bivalent darker staining.

10µ
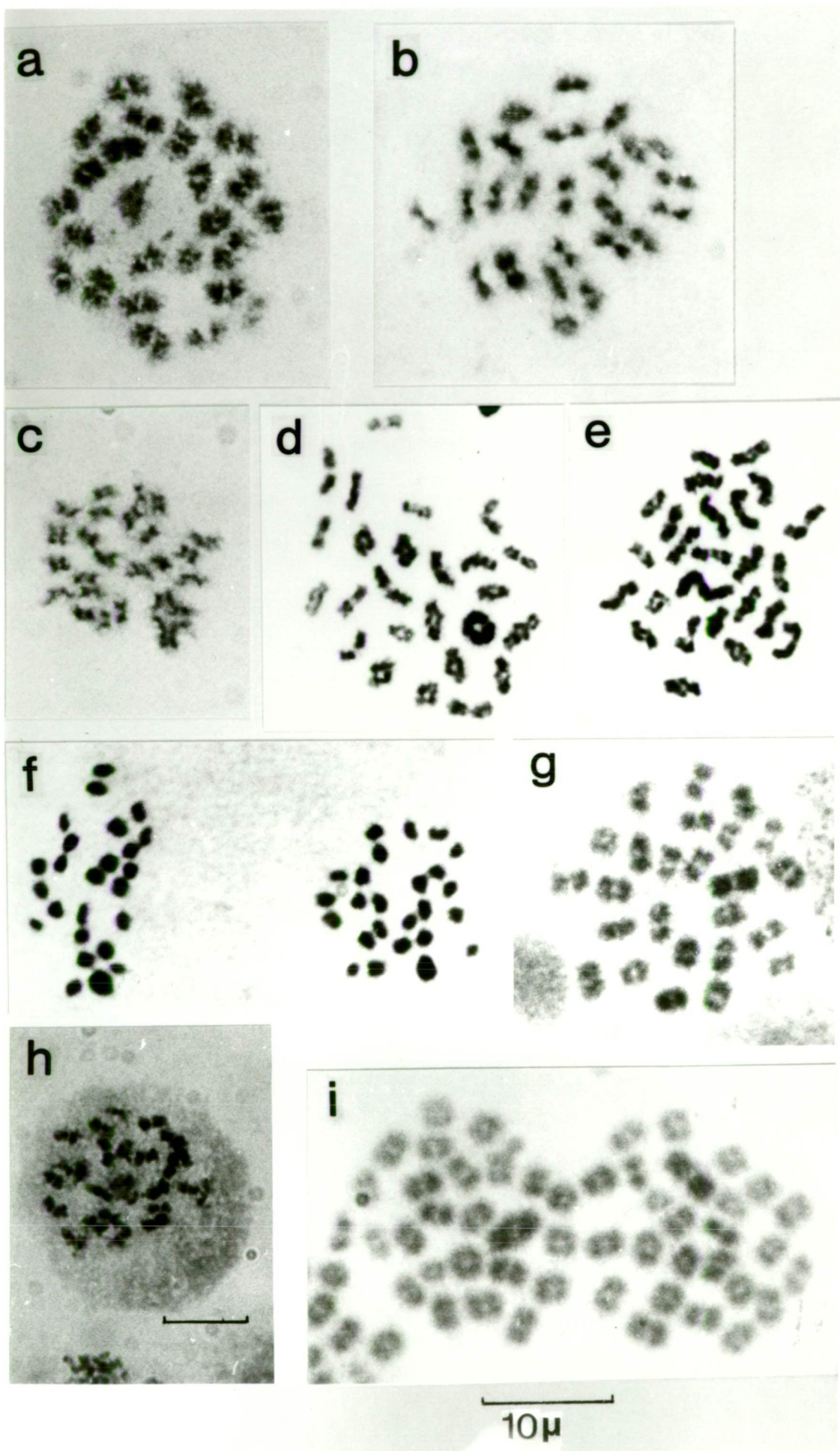
Plate 5.

a *Tamasia variegata* male; diakinesis; five chiasmata visible;

b *T. variegata* male; M I; well condensed;

c *T. variegata* male; anaphase; equatorial view;

d *Caenota plicata* male; M I; "linked" bivalents (arrowed);

e *C. plicata* male; " " "

f *C. plicata* male; diakinesis; many chiasmata; 2 elements missing;

g *C. plicata* male; M I.
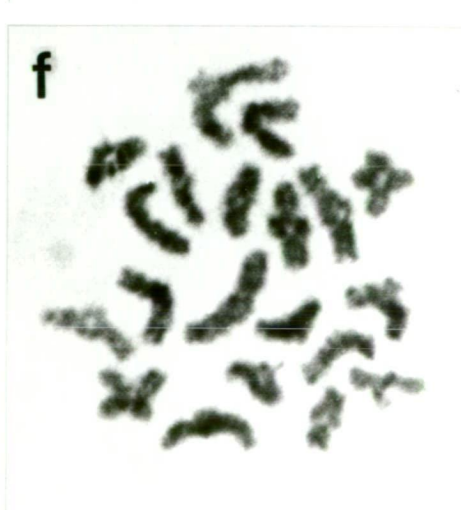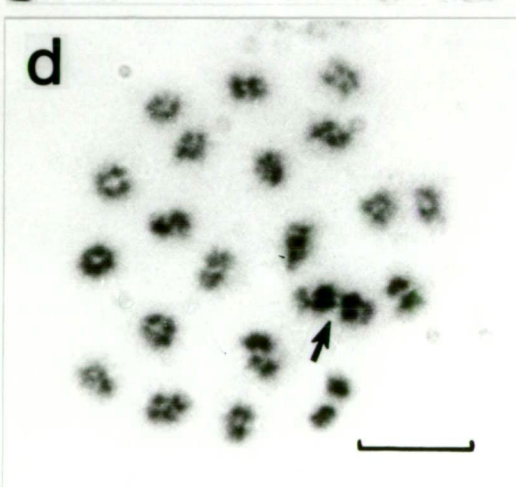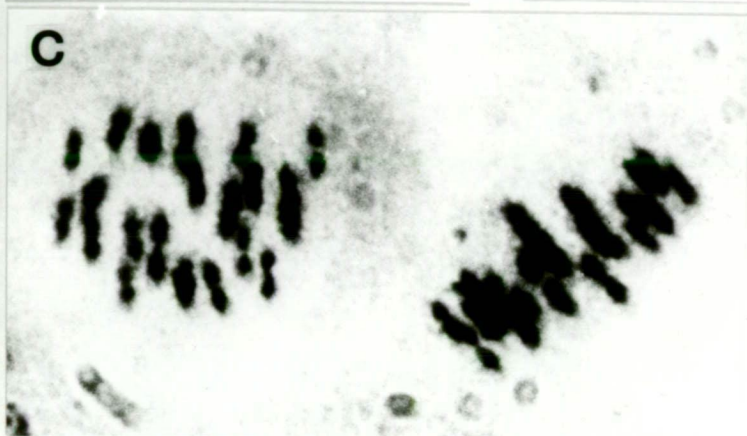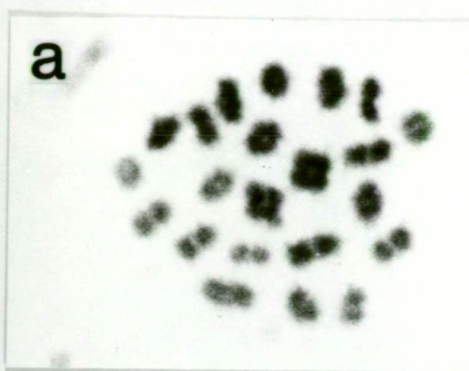
10μ

Plate 6.

a *Alloecella grisea* male; diakinesis-M I; fuzzy, possible chiasma;

b *A. grisea* male; M I; n=29?;

c *A. longispina* female; diakinesis; X pale, less condensed,central, univalent;

d *A. longispina* male; diakinesis?; possible chiasma (arrowed);

e *A. longispina* male; M I;

f *A. pilosa* male; M I; n=26;

g *A. pilosa* male; M I; showing "linkage"; n=25;

h *A. pilosa* male; M I;   "   "   ;   "

a

b

c

d

e

f

g

h

10μ
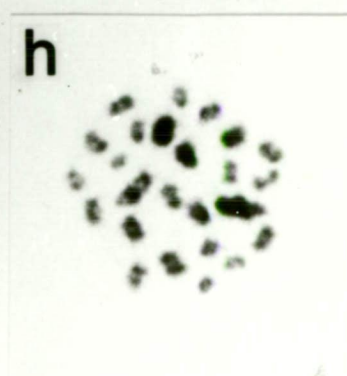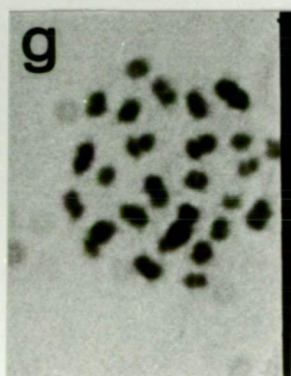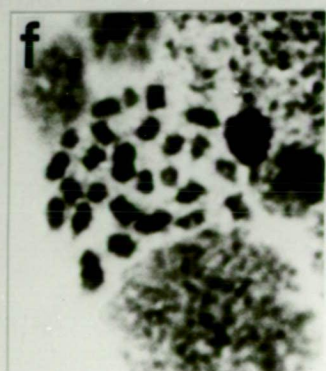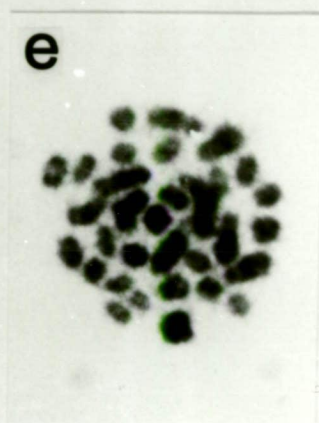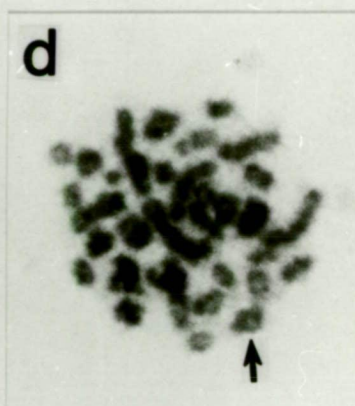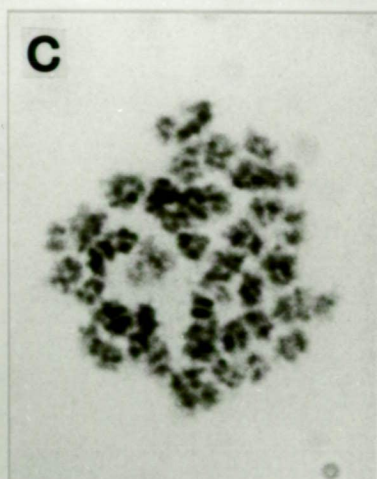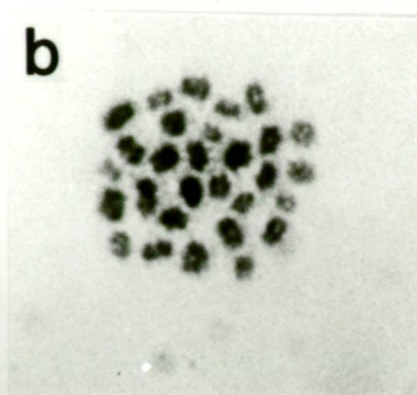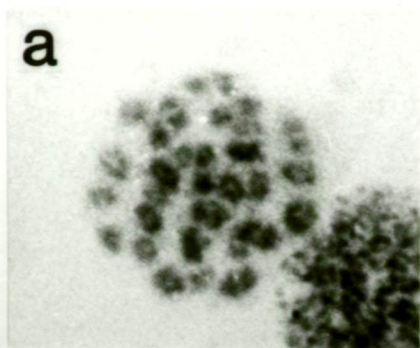
Description of the complement.

Conoesucidae. (Plates 1-4). Chromosome numbers observed were male n=25, female n=25, 24, 2n=50. Females heterogametic (XO), with X distinct at diakinesis in many species as a paler (negatively heterochromatic), little-condensed, univalent element, positioned at or near the centre of the metaphase plate and somewhat separate from the other elements. In *Conoesucus nepotulus*, *C. digitiferus*, *C. brontensis* (Plates 1g, 1e), X did not appear heterochromatic but was distinct as a univalent. In *Costora delora* (Plate 3d), X was darker than the autosomes. The X could be up to twice as long as the next largest element.

Mitotic divisions were observed rarely, and only in females of *Conoesucus nepotulus* (Plate 2d), *C. fromus*, and *Costora rotosca*. Lengths of mitotic elements ranged from 0.9-2.2μ in *C. nepotulus*. Counting of mitotic elements (2n) confirmed counts from meiotic divisions (n).

In general, the size range of elements (Table 2.1) was small and continuous i.e. there were no size classes; absolute size depended on degree of contraction, which differed between cells.

In males of all species examined (except *C. brontensis* and *Costora krene/ramosa*, for which no male divisions were obtained) the largest bivalent stained distinctly darker. Although this may be the XX sex bivalent, there is no definite evidence to confirm this.

Stages of division observed in male meiosis were pachytene, diakinesis, metaphase 1, metaphase II, and early anaphase; in females, pachytene, diakinesis, meiotic metaphase I, and mitotic metaphase. Metaphase I was by far the most common and was observed in all species.

Chiasmata were observed at diakinesis in the males of *Conoesucus norelus* (in 2-11 bivalents per nucleus, Plate 2f, g), *C. notialis*sp.n. (possibly in one bivalent, Plate 3b), *Costora luxata* (in one bivalent, Plate 4c), *C.seposita* (in 5-8 bivalents per nucleus, Plates 4d,e). Ring bivalents, indicating two terminalized crossovers (chiasmata) on one bivalent (White 1973), were observed in *Costora seposita*, and for most bivalents in *Conoesucus norelus*. Other species in which chiasmata were seen (Table 2.1) showed no more than one chiasma per bivalent. No chiasmata were seen in any female cell.

Calocidae (Plate 5a-g). Chromosome numbers were n (male) =22 (no female divisions were countable). Division stages observed in *Tamasia* males were diakinesis, metaphase I, early anaphase; and in females mitosis. In *Caenota*, stages seen were male diakinesis and metaphase I.

In *Tamasia* there were no darker staining elements, and length range was negligible. *Caenota* showed unusual pairing at metaphase I in many nuclei, with a large and small bivalent appearing linked. The length range of *Caenota* metaphase I elements was 1.6-2.5μ.

Most individuals had many nuclei with chiasmata: in *Tamasia* up to 5

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bivalents per nucleus had 1 chiasma (Plate 5a); in *Caenota* up to 16 bivalents per nucleus had 1 crossover. No chiasmata were seen in any female cell.

Helicophidae (Plate 6a-h). Definite counts were not obtained, but it can still be seen that chromosome numbers are different for each species (*A. grisea* n=29-30; *A. longispina* n= 32-40; *A. pilosa* n= 26-27), and higher than those of conoesucids and calocids; in general divisions were not very clear. Stages of division observed in males were meiotic metaphase I and II; no countable divisions were seen in females. The X chromosome was distinct in a few cells in *Alloecella longispina*, as a central, paler, less-condensed element (Plate 6c). In *A. pilosa* males the largest bivalent stained darkest (Plate 6f-h).

Chromosomes were small relative to those of Conoesucidae and Calocidae; the greatest length range of 0.9-1.7μ was in *A. grisea*.

No clear chiasmata were seen although there are possible crossovers in *A. grisea* (Plate 6a) and *A. longispina* (Plate 6d). In *A. pilosa* there is unusual arrangement, with the largest bivalent appearing to have an "extra" small element at one end (Plate 6g, h).

In addition to karyotype information, data on gonad structure was obtained during dissection. Testes lobes were clearly either round or long. In the Conoesucidae, testes of all *Conoesucus* species have 4 round lobes; *Costora* species 4 long lobes; *Matasia* and *Lingora* 2 long lobes. *Tamasia* and *Caenota* have 4 round lobes. *Alloecella* species have 4 round, relatively large, clear lobes.

2.4 DISCUSSION.

Observations on chromosomes of 21 species of sericostomatoid Trichoptera (*sensu* Weaver & Morse 1986) made in this study contribute significantly to the karyological information on the order. All the species studied are new to cytology, and the results include the most complete karyological study of any trichopteran family.

Although light microscope preparations of such small chromosomes are not really satisfactory for study of detailed structure and a method such as the ion-etching of Wenqing *et al.* (1984) would be better, the advantages of the method used in this study were its simplicity, speed and low cost. No special materials or microscopes were required, enabling many individuals to be prepared quickly, compared with 3-4 days before results of ion-etching are obtained. The type of results likely to be obtained were largely unknown, so it was considered better to begin with a simple technique; other methods such as ion-etching and banding are possibilities for future investigations.

All the characters observed are involved in the genetic system on which speciation and evolution depend. The only character found to vary in a taxonomically useful way was chromosome number. Possible differences in

chromosome size between families were apparent, but were not quantified by the measurements made. No other character was consistently definable. Most other characters observed conform with known karyological characteristics of Trichoptera (holocentric chromosomes, heterogametic females, achiasmatic oogenesis, small size), all of which relate to the population genetics and evolution of the group by affecting amount of recombination, rate of change in number, etc. These characteristics are shared with the sister order Lepidoptera (Suomalainen 1966), and comparison is valuable when considering chromosomal evolution in Trichoptera.

Numbers.

The chromosome numbers of Conoesucidae (n=25) and Calocidae n=22) are within the range previously reported for Trichoptera (Lankhorst 1970,1972, White 1973, Kiauta & Kiauta 1979) (Table 2.2). The numbers for *Alloecella longispina*(32-40), however, are the second highest so far recorded in Trichoptera, although failure to determine the precise number means that this species requires further study. Determination of numbers for *Helicopha*, for which larvae are not known, would also be informative.

The difference in number between families confirms their separation from each other, and supports separation of Conoesucidae from Sericostomatidae; however, the only sericostomatid number known is n=22 (Pchakadze 1930, cited by Kiauta 1968). The calocid number is also n=22. This variation at familial level means that chromosome data would be particularly valuable for clarification of the status of Antipodoeciidae.

Due to the lack of variation in number within the Conoesucidae, karyotypic evidence is uninformative in relation to generic delimitation within the family, particularly with respect to the present separation of genera *Hampa*, *Matasia* and *Lingora*, which morphological data (ch. 5) indicate should probably be congeneric. Nor do karyotypic data clarify problems of species designation and diagnosis, such as diagnosis of *Costora ramosa* and *Costora krene* larvae.

This lack of intrafamilial variation contrasts with karyotypic variation within the previously best known family Limnephilidae, which shows intrageneric variation in chromosome number (Table 2.2). No other group of Trichoptera has been studied completely enough to make general patterns of variation apparent, for example whether there are other families in which chromosome number is constant. It seems likely that amount of variation will vary from group to group within the order, as the rate of karyological evolution can vary erratically (Crozier 1983). In Lepidoptera, intraspecific variation in number has revealed or confirmed the separation of cryptic species (Suomalainen 1965, Suomalainen and Brown 1984), with diverse numbers in a butterfly "species" belonging to good sibling species with minor external differences.

In contrast to the conservatism in Conoesucidae, within Helicophidae

Table 2.2. Chromosome numbers recorded in Trichoptera.

Family	Genus	n	No.species	Reference
Hydropsychidae	*Hydropsyche*	15	1	Pchakadze (1930) in Lankhorst (1970).
Polycentropodidae	*Plectronemia*	13	1	"
Stenopsychidae	*Stenopsyche*	13	1	Makino & Kichijo (1934) in Lankhorst (1970).
Rhyacophilidae	*Rhyacophila*	23	3	Pchakadze (1930) in Lankhorst (1970); Lankhorst (1970); Lankhorst (1972).
Glossosomatidae	*Agapetus*	17	1	Lankhorst (1972)
Hydroptilidae	*Oxyethira*	14	2+?	Higler (1969) in Lankhorst (1970);
	Hellyethira	14	2	A. Wells pers. comm.
	Maydenoptila	14	1	"
Limnephilidae	*Anabolia*	30	1	Pchakadze (1930) in Lankhorst (1970); Klingstedt (1931) in Lankhorst (1970)
	Chaetopteryx	30	1	Pchakadze (1930) in Lankhorst (1970).
	Glyphotaelius	30	1	Kiauta & Lankhorst (1969).
	Halesus	21	1	Pchakadze (1930) in Lankhorst (1970).
	Hesperophylax	30	1	Lutman (1910) in Lankhorst (1970).
	Hydatophylax	30	1	Pchakadze (1930) in Lankhorst (1970).
	Limnephilus	6	1	Pchakadze (1930) & Higler (1969) in Lankhorst (1970)
		10	1	Soumaleinen (1966)
		13	1	Klingstedt (1928,1931) in Lankhorst (1970).
		16	1	Pchakadze (1930) in Lankhorst (1970).

cont....

Table 2.2 cont

Family	Genus	n	No. species	Reference
Limnephilidae	*Limnephilus*	29	1	Higler (1969) in Lankhorst (1970).
		30	5	Pchakadze (1930) in Lankhorst (1970).
	Potamophylax	30	2	Gresson (1933, 1935) in Lankhorst (1970); Lankhorst (1972).
	Allogamus	30	1	Kiauta & Kiauta (1979)
Goeridae	*Goera*	22	1	Pchakadze (1930) in Lankhorst (1970); Lankhorst (1970).
Phryganeidae	*Agrypnetes*	± 50	1	Klingstedt (1931) in Lankhorst (1970)
	Dasystegia	28	2	Klingstedt (1931) in Lankhorst (1970)
	Phryganea	28	2	Pchakadze (1930) & Klingstedt (1931) in Lankhorst (1970).
	Trichostegia	19	1	Klingstedt (1931) in Lankhorst (1970).
Odontoceridae	*Odontocerum*	30	1	Lankhorst (1972)
	Drusus?	30	1	"
Molannidae	*Molanna*	27	1	Pchakadze (1930) & Klingstedt (1931) in Lankhorst (1970).
Leptoceridae	*Athripsodes*	25	2	Pchakadze (1930) in Lankhorst (1970).
Sericostomatidae	?	22	?	Kiauta (1968)
Conoesucidae	*Conoesucus*	25	7	this study
	Costora	25	6-7	"
	Matasia	25	1	"
	Lingora	25	1	"
Calocidae	*Caenota*	22	1	"
	Tamasia	22	1	"
Helicophidae	*Alloecella*	26	1	"
		29/30	1	"
		32-40	1	"

chromosome number differed for each of the three *Alloecella* species (no data were obtained for the other genus in the family). The range of number given for *A. grisea* and *A. longispina* should not be interpreted as intraspecific variation, it is due to lack of very clear preparations. In Calocidae, the two species from different genera had the same number, although too few species were studied to enable any valid generalizations to be made. Possible phylogenetic implications of intrafamilial variation is discussed later.

Change in chromosome number in the species studied must involve only mechanisms of fusion and fission, not polyploidy. Any chromosomal heterozygotes, which would result from polyploidy, can be recognized by the formation of multivalents at meiotic metaphase I (White 1973); only bivalents were observed in this study. Nor are the highly variable numbers in Lepidoptera, 7-220 (White 1973), a result of polyploidy, as species with diverse numbers have the same amount of DNA (Suomalainen 1965, 1969). Therefore, species with larger numbers have smaller chromosomes. Size, with number, gives an indication of total DNA, and although size could not be measured accurately in this study, it was observed that chromosomes of species with higher numbers (i.e. *Alloecella*) appeared smaller than those with lower number (Conoesucidae) which were in turn smaller than those of Calocidae. The small absolute size and narrow range found in this study is similar to findings of other studies on Trichoptera (e.g. Kiauta & Kiauta 1979, Lankhorst 1972).

Suomalainen (1965) suggested that holocentric chromosomes make more feasible such rearrangements as fission and fusion, thus allowing greater range of numbers (the spindle attaches at the centromere, so for holocentric chromosomes, each fragment will still have a spindle attachment point). However, the mechanisms of fission and fusion are unknown, for example whether simple breaks and joins can occur (White 1973).

The cytological restraints on changes in number and selective pressures acting on number are unknown. Most animal groups have haploid numbers between 6-20 (White 1973); numbers may be limited by the mitotic mechanism, which could have different limiting factors in holocentric and monocentric chromosomes.

Recombination.

Another factor important in population genetics and evolution, influenced by chromosome number, is the amount of genetic recombination that occurs. This depends on the number of chiasmata (crossovers) per nucleus, which will depend to some degree on the number and size of the chromosomes: species with high chromosome number will show more genetic recombination than ones with low number (White 1970), and large chromosomes can have more than one chiasma (Y.A.E. Bick pers. comm.). In this study, nuclei in diakinesis were not observed often enough to enable meaningful estimation of

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amount of recombination, expressed as the recombination index: haploid number + mean number of chiasmata per nucleus (White 1973), which represents the mean number of blocks of genes segregating at meiosis. In addition, the small size of trichopteran chromosomes makes it difficult to observe such details as chiasmata.

The highest recombination seen in the species studied occurred in *Caenota*, where frequently all bivalents in a nucleus were crossing over. Such nuclei were also observed, rarely, in *Conoesucus norelus*.

In their study of *Allogamus auricollis*, a limnephilid with a recombination index higher than any confamilial species, Kiauta & Kiauta (1979) suggest that the adaptive significance of a low recombination index is genetic stability, whereas a high recombination index will promote long-term flexibility, i.e. the ability to adapt to changing conditions, which they relate to its ecology. However, expression of adaptation in this way implies forward planning to cope with conditions, rather than conditions influencing the features (such as rapidly fluctuating conditions providing selective pressure towards a system that can adapt to them, for example with a higher rate of recombination). Such pressures may not be exerted in a more stable environment. Since so little is known about selective pressures acting on karyological characteristics, and the rate of their evolution, asssociation of karyotypic and ecological features must be tentative.

Achiasmatic oogenesis, which was observed in the species in this study and appears to be a general feature of the order and of Lepidoptera (Suomalainen 1965, White 1970), reduces recombination by half. Suomalainen (1965) suggests that the relatively high chromosome number in these groups compensates for this. The reason for absence of crossing over in female meiosis is unclear; achiasmatic meiosis occurs in other insect groups (White 1970), and is restricted to the heterogametic sex, indicating that chiasmata formation may depend on pairing of all elements.

Holocentric chromosomes.

Another characteristic of the Trichoptera shared with Lepidoptera that was observed in this study is that chromosomes are holocentric, or at least have no distinct centromere. This must have profound effects on the recombination and cell division system. For example, Suomalainen & Brown (1984) propose that, because fissions and fusions may survive more often than in monocentric chromosomes, holocentric chromosomes allow for greater variation in chromosome number. If so, this potential has not been realised in the Conoesucidae and possibly Calocidae.

Sex determination.

The findings of this study for Conoesucidae and Helicophidae (no clear female metaphases were seen for Calocidae) agree with other studies on Trichoptera, showing that the female is heterogametic and that the X is the only sex chromosome (i.e. XO).

The X chromosome was distinct in most dividing female cells as a paler, less condensed, central univalent. These characteristics differed in a few species, but appearance probably depends on stage of division (for example as it does in Acridoidea (Orthopera) males (White 1970)), as X appeared to be later condensing than the autosomes. These characteristics differ from observations made in other studies, in which X was distinct as a positively heteropycnotic[2] univalent at prometaphase and metaphase (e.g.*Chaetopteryx villosa* , *Rhyacophila vulgaris* (Lankhorst 1972) and *Glyphotaelius pellucidus* (Kiauta & Lankhorst 1969)); at all stages (*Allogamus auricollis* (Kiauta & Kiauta 1979)); or only as a univalent (*Drusus? alpinus* (Lankhorst 1972)).

The central position of the X chromosome in polar views of the metaphase plate means that it is nearer the pole than the autosomes, perhaps ensuring that it reaches the pole safely before cytokinesis (Y.A.E. Bick pers. comm.).

The largest, darker staining bivalent usually seen in males of the Conoesucidae, Calocidae and Helicophidae could be the sex bivalent (XX) (Lankhorst 1972), but in this study there is no clear evidence that this is so. Although the X chromosome in females is differentially contracted with respect to the autosomes, it nevertheless appears to be one of the larger elements. Also supporting the possibility that these large dark elements are the sex chromosomes is Suomalainen's suggestion (1965) that, as fragmentation of the sex chromosome is likely to disrupt the sex determination mechanism, the large dark unfragmented chromosome often found in butterflies is a sex chromosome. Why the sex determination mechanism should be more sensitive to disruption by chromosome fission than other vital processes is not clear; nor is it clear whether the same situation could apply in Trichoptera.

The Lepidoptera also have heterogametic females; all other insects studied have male heterogamety (White 1970). Both XY and XO systems occur in the Lepidoptera, with XY most widespread (White 1973). White's (1973) comment that there have been few really detailed studies of the sex chromosomes in Trichoptera and Lepidoptera remains true.
Stages showing division.

Not all life history stages were surveyed for cell division activity in this study, but the stages in which activity was observed can be compared with findings of other studies. Divisions were rarely observed in male pupae in this study, although Lankhorst (1970) found intense mitotic and/or meiotic activity in male pupae of three species, which did not confirm earlier records. Kiauta and Lankhorst (1969) found only pupal males and adult females to be mitotically active; in this study mitosis was not seen in any males, and rarely in

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[2] Positive heteropycnosis=some regions which are condensed and heavily staining at stages when the rest of the karyotype is diffuse and weakly staining (White1973).

female larvae and prepupae. Mitotic activity can be more frequently observed by treatment of larvae with colchicine (live animals for up to 5 hours (C. Parker pers. comm.)), although this had no apparent effect in this study.

Most studies have found meiotic divisions occurring in larvae, relatively few recording divisions in pupae and adults (Lankhorst 1970, Table 1). Overall, observations of this study agree with Lankhorst's conclusion (1970) that meiotic activity occurs only from the last larval stage until the pharate adult, and that spermatogenesis usually starts one instar or at least a few days earlier than oogenesis, although the duration of divisional activity is about equal in males and females.

Tissues showing division.

No other study on Trichoptera has recorded examination of tissues other than gonads for cell division, thus the failure in this study to find division in neural ganglia and silk glands cannot be compared with other results. No silk gland chromosomes were seen in this study although White (1973) thought that the much-branched nuclei in the spinning glands of Trichoptera and Lepidoptera probably have a similar structure to those of the salivary glands of the pondskater *Gerris* (Hemiptera), with polyploid chromosomes.

Speciation.

All the karyotypic characteristics (number, size, chiasmata, centromeres, sex determination) interrelate and are involved in the population genetics system (White 1973), and therefore the evolution, of the animals. For most groups of animals studied in detail cytologically, even closely related species can be distinguished by differences in chromosome number, shape, size or other features (White 1973). Chromosome rearrangements result in speciation, although clearly speciation can occur without chromosome rearrangements, and such changes may occur after speciation; in addition, there may be rearrangements such as inversions which do not affect the gross morphology of the karyotype.

The conoesucid species studied were karyotypically indistinguishable, as were the two calocid species; only *Alloecella* species were distinct from each other. Thus, for most of the species studied, there is apparently no gross karyological change causing or associated with speciation, although the chromosomes were small and rather uniform. No rearrangements such as inversions could be detected with the method used, so their incidence is unknown. In *Alloecella*, preparations were not clear enough to enable comparison of chromosome sizes, which may have shown where fissions or fusions resulting in the difference in numbers had occurred.

The vagility and the population structure of a group seems to be very important with respect to determining what kinds of cytotaxonomic change can establish in populations and hence play a role in speciation (White 1973). However, no reports of population genetics studies on Trichoptera are

available, and little is known of trichopteran vagility.

Direct and objective measures of the extent of genetic divergence between species, such as allozyme electrophoresis, are needed to study speciation in groups such as these. The small amount of electrophoretic data from the present study (ch. 3) shows that allozymically distinct species (*Conoesucus brontensis* and *C. adiastolus* sp. n.) may have no gross chromosome differences. Females of these species were distinct in chromosome size and appearance of X, but these differences may result from different degrees of condensation; there is no chromosome information on *C. brontensis* males for comparison.

Phylogeny.

The karyotypic character discussed by previous authors in relation to trichopteran phylogeny is chromosome number. This is a clearly defined character, unlike others which may depend on treatment or stage. With the degree of variation in chromosome number differing within different groups, it may seem reasonable to imply a relative time since divergence of the members of each group, for example to say that the Conoesucidae speciated more recently than *Limnephilus*. However, such conclusions are invalid, as the rate of chromosome evolution is unknown and can vary from group to group and even within a group (Crozier 1983), and taxonomic designations may not be comparable. Thus, karyotype information can only be informative of the phylogenetic branching sequence, not of the temporal extent of phylogenetic divergence (Crozier 1983). Nothing is known about the rate of chromosome evolution in Trichoptera or Lepidoptera.

Relating chromosome number to phylogeny requires knowledge of the processes resulting in the observed distribution of numbers; without it, proposed directions of change remain speculative, and are deduced by comparison of the distribution of numbers with an existing phylogeny based on morphological and other criteria, such as those of Ross (1967) and Weaver & Morse (1986) (figs 1.1 and 1.3). This approach has been taken for Trichoptera, with phylogeny discussed at the family level. However, in a detailed study of ant karyotypes, Imai *et al.*(1977) concluded that there appeared to be little correlation between whether a species is morphologically primitive or advanced and its karyotype organization.

The detection of ancestral number clearly is not easy, as theoretically it can increase or decrease (Swanson 1963). Swanson takes the view that there is no direct connection between basic number and phylogenetic position unless it is within narrower limits of the family or genus.

By examining distribution of known numbers throughout the Trichoptera in terms of Ross' (1967) phylogeny, Kiauta (1968) concludes that for the Trichoptera, low number indicates primitiveness, and that low number in "advanced " families is of secondary origin arising by fusion (thereby resulting in larger elements). He claims that there is a correlation between advanced phylogenetic position and increase in chromosome number in most insect

orders with holocentric chromosomes, for example Odonata (although they are almost certainly monocentric according to White (1970)), Heteroptera and aphids.

Thus, according to Kiauta (1968), the number n=30 proposed as the "type" or ancestral number for the order by White (1973), on the basis that it was the commonest (modal) number in the order, is not the type number but simply the state of one of the advanced families, and the similarity with the modal number in Lepidoptera (29-31 (Suomalainen 1966, Robinson 1971)) is incidental. Prior to this study, the commonest number for Trichoptera was n=30, but with this study recording n=25 for 16 species, this is now the most common number for the order (Table 2.2). The additional data on the order obtained in this study (a 67% increase in species known karyotypically) enable no reliable estimate of the modal number of the order to be made, as the proportion of species karyologically known is still so small. However, chromosome number modes may not represent movement in one direction or persistence of ancestral number, but equilibria, determined by relative rates of fission and fusion and not by selection acting on chromosome number, size etc. (Imai *et al*. 1977). Kiauta (1968) considered that there were no indications as to the probable ancestral number in Trichoptera, but that a number of about 13 might characterize Ross' (1967) "ancestor 1".

In comparison to Kiauta's conclusions relating to the Trichoptera, Suomalainen & Brown (1984) found that in Lepidoptera, a decrease in number was more usual. In Lepidoptera, the modal number of 29-31 (Suomalainen 1966) is considered by most (Beliajeff 1930, Federley 1938, Lorkovic 1941, White 1954, 1957a, cited by Suomalainen 1965; Robinson 1971) to be ancestral, with other numbers (ranging from 7-220) derived from it. If the mode is taken as ancestral, there are more species with n< 29 than with n> 31, indicating that fusions are more likely to survive (White 1973). However, interpretation of the modal number as ancestral may not be correct: the ancestral number could be low and fissions predominant. The direction of change will depend not only on the frequency of fusion and fission, but the rate at which such changes survive, as mitotically unstable chromosomes will not survive in evolution (White 1973). This rate will depend on characteristics of the chromosomes such as centomere type.

For the Trichoptera, no information is available to indicate possible rates of fission and fusion, and data on numbers is scant and scattered. Type numbers for families given by Kiauta (1968) are based on only one or a few species, which would be representative if the family had the same degree of variation in number as the Conoesucidae. This seems unlikely, as the entire range of numbers previously recorded occurs in one genus, *Limnephilus* (Lankhorst 1970).

For considering the phylogenetic relationships of Conoesucidae,

Calocidae and Helicophidae to each other, the phylogeny proposed by Weaver & Morse (1986) is not useful as they did not resolve family relationships within Sericostomatoidea. Within this superfamily, chromosome numbers are known only for the three families studied and Sericostomatidae (Pchakadze 1930, cited by Kiauta 1968). Ross (1967) placed Calocidae (=Pycnocentrellidae) and Sericostomatidae (then including Conoesucidae) as branches at the same level, derived from "ancestor 15"; Helicophidae and Antipodoeciidae were considered more advanced. Ross (1978) concurs with this although Antipodoeciidae is included in Beraeidae, at the same level as Calocidae and Sericostomatidae. Thus there is no differentiation in the phylogenetic position of Conoesucidae and Calocidae, and Helicophidae are considered more advanced. Therefore, to a very limited extent, chromosome numbers of the three families tend to support the idea that morphologically advanced families have higher numbers.

The pattern discernable within the whole order is that most families in the suborder Annulipalpia (*sensu* Weaver & Morse 1986), generally considered the more primitive suborder, have low chromosome numbers (n=13-17); Integripalpia have higher numbers (n=19-30/40). The exception is the Annulipalpian family Rhyacophilidae, with a relatively high number (n=23). Rhyacophilidae, Glossosomatidae and Hydroptilidae were placed by Ross (1967) at the base of the Integripalpian branch; Schmid (1980) and Weaver & Morse (1986) included them in the Annulipalpia. Chromosome numbers of the Glossosomatidae (n=17 (Lankhorst 1972)) and Hydroptilidae (n=14 (Higler 1969, cited by Lankhorst 1970, A. Wells pers. comm.)) are consistent with this placement in Annulipalpia, but those of Rhyacophilidae are not. However, as the number given for most families is based on only a single species, any conclusions relating to distribution of numbers within the order are tentative.

The group of sericostomatoid families studied here are included in the phylogenies of Ross (1967) and Weaver & Morse (1986) amongst the most advanced families, and therefore according to Kiauta (1968) would be expected to have numbers amongst the highest in the order. Numbers recorded for *Alloecella longispina* (Helicophidae) in this study are the highest known for the order, and *A. grisea* number equals the highest previously recorded (n=30 in Limnephilidae and Odontoceridae (Lankhorst 1972)). However, numbers for Conoesucidae and Calocidae are not remarkably high. Therefore, the proposed pattern of primitive families having low chromosome number is apparent only at the very broad level of suborders.

In relation to phylogeny within the class Insecta, the sister group relationship of Trichoptera and Lepidoptera is well established (Kristensen 1981). Both show female heterogamety, although male heterogamety occurs in all other insects studied (White 1970), including the mecopteroid sister group of Trichoptera + Lepidoptera. The karyological characters found in this study conform with the characters previously reported as being shared by Trichoptera and Lepidoptera (Suomalainen 1966): female heterogamety, achiasmatic

oogenesis and holocentric chromosomes. These cytological features must have originated before the divergence of Trichoptera and Lepidoptera, i.e. before the Tertiary, 60-70 million years ago (Shields 1988). Such persistence indicates the stability of these features. Suomaleinen & Brown (1984) have interpreted the similarity of the modal number for Lepidoptera (29-31) and White's proposed type number of Trichoptera (30) as an indication that this is the primitive number, typical for the common ancestor of Trichoptera and Lepidoptera which probably lived in the Cretaceous (Suomalainen 1969). However, as discussed earlier, these modal numbers are not necessarily the ancestral number.

Shields (1988) interprets the chromosome numbers of the ancestral Mecoptera (n=21, 22, 23 (Makino 1951, cited by Shields)) as indicating a trend of increase in number from Trichoptera to Microlepidoptera, while Mecoptera and primitive Trichoptera retained approximately the same number of chromosomes. Available data do not support such statements, as primitive Trichoptera have numbers much lower than Mecopteran numbers.

Gonad structure.

Although chromosome numbers in Conoesucidae are uninformative of taxonomic divisions below family level, gonad structural characters provide valuable evidence relating to generic division within Conoesucidae. *Conoesucus* and *Costora* are separated by the shape of testes lobes (round cf. long); *Matasia* and *Lingora* share the unique structure of two long lobes, which supports the idea that they are congeneric. Information on testes structure of *Hampa*, the other monospecific genus which possibly should be included in a group with *Matasia* and *Lingora*, is required for resolution of this problem.

Shields (1988) has noted that the Lepidopteran family considered most primitive has a 4-lobed testis structure similar to Trichoptera. However, as this study has shown, not all Trichoptera have 4-lobed testes, which raises questions of the distribution of this character throughout the order and its phylogenetic significance.

In conclusion, karyological data obtained in this study support the separation of the Conoesucidae, Calocidae and Helicophidae from each other, and of Conoesucidae from Sericostomatidae. These families conform in general karyotypic features with previously known characters of Trichoptera, which are also shared with Lepidoptera. Chromosome numbers agree at a broad level with those expected from known phylogenetic distribution of numbers within the order. Internal morphological characters of gonad structure are taxonomically useful at the generic level.

Further investigation of conoesucid karyotypes may be taxonomically unrewarding due to the uniformity of those studied, although karyotyping of the New Zealand species would be particularly interesting, since geological evidence enables approximation of the time of their separation from Australian species. On the basis of results of this investigation, study of more calocid and

helicophid species is likely to yield taxonomically valuable information, and may help in tracing karyological evolution in Trichoptera. Use of methods of preparation that reveal detailed chromosome structure, such as staining to show bands, may enable detection of important characteristics that were not seen in this study, although small chromosome size is likely to make this difficult. Investigation of basic karyotypic features for entire groups within the order is more urgent for solution of systematic problems in Trichoptera.

CHAPTER 3. ELECTROPHORESIS

3.1 INTRODUCTION

The aim of this electrophoretic study was to test the validity of the species status of pairs of species for which adult and/or larval stages are morphologically very similar: *Conoesucus brontensis* and *C. adiastolus* sp. n.; *Costora ramosa* and *C. krene*; *Costora luxata* and *C. seposita*. These species were designated *a priori* on the basis of morphological diagnostic features (Neboiss 1977, this study), and allozyme electrophoresis was used to determine whether the species designated do in fact consist of independent gene pools.

There are two approaches to this problem of species delimitation, depending on whether the species are sympatric or allopatric. If sympatric specimens have allelic frequencies that do not deviate from those predicted by the Hardy-Weinberg Equilibrium, they represent one interbreeding population. However, a single genetically determined fixed difference is sufficient to show that the populations are not interbreeding and therefore are separate species. As it is possible in practice that a single difference found may not be under simple genetic control, the criterion of two or more fixed differences should be used (Richardson *et al.*1986).

For allopatric populations, the assumption of panmixis is not justified and therefore Hardy-Weinberg cannot be invoked. Instead, the biological significance of the genetic distance between populations must be determined, i.e. how large an electrophoretic difference reflects a species difference? Where different populations show extensive electrophoretic divergence, they can be interpreted as full species, but the converse is not true, as "good" species may show little electrophoretic divergence (e.g. Matsuoka *et al.* 1983; Richardson *et al.*1986).

Genetic divergence can be expressed in several ways. Nei's D (Nei 1972, 1978) and Roger's R (Rogers1972) are based on allele frequencies. Nei's D measures a biological phenomenon, i.e. the accumulated number of gene substitutions per locus since separation of the populations (cf. the geometric distance measured by R), and has been the most widely used index. However, in interspecific taxonomic studies, allele replacement is more important than allelic frequency differences (Ferguson 1980, Richardson *et al.*1986). Richardson *et al.* suggest that therefore the proportion of fixed differences is a more practical and biologically significant measure of genetic divergence. An added advantage is its ease of calculation. A fixed difference is defined by Richardson *et al.* (1986 p. 306) for practical purposes as "when, for a particular locus, any alleles common to the two taxa occur at a frequency of < 0.05 in one of the two taxa.", although in this study two taxa are considered to show a fixed difference only when the two species fail to share any alleles at a locus.

Nei's D makes the assumption that the rate of gene substitution is the same for all loci, unless geometric means are used instead of arithmetic means (Nei 1972). As this assumption is rarely met (Nei 1972, Hillis 1984), Hillis (1984) has suggested a modification to the algorithm of D so that it is not adversely affected by varying rates

of change at different loci.

In this study, the proportion of loci with fixed differences, Nei's D and Hillis' modified D were used as measures of the extent of divergence between species. Proportion of fixed differences is a practical and easily calculated measure, and Nei's D enables comparison with other studies which have used it.

Knowledge of the level of interspecific divergence previously recorded from related taxa gives a background against which to assess the biological significance of the divergence found. No such information is available for Trichoptera, as previous electrophoretic studies on the order examined intraspecific variation only (Ingold *et al.* 1988, C. Parker pers. comm.). Therefore, previous studies of other insect groups were surveyed to provide comparative data. Values of D found in some previous studies on insects, particularly the trichopteran sister group Lepidoptera, are given in Table 3.1.

It is evident from Table 3.1 that interspecific values of D between congeners vary considerably, giving little basis on which to determine species boundaries. Large D values may indicate separate species, but small values do not demonstrate conspecificity.

The proportion of fixed differences is likely to be more reliable as an indicator of specific status, due to its biological significance. Richardson *et al.* (1986) suggest, on the basis of empirical data, that a lower limit of 15% fixed differences between allopatric populations indicates specific status, and this criterion of specific status was applied in this study.

In addition to delineation of species, an electrophoretic character set is also useful for elucidating phylogenetic relationships. Although a phylogenetic analysis based on allozyme data of all the conoesucid, calocid and helicophid species studied would be valuable for comparison and integration with the phylogeny based on morphology (ch. 6), such a study was not undertaken because the of the large number of species involved, and the lack of any prior information on the suitability of the group for such a study (i.e. the extent of their genetic divergence). It is likely that the animals are too distantly related to be amenable to phylogenetic analysis with allozyme data (P. Baverstock pers. comm.).

3.2 MATERIALS AND METHODS
Collection and preservation of specimens

To obtain a sample with a high probability of representing all the genetic variation in a species (Richardson *et al.* 1986), individuals were collected from widely spaced sites shown on Figures 3.1-3.6.

Specimens used were generally adults, except when none were available and larvae could be specifically identified. Adults of those species for which adults could not be distinguished but larvae were distinct (*Conoesucus adiastolus* and *C. brontensis*) were obtained by rearing from larvae and/or pupae, as were *Costora seposita* and *C. luxata*. Larvae could not be distinguished for *Costora ramosa* and

TABLE 3.1. Interspecific values of Nei's D for congeneric insects.
* indicates that specific status of the forms studied was uncertain

Group	Nei's D	no. species	no. Loci	Reference
ODONATA				
Austrolestes	0.418-1.946	4	7	Krasnicki (1988)
Ischnura	0.405	2		
Austroaeschna	1.151	2		
DIPTERA				
Drosophila willistoni gp.	0.413-1.325	6		Ayala (1975)
Culex pipiens gp	0.386 av.			Miles (1974) in Berlocher (1979)
PLECOPTERA				
Nemoura	0.93-1.61	4	16	Lees & Ward (1987)
Protonemoura	0.53	2		
Amphinemura	0.67	2		
HYMENOPTERA				
Formicidae	0.136 av.	5	11	Ward (1980b)
LEPIDOPTERA				
Nymphalidae	0.012-0.384	10		Brittnacher et al. (1978)
	0.043	2	15	Matsuoka et al. (1983)
Noctuidae	0.34	2	19	Daly & Gregg (1985)
	0.874	2	19	Sluss et al.(1978)
Satyridae	0.003	2		Angevine & Brussard (1979)
Geometridae	0.084*	2	10	Jelnes (1975b)
Pyralidae	0.003*	2		Harrison & Vawter (1977)
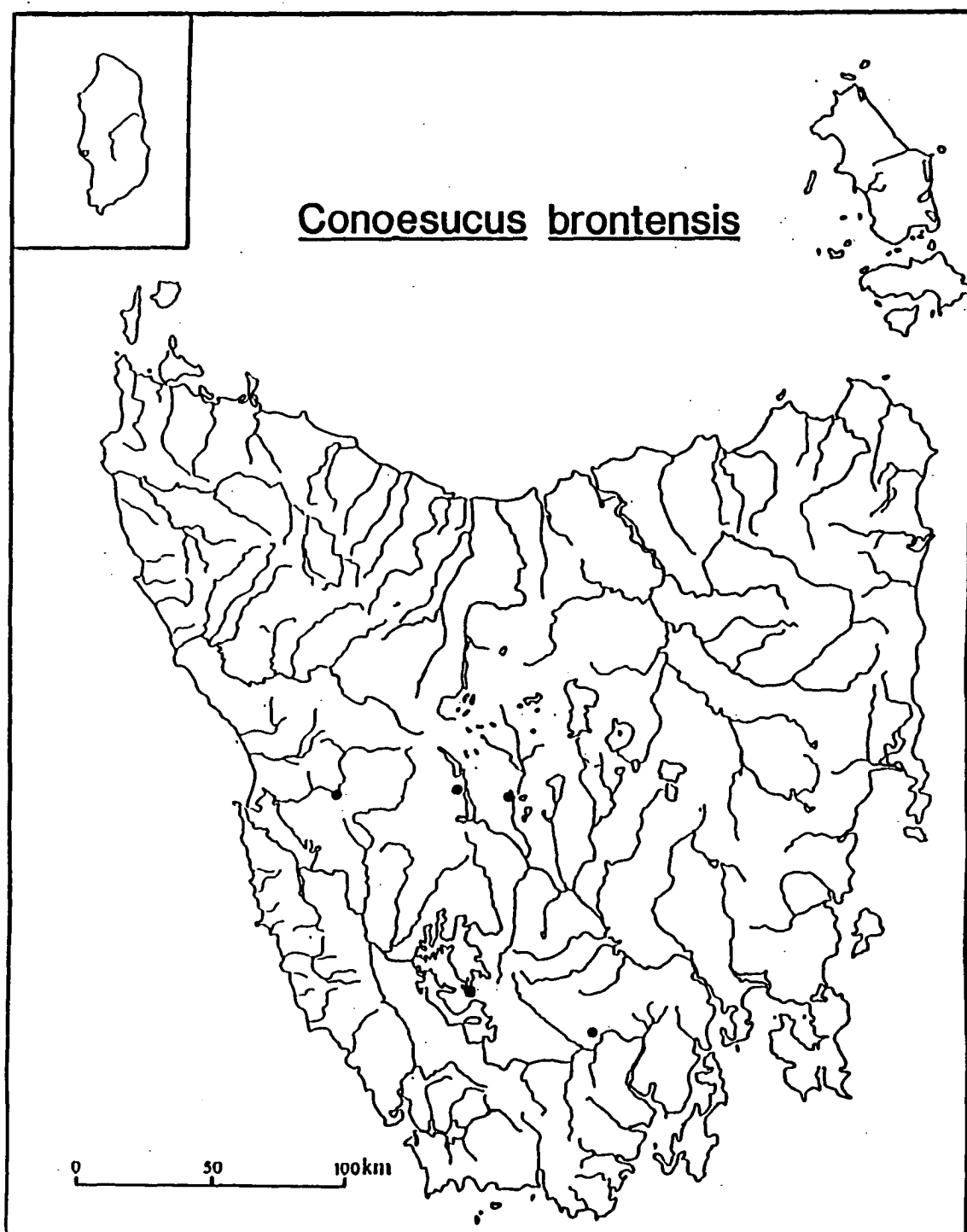
Figure 3.1. Collection sites of *Conoesucus brontensis* electrophoresis specimens.
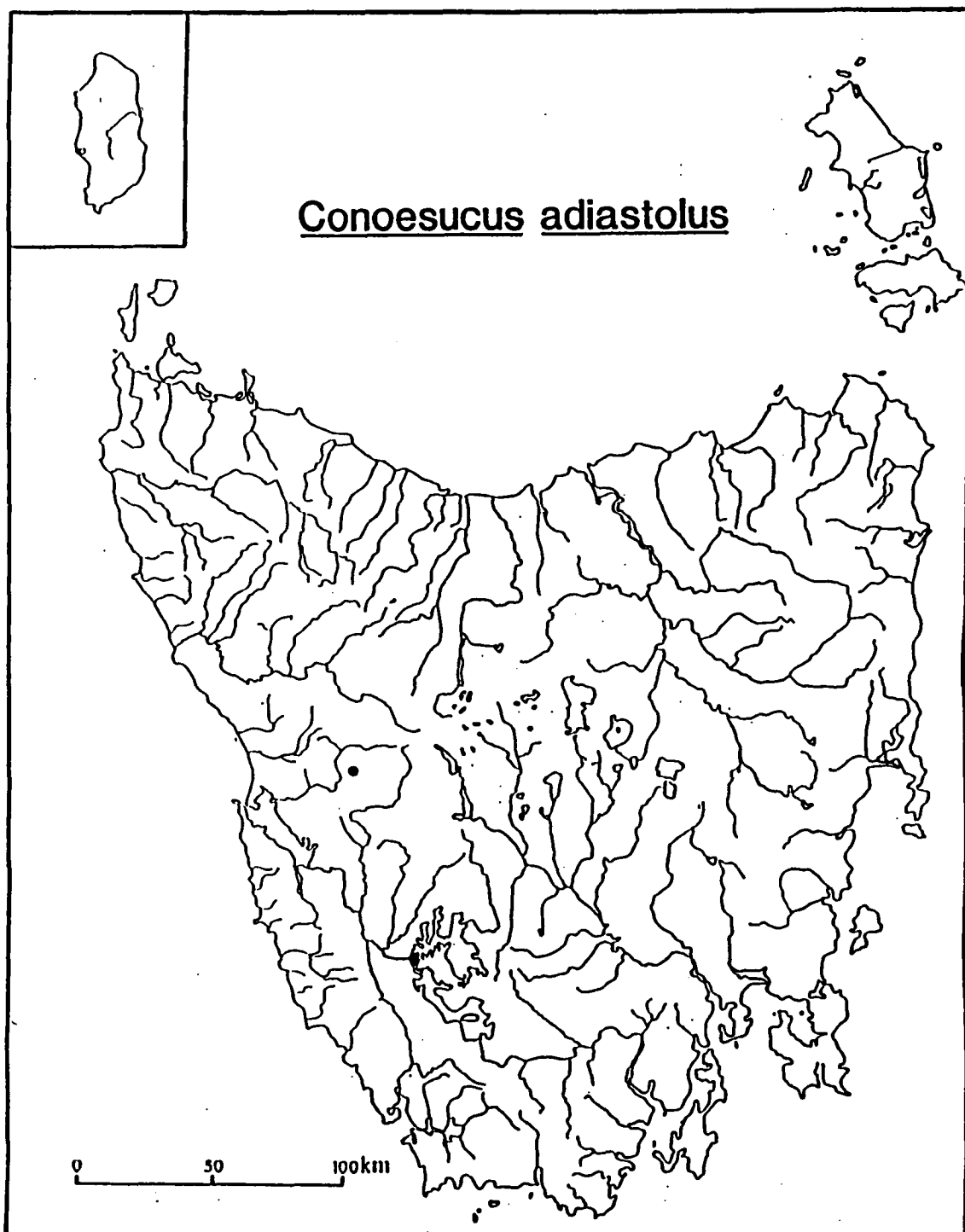
Conoesucus adiastolus   unnamed creek 13, Serpentine Dam road
                           Nelson Valley Creek, Lyell Hwy

Figure 3.2. Collection sites of *Conoesucus adiastolus* sp. n.
electrophoresis specimens.
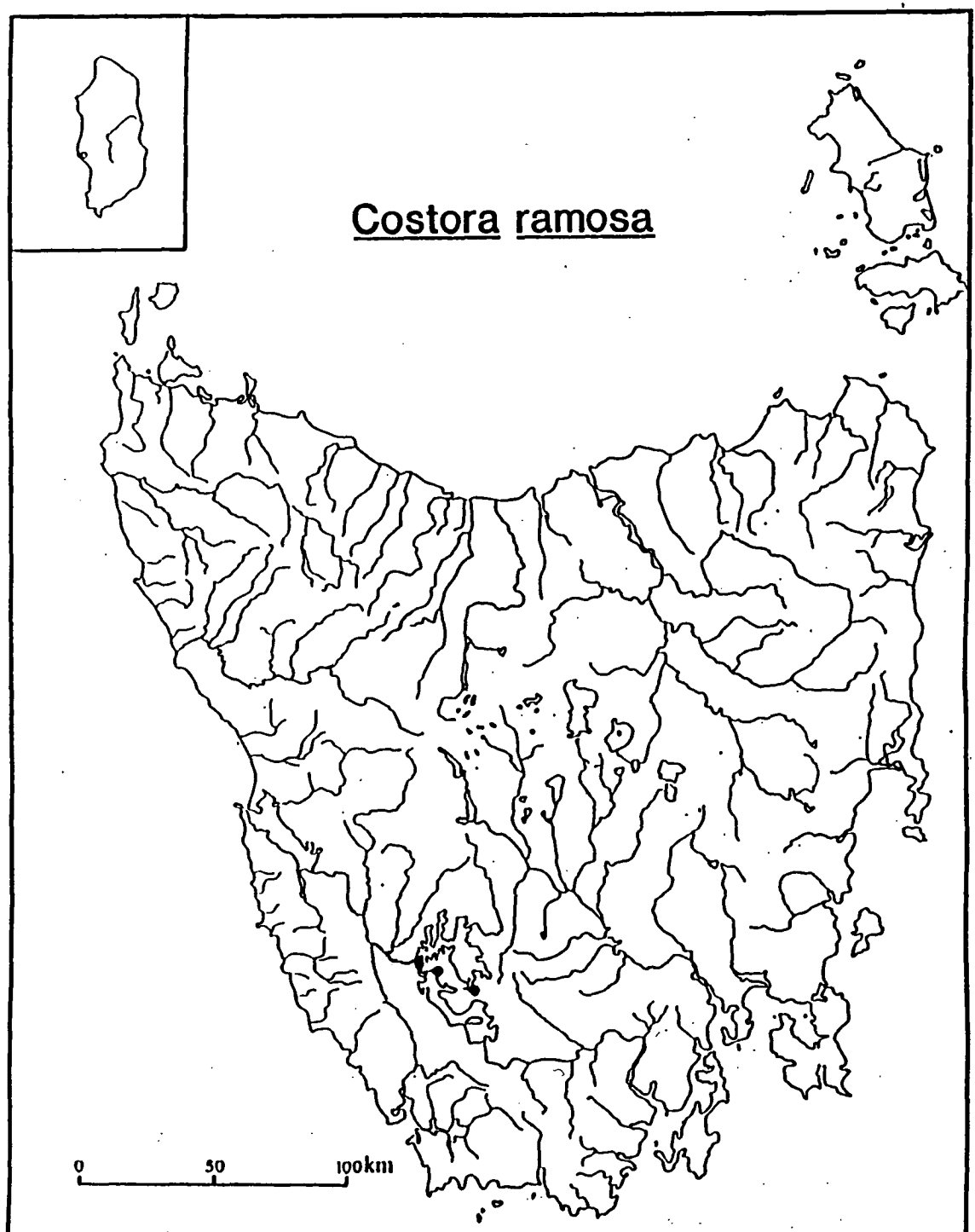
Costora ramosa

Costora ramosa	Wedge River, Gordon Rd
	unnamed creek 13, Serpentine Dam road
	unnamed creek 11 near Ted's Beach, Gordon Rd

Figure 3.3. Collection sites of *Costora ramosa* electrophoresis specimens.
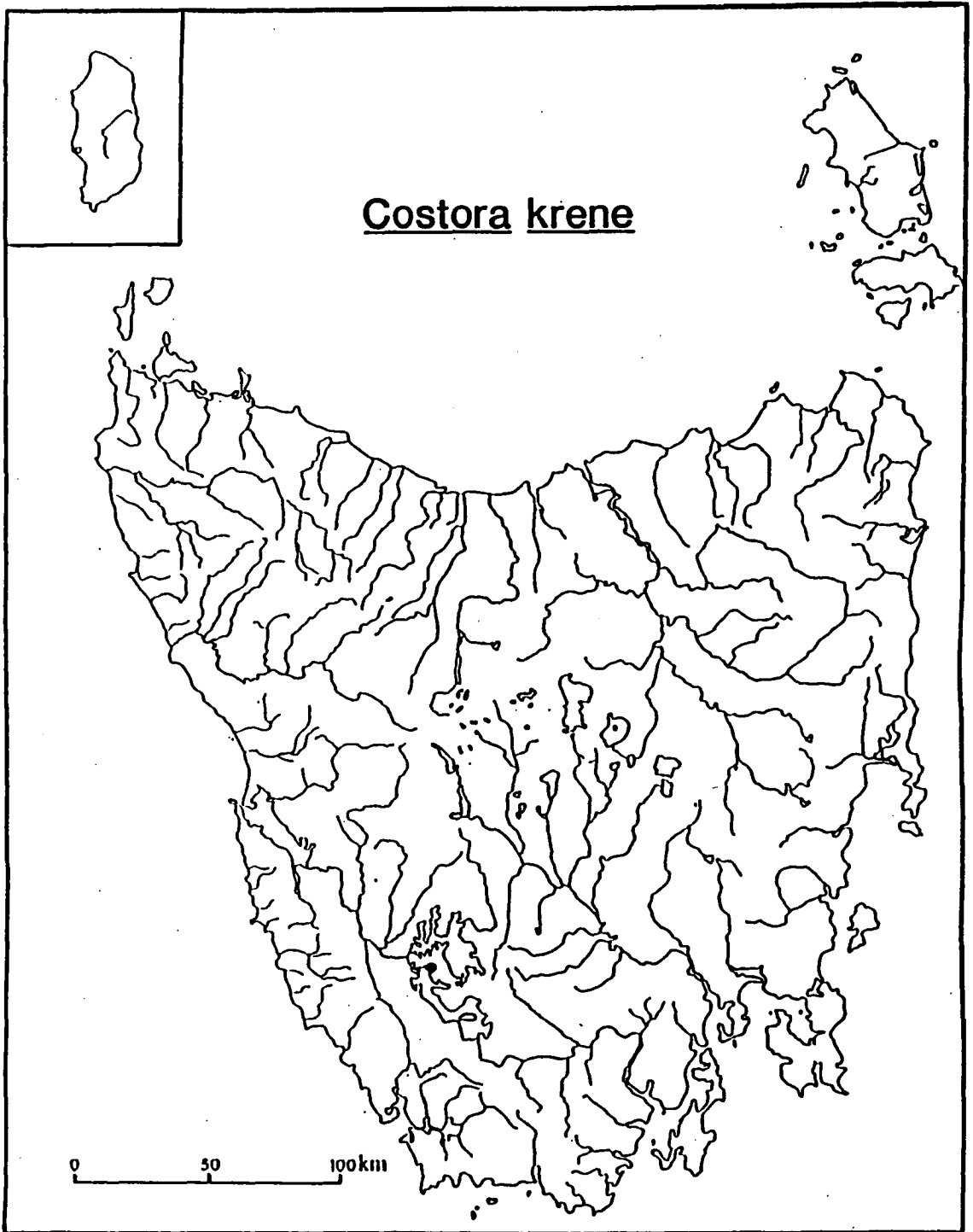
Costora krene

| *Costora krene* | unnamed creeks 15 &16 near Ted's Beach, Gordon Rd |
| | unnamed creek 11, 200m E of Ted's Beach, Gordon Rd |

Figure 3.4. Collection sites of *Costora krene* electrophoresis specimens.
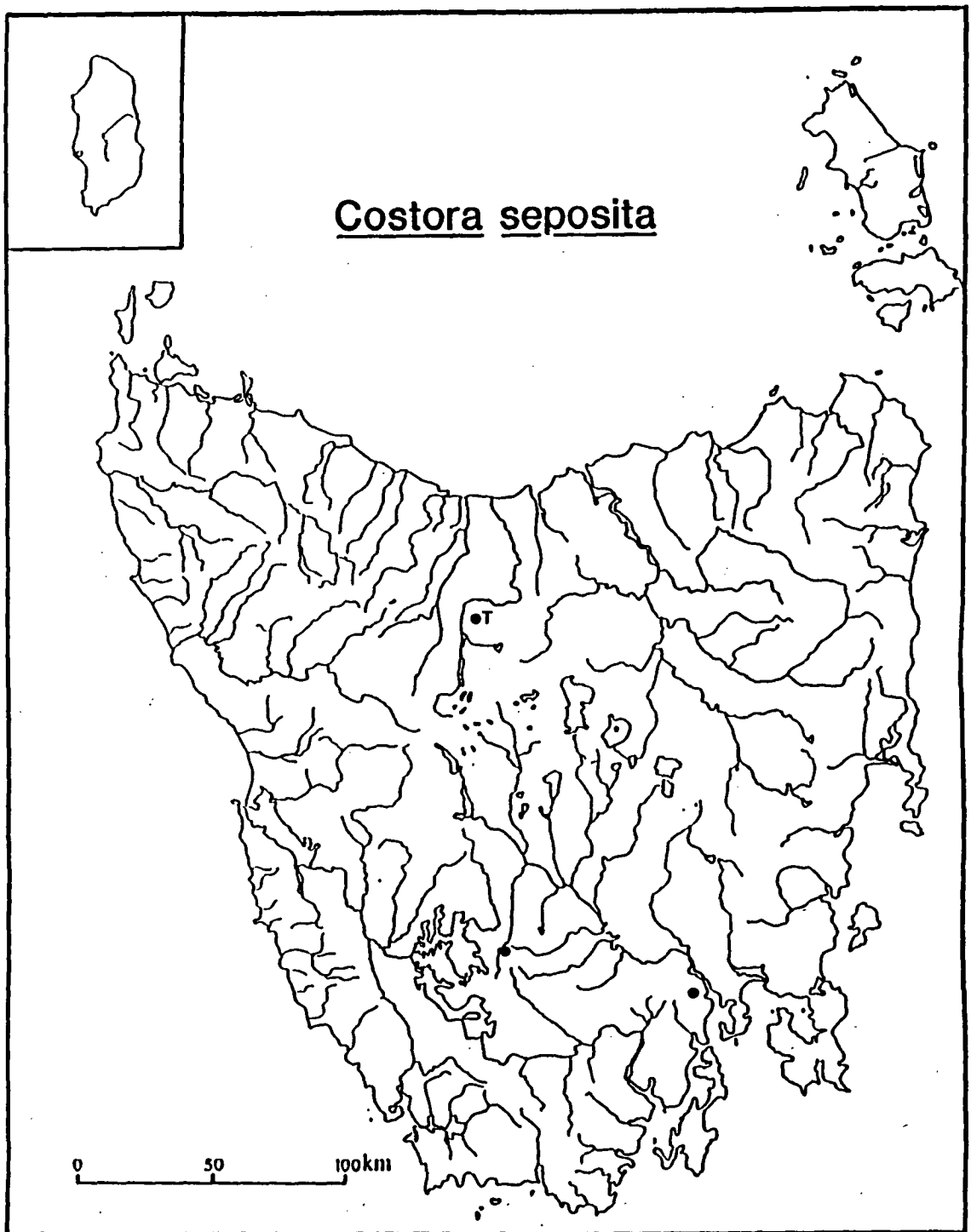
Costora seposita

Costora seposita	Little Florentine River, Gordon Rd
	creek near Marakoopa Cave, Mole Creek
	Hobart Rt, Strickland Falls

Figure 3.5. Collection sites of *Costora seposita* electrophoresis specimens.

Costora luxata   Lilla Creek, Cradle Valley

                            unnamed creek 50, Lyell Hwy
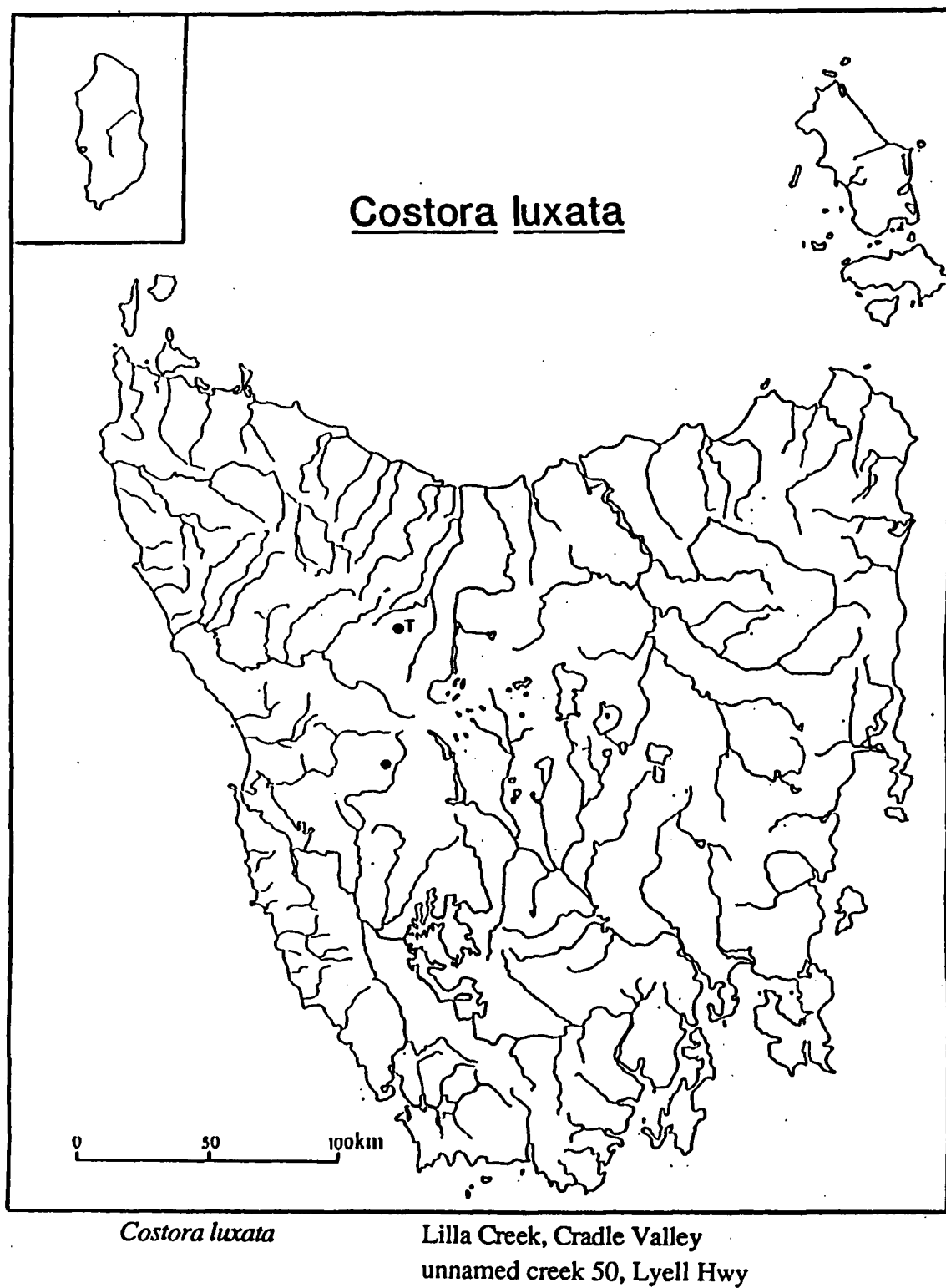
Figure 3.6. Collection sites of *Costora luxata* electrophoresis specimens.

C. krene, so adults were collected by sweep netting and assigned to species on diagnostic criteria (Neboiss 1977).

Live adults were transported to the lab in a vial with paper tissue, on ice. Adults were anaesthetized with CO_2 gas to enable handling. Diagnostic features were checked and all wings removed with eye surgery scissors, before enclosing the animal in folded aluminium foil onto which an identifying number was scratched. About 5 individuals were then placed into a cryotube (Nunc, 1.8 ml) and stored in liquid nitrogen.

Larvae were removed from cases by pressing and pushing from behind, then blotted to remove excess water, foil-wrapped and frozen.

Tissue preparation

Preparation of animals for electrophoresis was carried out in a coldroom (5 °C) with samples kept on ice when possible. Whole individuals were homogenized by hand in eppendorf tubes with 5 µl of cold homogenizing buffer (100ml distilled H_2O, 10mg NADP, 100µl ßmercaptoethanol; stored in sealed glass at 4°C), then centrifuged for 7 minutes at 10,000g. The supernatant was stored in aliquots of about 5 µl in capillary tubes plugged with plasticine, kept at -20°C.

Electrophoresis

Methods of preparation of gels before loading and techniques for loading, running, staining, scoring and interpretation of gels are given in detail in Richardson *et al.* (1986).

Gels used were cellulose-acetate (Cellogel, Chemetron, Italy). Mobility controls (repeated loading of a sample) were included to minimize the need for line-up gels.

All gels were run at 200V in a 4 °C refrigerator for 2 hr, except gels stained for ADA, IDH and LDH, which were run for $1^1/2$ hr, and GDA which was run for 1 hr.

Enzymes

The enzymes screened, their abbreviation used in the text, Enzyme Commission (E.C.) number, number of scorable loci found, and running buffer used are given in Table 3.2.

Analysis

Genetic distance between species was calculated as Nei's D (Nei 1972), Hillis' (1984) modified D (D*), and proportion of loci with allelic fixed differences. Nei's D is calculated as:

$$D = -\ln I$$
$$I = \Sigma x_i y_i / \sqrt{\Sigma x_i^2 \Sigma y_i^2}$$

where x_i and y_i are the frequencies of the ith allele at the jth locus, for populations x and y.

Over all loci,

$$I = Jxy/ \sqrt{JxJy}$$

where Jxy, Jx, and Jy are the arithmetic means of $\Sigma x_i y_i$, Σx_i^2, and Σy_i^2 over all loci, respectively (Nei 1972).

Hillis' D* is calculated as:

$$D* = -\ln I*$$

TABLE 3.2. Names, abbreviations and E.C. numbers of enzymes screened, the number of scorable loci, and running buffer used.
Buffer A = 0.01 M Citrate-phosphate pH 6.4; B = 0.02 M Phosphate pH 7.0;
C = 0.05 M Tris-maleate pH 7.8; F = 0.1 M Tris-EDTA-maleate-MgCl2
(more details are given in Richardson et al. 1986).

Enzyme	Abbreviation	E.C. no.	No. of loci scorable	Buffer
Aconitate hydratase	ACON	4.2.1.3	2	B
Adenosine deaminase	ADA	3.5.4.4	0	B
Adenylate kinase	AK	2.7.4.3	0	A, B
Aldolase	ALD	4.1.2.13	0	A
Fructose 1,6 diphosphatase	FDP	3.1.3.11	0	B
Guanine deaminase	GDA	3.5.4.3	0	B
Glutamate dehydrogenase	GDH	1.4.1.3	0	F
Glucose dehydrogenase	GLDH	1.1.1.47	0	B
Glucose-6-phosphate dehydrogenase	G6PD	1.1.1.49	0	B
Glycerol-3-phosphate dehydrogenase	αGPD	1.1.1.8	0	C
Glucose phosphate isomerase	GPI	5.3.1.9	1	C
Hexokinase	HK	2.7.1.1	2	C
Isocitrate dehydrogenase	IDH	1.1.1.42	2	C
Lactate dehydrogenase	LDH	1.1.1.27	0	B
Malate dehydrogenase	MDH	1.1.1.37	1	C
Malic enzyme	ME	1.1.1.40	1	B
Mannose-phosphate isomerase	MPI	5.3.1.8	0	B
Purine nucleoside phosphorylase	NP	2.4.2.1	0	B
6-Phosphogluconate dehydrogenase	G6PD	1.1.1.44	0	B
Phosphoglucomutase	PGM	2.7.5.1	1	C
Superoxide dismutase	SOD	1.15.1.1	1	A
L-iditol dehydrogenase	SORDH	1.1.1.14	0	C
Triose-phosphate isomerase	TPI	5.3.1.1	0	A, B
Xanthine oxidase	XO	1.2.3.2	0	F

where $I^* = \Sigma I_j / L$ (L is the number of loci)

    Nei's D was not corrected for small sample size, as the bias was considered negligible due to the size of D in relation to the amount of heterozygosity and the number of individuals used (Nei 1978, Gorman & Renzi 1979). Typically about 5 individuals per population will give a reliable estimate of D except when D is small (<0.1) (Richardson *et al.* 1986).

    A conservative approach was taken to analysis, and those heterozygotes for which there were no homozygotes (i.e. *Conoesucus adiastolus* MDH allele A, *C. brontensis* and *C. adiastolus* alleles A & D) were not included in calculations of genetic distance.

3.3 RESULTS

Electrophoresis

    Loci scored and allele frequencies for the three pairs of species are given in Tables 3.3, 3.4 and 3.5. Gel diagrams for scorable loci are shown in Appendix 1. A total of 8 enzymes of the 24 screened were found to give scorable bands (representing 11 loci), although not all loci were scorable for all species.

    No difference in activity or banding pattern was seen between stored frozen homogenates and freshly frozen or homogenized samples.

    The activity of some enzymes differed between larval and adult specimens. Activity of αGPD and IDH 1 and 2 was weak/absent in all larvae sampled (for αGPD:*C. adiastolus*, *Costora seposita* and *C. luxata;* for IDH, all species except *C. brontensis*), except for one specimen of *C. luxata* which showed activity in both αGPD and IDH. MDH activity was low or absent in *C. adiastolus* larvae, although in other species all larvae showed activity. Although TPI bands were not scorable, it was apparent that larvae showed no activity.

    Problems were encountered with homogenizing adult females, particularly of *C. brontensis*. Supernatant was difficult to obtain regardless of the amount of homogenizing buffer added, possibly because of the large amount of body fat, or egg jelly absorbing water to form a gel.

    No patterns of geographical variation were apparent, although discovery of such patterns was not an aim of the study and thus the sampling program was not designed to detect such variation.

Species discrimination

    Values of Nei's D, Hillis' D* and proportion of fixed differences between species are shown in Table 6. The only pair of sympatric species is *Costora ramosa* and *C. krene*; although the ranges of the other species overlap (ch.5), *C. brontensis* and *C. adiastolus* were never collected at the same site, and *C. luxata* and *C. seposita* were found together at only one site (from which electrophoretic samples were not taken).

    For *Conoesucus brontensis* and *C. adiastolus* sp. n., 11 loci were scored. Two of these were monomorphic (αGPD, MDH), and three showed absolute fixed

TABLE 3.3. Results for <u>Conoesucus</u> <u>brontensis</u> and <u>C. adiastolus</u> sp.n. Loci scored, number of specimens scored, and allele frequencies found.

Allele A is the slower running allele; locus 1 is the slower locus.

Numbers in parentheses are allele frequencies used in calculations, i.e. not including heterozygotes for which there were no homozygotes.

*= fixed difference between the species

Locus	Allele	C. brontensis		C. adiastolus sp. n.	
		No. specs	Allele freq.	No. specs	Allele freq.
ACON 1	A	13	96	9	28
	B		4		72
ACON 2	A	7	14	7	50
	B		86		50
αGPD	A	13	100	12	100
GPI	A	13	15	12	96
	B		85		4
PGM	A	13	0	12	4 (0)
	B		65 (71)		83 (86)
	C		31 (29)		13 (14)
	D		4 (0)		0
IDH 1*	A	12	0	8	100
	B		100		0
IDH 2*	A	13	100	7	0
	B		0		100
HK 1	A	13	100	9	39
	B		0		61
HK 2	A	13	100	12	38
	B		0		62
MDH	A	13	0	9	6 (0)
	B		100		94 (100)
ME*	A	10	0	11	100
	B		100		0

TABLE 3.4. Electrophoretic results for <u>Costora ramosa</u> and <u>C. krene</u>. Loci
scored, number of specimens scored, and allele frequencies.
In addition to the number of specimens shown, larvae which
could belong to either species were also run (see gel diagrams, Appendix 1)

| Locus | Allele | C. ramosa | | C. krene | |
		No. specs	Allele freq.	No. specs	Allele Freq.
GPI	A	2	100	2	100
PGM	A	13	100	3	100
HK 1	A	9	100	2	100
HK 2	A	9	100	2	100
IDH 1	A	8	100	5	100
IDH 2	A	8	100	5	100
MDH	A	10	100	5	100

TABLE 3.5. Electrophoretic results for <u>Costora luxata</u> and <u>C. seposita</u>.
Loci scored, number of specimens scored, and allele frequencies.
Numbers in parentheses are allele frequencies used in calculations, i.e. not
including heterozygotes for which there were no homozygotes.
*= locus showing fixed difference between the species.

Locus	Allele	C. seposita		C. luxata	
		No. specs	Allele freq.	No. specs	Allele freq.
α GPD	A	6	100	8	100
GPI	A	15	0	9	11 (0)
	B		100		89 (100)
IDH 1	A	5	100	8	100
IDH 2	A	5	100	9	100
MDH*	A	10	0	9	100
	B		100		0
ME	A	12	100	5	100
SOD*	A	15	0	8	100
	B		100		0

TABLE 3.6. Genetic distance between the species, calculated as Nei's D, Hillis'
modified D (D*), and proportion of loci showing absolute fixed difference (F. D.).

Species pair	D	D*	F. D.
Conoesucus brontensis-<u>C. adiastolus</u>	0.778	0.715	0.27
Costora ramosa-<u>C. krene</u>	0	0	0
Costora seposita-<u>C. luxata</u>	0.337	0.337	0.29

difference (IDH1, IDH 2, ME). Some alleles occurred in one species but not the other: for PGM, allele A was found in *Conoesucus adiastolus* and not in *C. brontensis*, and allele D occurred in *C. brontensis* but not *C. adiastolus*. However, there were no homozygotes for these alleles, only one heterozygote of each.

HK 1 and 2 each have one allele which is present in *C. adiastolus* but not in *C. brontensis*, although alleles at the two loci were correlated (i.e. heterozygous or homozygous at both), indicating that the observed pattern is most likely to be a result of non-genetic factors (Richardson *et al.* 1986). Therefore, the HK loci were not included in calculations of genetic distance.

For *Costora ramosa* and *C. krene*, 7 loci were scorable. They were all monomorphic. However, *Costora krene* was represented by only a few specimens from a limited locality, so the sample may not fully encompass the genetic variation present.

Of the 7 loci scorable for *Costora seposita* and *C. luxata*, two showed a fixed difference (SOD, MDH), and three were monomorphic. *Costora luxata* had allele A of GPI which was not found in *C. seposita*, although as there were no homozygotes for A, it was considered possible that the pattern was due to non-genetic factors.

3.4 DISCUSSION
Species discrimination

This study of electrophoretic characters has confirmed the distinction between *Conoesucus brontensis* and *C. adiastolus*, and between *Costora seposita* and *C. luxata*, on the basis of the proportion of fixed differences between them (>15%). The values of Nei's D also indicated that the species could confidently be considered separate. (Subsequent detailed morphological study revealed clear morphological diagnostic characters for *C. brontensis* and *C. adiastolus* (section 4.2)).

Costora ramosa and *C. krene* could not be distinguished on the basis of electromorph characters; however, they are diagnosable on slight morphological differences, and in the absence of morphometric data on adults demonstrating that the forms are part of a continuum of variation, the current species separation remains. It seems likely that study of additional loci will reveal diagnostic differences, and the use of different methods (e.g. isoelectric focussing or SDS electrophoresis) may resolve alleles that were not distinguished in this study.

Although the values of D between species were within the range for other insect species, it is apparent that genetic distance values provide little basis for determining species boundaries, at least in insects, because of the range of values for any given taxonomic level (Berlocher 1979). The range of distances in vertebrate groups is also very large (Avise & Aquadro 1982).

In any case, if species are defined in terms of reproductive isolation, the genetic distance between them, which may have accumulated since speciation, is largely irrelevant to the problem of determining species boundaries (Zuckerkandl 1963). For

example, chromosome changes may cause reproductive isolation by preventing correct pairing at meiosis, without change in structural genes (Ferguson 1980). This has been documented in plants (Gottlieb 1973, 1974), and it may be the cause of the small electrophoretic difference between some butterfly species which have different chromosomes (e.g. Brittnacher *et al.* 1978, Matsuoka *et al.* 1983). Therefore, D is of limited use in systematic studies, and is more applicable to population genetic studies for which it was initially proposed.

Fixed differences provide a much more powerful criterion to distinguish species, although with allopatric species an appropriate level of divergence must still be determined. Therefore every effort should be made to obtain samples in sympatry.

When considering the results of this study, the fairly small number of loci scored must be taken into account. The statistical finding that a small number of individuals is adequate to represent the range of variation in a species (Nei & Roychoudhury 1974, Nei 1978) has been confirmed empirically (e.g. Gorman & Renzi 1979), but the number of loci examined should be relatively large. Ideally >50 loci should be used to reduce the sampling error in estimates of D (Nei 1978), although in practice technical difficulties often limit the number of loci studied. Only a small proportion of the loci screened in this study were scorable, although many showed activity, as has been found by others (e.g. Jelnes 1975a, Krasnicki 1988). Although manipulation of electrophoretic conditions such as running buffers may increase the proportion scorable, bands observed in invertebrates may generally be less well resolved than bands in vertebrates (Krasnicki pers. comm.). This could be the result of the use of whole animals rather than specific tissues.

Banding patterns

The differential expression of enzymes in different life stages observed for some enzymes in this study has been commonly recorded in other insects, and results from developmental changes in metabolism (Wagner & Selander 1974, Ferguson 1980). Such changes are likely to be particularly marked in holometabolous insects, compared to those without complete metamorphosis.

The many enzymes for which such a change in activity has been observed (e.g. Lokki *et al.* 1975; studies cited in Wagner & Selander 1974), include two that showed lower activity in larvae in this study: αGPD and IDH. The larva of *Costora luxata* which showed activity in IDH and αGPD where other larvae did not may have been at a slightly different stage. Presumably the reactions catalysed by these enzymes are occurring at a greater rate in adults; for example, the glycerol-phosphate shuttle in which αGPD functions is known to be especially prominent in insect flight muscle (Stryer 1981). All the enzymes showing lower activity in larvae in this study catalyse reactions in energy producing pathways, so the activity pattern may be due to the accumulation of energy reserves in the larval stage. The enzyme activity pattern in pupae is likely to be different again, during this non-active, metamorphosing stage.

The banding pattern for IDH 1 and 2 in *C. brontensis*, *C. adiastolus* and *C. luxata* shows evidence of what may be a null allele, as at least one locus is clearly absent for one specimen of each species. A null allele produces a non-functional

protein; they occur most commonly in polyploid organisms or, as here, where there are duplicated loci (Richardson *et al.* 1986). When interpreting these patterns, though, the conservative interpretation of missing activity due to non-genetic factors was taken.

None of the enzymes studied were highly polymorphic in the very limited number of species examined. PGM in *C. brontensis* and *C. adiastolus* had the highest number of alleles, with 4, although 2 of these are doubtful as there were no homozygotes for them. PGM has been found to be highly polymorphic in other insects, e.g. Krasnicki (1988) found 10 alleles in 14 species of Odonata. The degree of variation in a particular enzyme is correlated among different taxa and is apparently related to the metabolic function of the enzyme, with glucose metabolizing enzymes generally being less variable than non-glucose metabolizing enzymes (Powell 1975). However, the results of this study are not sufficient to support or oppose this conclusion.

The number of heterozygotes for some enzymes (i.e. ACON, GPI, PGM) was much greater than others, showing that the assumption of Nei's D (that the rate of gene substitution is the same for all loci) is not met. Therefore, if D is used as a measure of genetic divergence, it should be modified to allow for the failure of this assumption. In this study, however, the modification of Hillis (1984) made little difference to the value of D.

Further studies.

The extent of genetic divergence between species in this study shows that the level of divergence within the family Conoesucidae is likely to be appropriate for a phylogenetic study of the family using electromorph characters, although a more detailed pilot study would still be needed. To be phylogenetically informative, species should share at least 30% of alleles. The upper useful limit of divergence is about 60-70%, when the proportion of similarities that are due to chance convergence becomes considerable (Richardson *et al.* 1986); clearly the limiting distance is where no alleles are shared. A further pilot study would be needed to assess the similarity of species of Calocidae and Helicophidae, before examination of interspecific relationships of all the species studied.

Although not pursued in this study, one of the most useful practical applications of enzyme electrophoresis is for the identification and association of different life stages, using enzymes that have been checked for developmental changes and shown to be the same in all stages. Such association is valuable for identifying pest species in the egg and larval stage (e.g. Daly & Gregg 1985, Fisk & Daly 1989), and in ecological studies to avoid the need for time consuming rearing where immatures cannot be identified. Before such application, diagnostic loci must be found for the species in question.

This study, then, has shown the value of enzyme electrophoresis for species discrimination in Trichoptera, and provides initial information on interspecific genetic distances and specific genetic variation for the order, which can form a basis for future comparative studies.

CHAPTER 4. MORPHOMETRICS

4.1 SPECIFIC STATUS OF *LINGORA VESCA* Neboiss.
4.1.1 INTRODUCTION.

Lingora vesca was described by Neboiss (1977 p. 108, figs 580-583) from a single specimen obtained from the North Esk River, Blessington (Tasmap grid reference 8415 448 081).

L. vesca is distinguished from the Tasmanian congener, *L.aurata* Mosely, by characteristics of male genitalia. In addition to "rather short, narrow and (in lateral view) obliquely truncate apices of the inferior appendages" (Neboiss 1977), *L. vesca* is characterised by "diverging apices of segment 10, [and a] shorter and broader membraneous plate below phallus" (Neboiss 1977), and the tergite 9 process is rounded in *L. vesca*, compared to pointed in *aurata*. In other characters *L. vesca* is not distinct from *L. aurata*.

Examination of *Lingora* specimens collected and reared during the present study revealed some variation in these distinguishing characters, so it was considered possible that the *L. vesca* type specimen may not represent a distinct species, but a variant or abnormal specimen of *L. aurata*. No male *L. aurata* specimens were collected with the type of *L. vesca* (Neboiss 1977), although an undetermined *Lingora* female was collected.

Therefore, a morphometric study of *Lingora* was carried out to determine the range of variation in the "diagnostic" characters, and thereby test the validity of the specific status of *L. vesca*.

4.1.2 MATERIALS AND METHODS.

To support the validity of *L. vesca*'s specific status, discontinuous variation between the two forms must be demonstrated. Measurements of male genitalia were made to determine the range of variation of the *L. vesca* distinguishing characters.

Additional material was collected from the *L. vesca* type locality, and specimens from a wide geographical area were also examined (Fig. 4.1.1). Adults were collected from the type locality by sweep netting and light trapping; larvae and pupae were collected for preservation and rearing.

The following characteristics were recorded (Fig. 4.1.2): width (i) and length (ii) of the end of inferior appendages; divergence of segment 10 apices; total length of inferior appendages (iii); length (iv) and width (v) of membranous plate below phallus; whether segment 9 ventromesal processes were bowed out; shape of tergite 9 process. Measurements were made to the nearest 0.01mm with an eyepiece micrometer in a Wild M5 stereomicroscope.

Specimens measured were the *L. vesca* type, cleared *Lingora* males and whole *Lingora* males. In addition 80 male specimens, mostly reared from larvae, from 27 localities were examined but not measured. Localities are given as site numbers; for
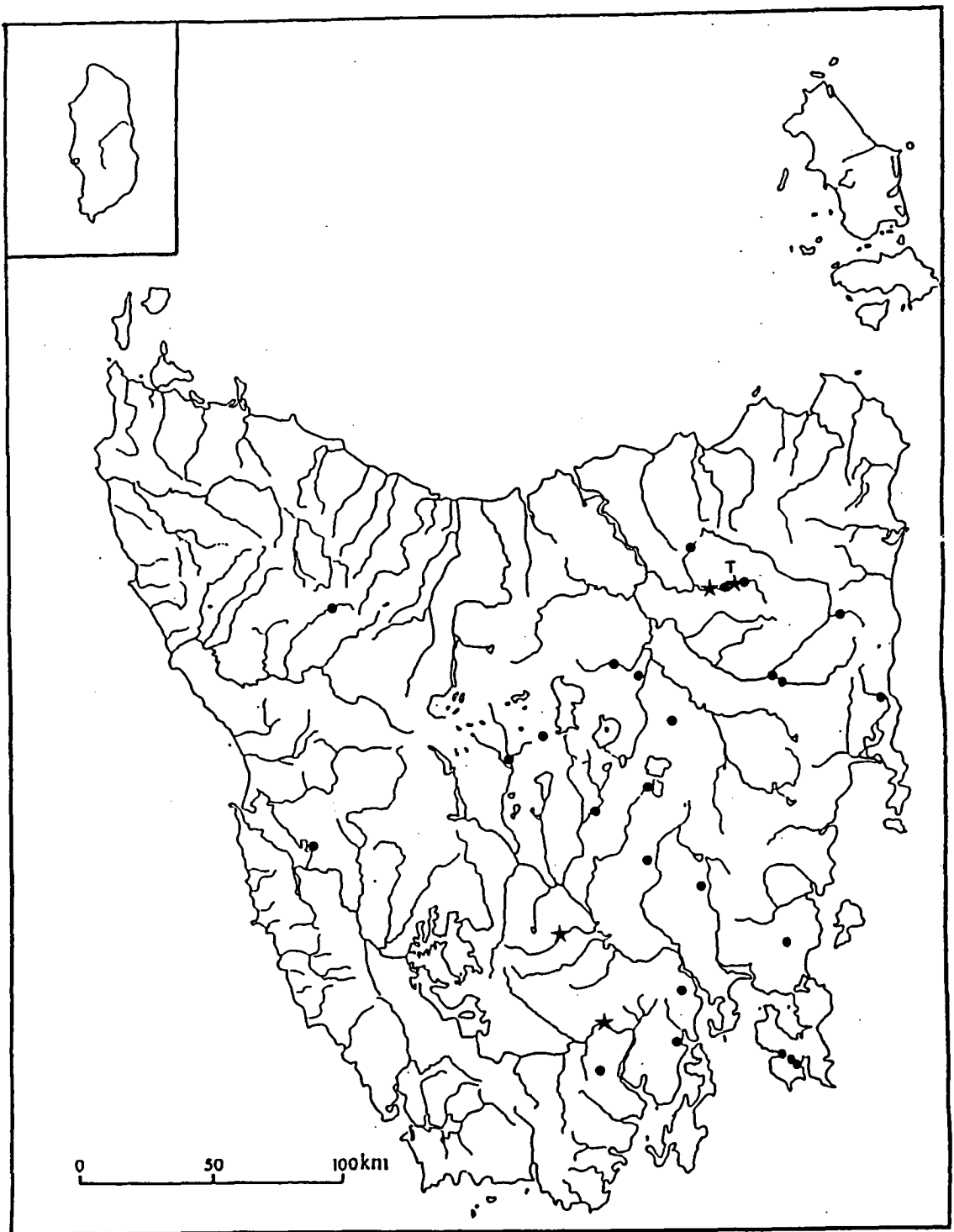
Figure. 4.1.1. Geographical distribution of the *Lingora* specimens examined to test the validity of *L. vesca* status. ★ = sites from which specimens with narrow appendages were recorded; T= *L. vesca* type locality.
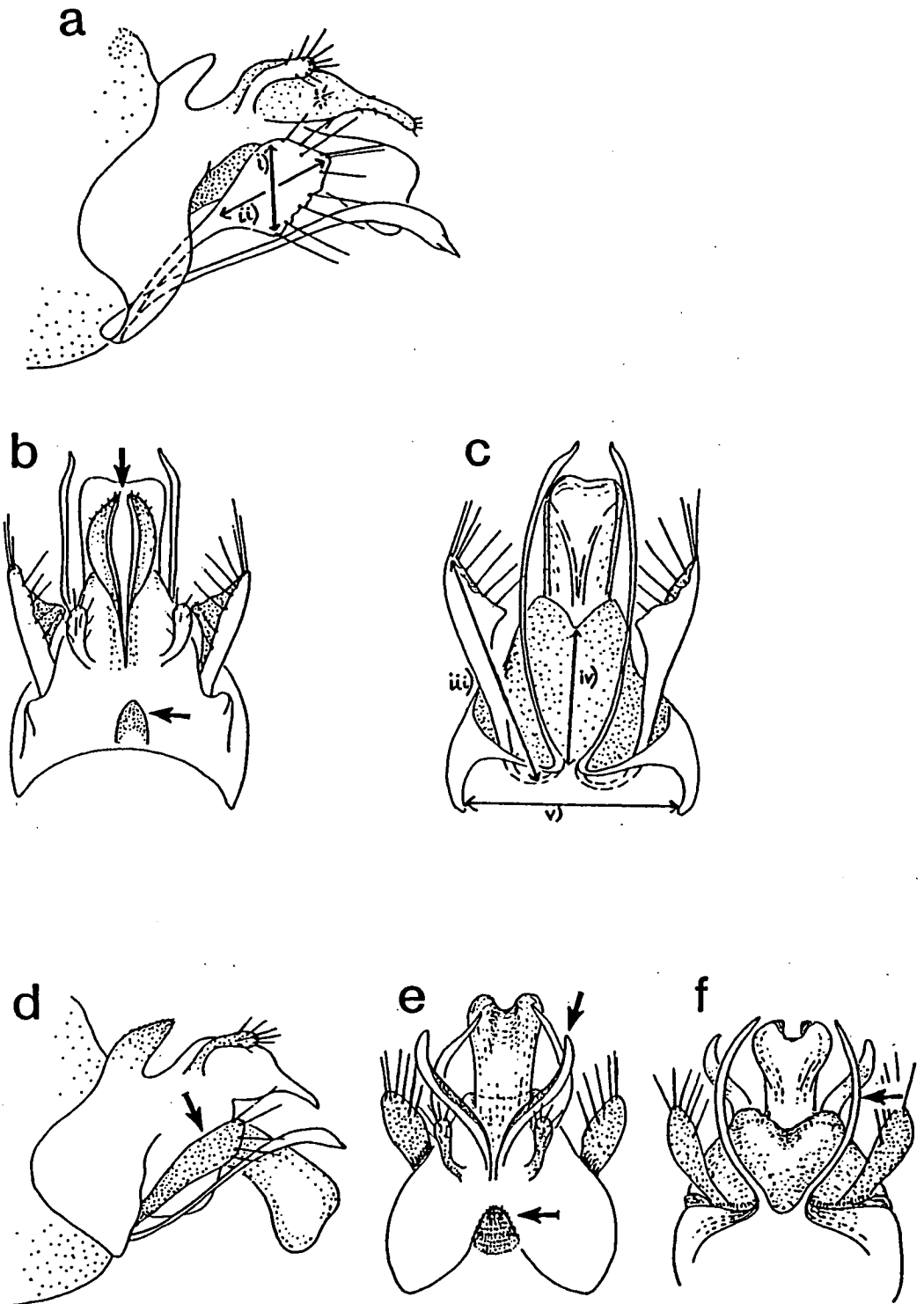
Figure 4.1.2 a)-c): *Lingora aurata* male genitalia in lateral, dorsal and ventral view (from Neboiss 1977), showing measurements taken of inferior appendage end width (i) and length (ii), total length of inferior appendages (iii), membranous plate length (iv) and width (v). Arrows indicate the apices of segment 10 and tergite 9 process. **d)-f):** *Lingora vesca* male genitalia in lateral, dorsal and ventral view (from Neboiss 1977), with arrows indicating the diagnostic characters.

details refer to Appendix 3. Specimens cleared and measured (males) were: *L. vesca* type male (site 91); 6, site 89; 2, site 90; 1, site 92; 1, site 275; 1, site 282; 1, site 284; 1, site 250; 1, site 273. Inferior appendage length and dimensions of membraneous plate could be measured only in these cleared specimens. Whole specimens that appeared unusual were cleared to enable measurement of all characters.

Uncleared specimens measured were: 4, *L. vesca* type locality (91); 13, site 89; 10, site 90. Specimens examined but not measured were: 10, site 282; 7, site 218; 3, site 84; 1, site 83; 1, site 266; 1, site 78; 2, site 210; 4, site 273; 7, site 284; 2, site 274; 2, site 275; 10, site 250; 3, site 208; 4, site 154; 1, site 223; 1, site 96; 1, site 273; 3, site 229; 1, site 86; 1, site 25; 1, site 72; 1, site 71; 4, site 268; 2, site 291; 5, site 107; 1, site 271.

The female from the type locality was compared with known (reared) *Lingora* females.

Lingora aurata specimens were stored in liquid nitrogen for electrophoretic study if enough *L. vesca* material was obtained.

4.1.3 RESULTS.

The *L. vesca* type locality is a bend in the river near the road, running through pasture. The river bed is rocky and water fairly shallow (about 50cm) with fast flow. Riparian vegetation is sparse and consists mainly of willows. Larvae and pupae were common on submerged willow roots. Other species collected were *Conoesucus norelus*, *C. fromus* and *Costora delora*.

Of the four *Lingora* specimens collected from the *L. vesca* type locality in this study, none had diverging segment 10 apices, narrow inferior appendages or rounded segment 9 process. Other *L. vesca* diagnostic characters were randomly distributed throughout the other specimens examined, i.e. there was no correlation in the occurrence of *L. vesca* diagnostic characters.

Occurrence of divergent apices of segment 10 was scattered. The apices are probably movable and specimens may be preserved with apices together or widely spread. One of the pharate adults examined had diverging segment 10 apices, indicating that their position is not related to occurrence of mating. In the *L. vesca* type, apices are wide apart; of the other 121 specimens examined, diverging apices were found in 13.

The tergite 9 process varied considerably in size and shape, with no pattern of variation apparent; it was usually difficult to designate it as round or pointed.

Segment 9 ventral processes were not bowed out in any specimen except the *L. vesca* type, although in three specimens they diverged.

The membranous plate below the phallus in *L. vesca* is both shorter and narrower than in most other specimens. The size of this plate is possibly changeable, depending on the position of genitalia parts.

Width of inferior appendage was found to vary continuously (Fig. 4.1.3), i.e. there is not an absolute character difference between broad and narrow. Specimens

34
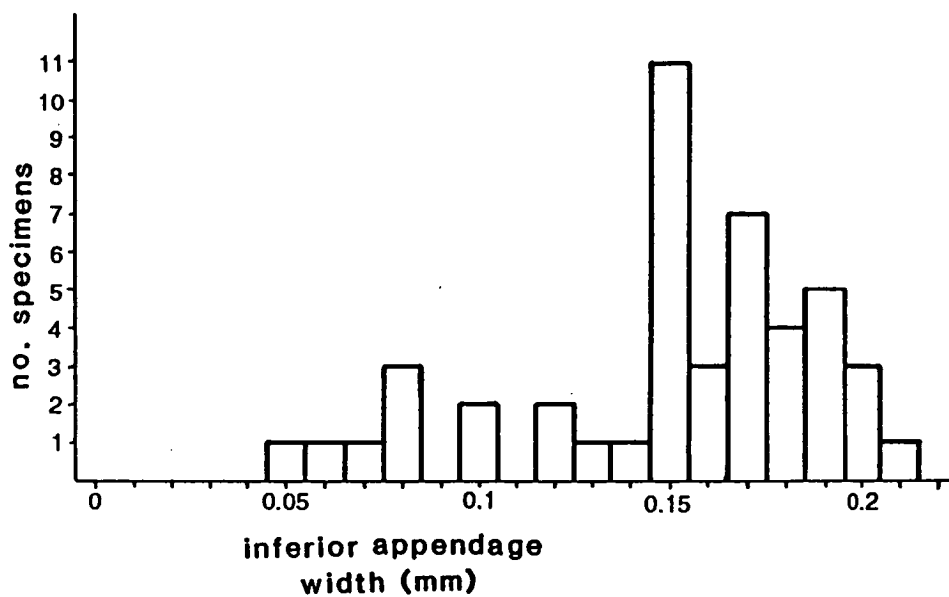
Figure 4.1.3. Frequency distribution of inferior appendage width of *Lingora* specimens measured.

with narrower inferior appendages (< 0.1mm) were recorded from a wide geographical range (Fig. 4.1.1): from North Esk R. Musselboro Rd. (5 specimens); Judds Ck (1 specimen); and Tyenna R. (1 specimen). This character is rare, and specimens occur in sympatry with specimens with wide inferior appendages. Inferior appendage width also varies in the other direction from the mode, i.e. there are specimens with unusually wide inferior appendages.

A single very unusual specimen was obtained from the North Esk River at Musselboro Rd, amongst normal specimens. It was distinct in having narrow inferior appendages that were not flattened, and very short and thick segment 9 ventral processes.

The female from the type locality was not distinguishable from *L. aurata* females, and no distinctly different larval forms were found.

Insufficient *L. vesca* morphs were obtained for electrophoretic analysis.

4.1.4 DISCUSSION.

No discontinuous variation has been demonstrated in any of the *L. vesca* diagnostic characters. Rather, the *L. vesca* morph is at the end of a continuous range of inferior appendage width, with other distinguishing characters randomly distributed. The occurrence of this morph in widely distributed populations, its sympatry with *L. aurata* morphs, and the lack of correlation of the various diagnostic characters, provides further evidence that *L. vesca* is a variant of *L. aurata*. Thus, results do not support the validity of *L. vesca* as a species distinct from *L. aurata*.

The original description of *L. vesca* was made on the basis of scanty material (a single male specimen). Opinions differ on how such material should be dealt with (Ross 1974), i.e. whether to set it aside until more material is available, or to describe forms as distinct species, as Neboiss (1977) has done. In the case of *L. vesca*, examination of further material in this study led to the conclusion that *L. vesca* is not separate from *L. aurata*. However, there are merits in splitting what may later be shown to be one variable species and describing the different forms, because a proposed name that proves to be a synonym can easily be assigned to its proper place and the correction is clear, whereas when a group is subsequently split, it will be difficult to remove the misidentification from literature, and will result in potential information loss from biological or other studies on a group which has been later split into more than one species.

For *L.vesca* to be a separate species, the *L. vesca* and *L. aurata* forms would have to be reproductively isolated. As they are contemporaneous there is no geographic or temporal isolation, so the barrier could be morphological, ecological, behavioural, biochemical or a postmating mechanism preventing fertilization or development. There is no information relating to ecological, behavioural or postmating isolation in this case; the difference in genitalia would make a morphological barrier to mating most likely. However, nothing is known about how *Lingora* male genitalia function in

mating, and thus no impairment of function of genitalia with narrow inferior appendages can be inferred.

The rarity of narrow inferior appendages in most populations may indicate selective pressure against it, although the basis of the variation is unknown and may not be genetic, but developmental. Collection of the *L. vesca* type late in the flight period (March 1st) may increase the likelihood that it is an abnormal form resulting from non-optimal development conditions.

No environmental parameters, such as the amount of chemical or organic pollution in the water, were measured to examine possible correlation with the number of variants found, although such factors may affect other freshwater insects.For example, recent studies have indicated a link between structural deformities in chironomid larvae and high levels of some pollutants (Pettigrove 1989).

In conclusion, the designation of *L. vesca* as a species distinct from *L. aurata* is not supported by the results of this study and therefore *L. vesca* is synonymous with *L. aurata*.

4.2 DIAGNOSIS OF *CONOESUCUS NEPOTULUS, C. BRONTENSIS* AND *C. ADIASTOLUS* SP.N.

4.2.1 INTRODUCTION

Male specimens of *Conoesucus nepotulus*, *C. brontensis* and *C. adiastolus* sp.n. were found to be difficult to correctly assign to species due to a lack of any obvious diagnostic characters. They can be separated from other *Conoesucus* species by genitalic morphology, but could not be distinguished from each other. As the type specimens of *C. nepotulus*, *C. brontensis* and other trichopteran species are adult males, it is important that they be distinguishable on the basis of morphological or other characters. Larvae of the three species are distinct, enabling reared adults of known identity to be examined for diagnostic characters.

Examination of *C. nepotulus* and *C. brontensis* male specimens revealed that the diagnostic character given by Neboiss (1977 p. 109) for separation of these species (posterior wing fork 1 footstalk present in *C. nepotulus* (Fig. 4.2.1b), fork 1 "sessile or nearly so" in *brontensis* (Fig. 4.2.1c)), was variable and did not correctly diagnose all specimens. In fact, venation could differ on the left and right sides of the same individual, a problem also reported for the New Zealand conoesucid genus *Pycnocentrodes* by Cowley (1976a).

In addition, specimens from the Gordon River 2km below the Serpentine junction (site 163), some of which were determined by Neboiss as *C. nepotulus* and some as *C. brontensis*, were shown by collection and rearing of larvae to be a new species (*C.adiastolus*). However, adult males could not be clearly distinguished from either *C. nepotulus* or *C. brontensis*.

On examination of reared specimens of the three species it appeared that *C. brontensis* and *C.nepotulus* could possibly be distinguished by the ratio of posterior wing fork 1 footstalk length to discoidal cell length. *C. nepotulus* and *C. brontensis* also apparently differ in size, measured as anterior wing length (Neboiss 1977). Characteristics of the male maxillary palps were also observed to differ between the species.

In order to test the value of these perceived differences as diagnostic characters, specimens of known identity (i.e. reared) were examined in detail.

4.2.2 MATERIALS AND METHODS

The following characteristics of wings were measured for males and females of each of the three species: anterior wing length (Fig. 4.2.1a); posterior wing length; posterior wing fork 1 footstalk length (f) (Fig. 4.2.1b); posterior wing fork 1 discoidal cell anterior margin length (dc) (Fig. 4.2.1b). The ratio f: dc was calculated.

Measurements were made to the nearest 1mm from drawings (25x) prepared as detailed in Taxonomic Methods (5.2),i.e. measurements were to the nearest 0.04mm. Localities are given as site numbers, for details refer to Appendix 3.
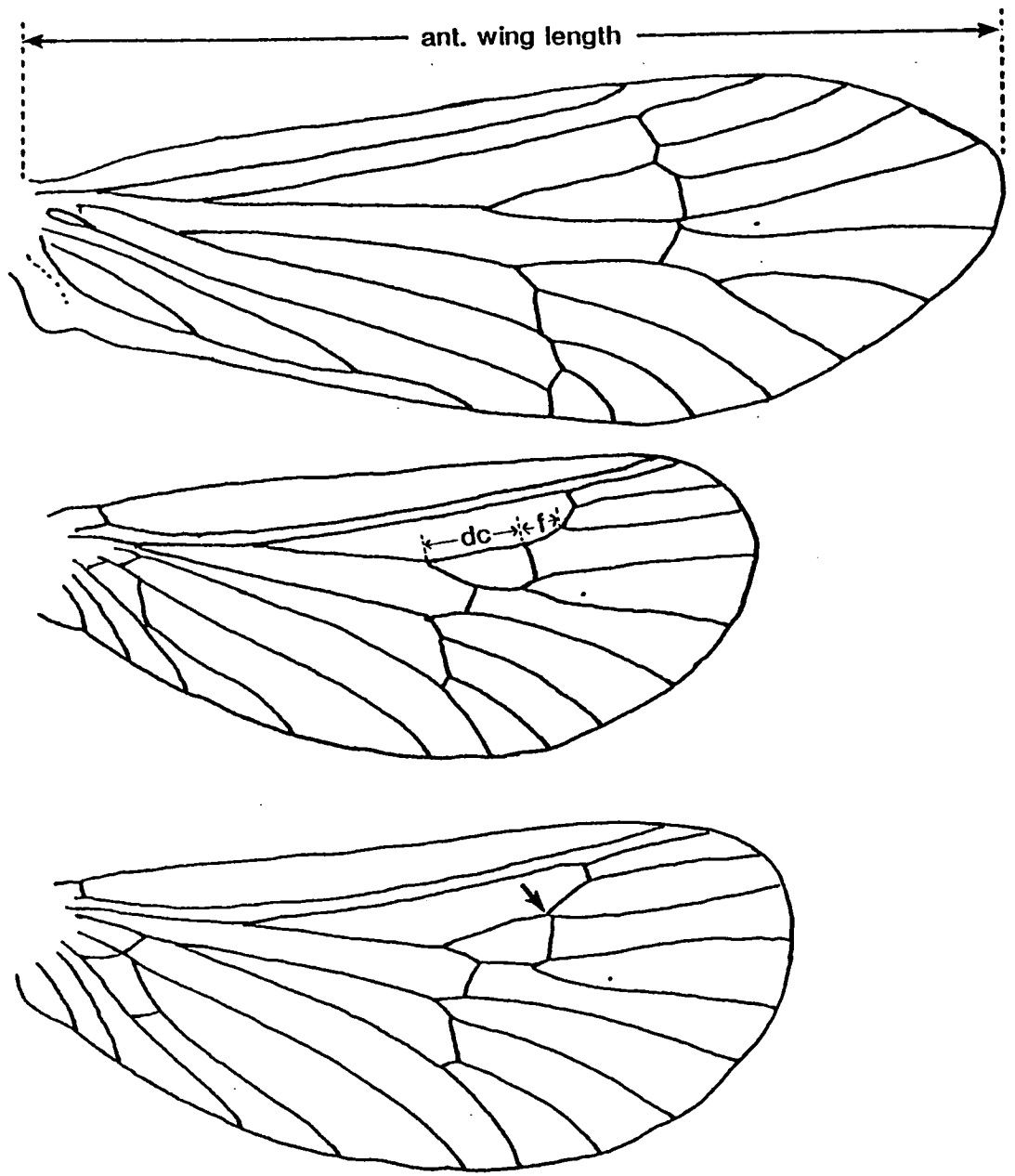
Figure 4.2.1. a) Anterior wing showing measurement taken; **b)** posterior wing of *Conoesucus nepotulus* showing measurements taken of f (posterior wing fork 1 footstalk length) and dc (discoidal cell upper margin length); **c)** posterior wing of *C. brontensis*, without fork 1 footstalk.

Specimens measured were: *Conoesucus brontensis*: 1♂, 1♀ netted, 1♀ reared, site 212 2.xi.1988; 2♂,1♀ reared, site 269 18.vii.1988; 3♂, 5♀ reared, site 150 1.xi.1988; 3♂, 1♀ reared, site 169 11.xi.1988; 1♂, 1♀ reared, site 246 22.x.1987.

Conoesucus nepotulus: 1♂, 4♀ reared, site 223 4.ix.1987; 1♂, 1♀ reared, site 223 12.x.1987; 4♂ reared, 233 5.x.1987, 22.x.1987 & 12.xi.1987; 3♂, 2♀ reared, site 152 27.x.1987; 2♂, 4♀ reared, site 170 14.x.1987.

C. adiastolus sp.n.: 2♂, 2♀ reared, 4♂ netted, site 164 29.xii.1988; 1♂ reared, site 164 11.xi.1988; 1♀ reared, site 164 29.xi.1988; 1♂ netted, 5♀ reared, site 133 13.i.1988; 2♀ reared, site 133 31.x.1988; 1♂ reared, site 166 13.i.1988.

Wing measurements were tested for normality of distribution using the Kolmogorov-Smirnov goodness-of-fit test (Biostat I, Pimentel & Smith 1990). Analysis of the proportions of the normal distribution (Zar 1984 p. 83) enabled calculation of the probability of correctly identifying a species on the basis of the f:dc ratio, and on the basis of anterior wing length. The normal deviate Z was calculated, where

$$Z = \frac{X_i - \mu}{S.D.}$$

for any measured value (X_i) from a normal population with mean μ and standard deviation SD. The proportion of the normal curve lying beyond Z (P) was then obtained from tables. The X_i values between which the species overlapped were calculated using an arbitrary limit P value of 0.005, i.e. only 0.5% of the population lie beyond the calculated X_i and are therefore not included in the calculated zone of overlap.

Lengths of male maxillary palp segments 2 and 3 (Fig. 4.2.2a) were measured at 50x using an ocular micrometer in a Wild M5 stereomicroscope, and the degree of sclerotization and setation noted. Specimens measured (reared males) were: *Conoesucus adiastolus*: 16, site 164; 2, site 133; 2, site 166.

Conoesucus brontensis: 3, site 150; 2, site 259; 1, site 169; 1, site 212.

Conoesucus nepotulus: 3, site 223; 1, site 171; 6, site 152; 7, site 233; 2, site 133; 1, site 170.

Specimens from the Victorian Museum (Appendix 2) were examined to check identities in the light of new diagnostic characters.

4.2.3 RESULTS
Wing measurements

The number of specimens measured and the mean, standard deviation and range of values measured are given in Table 4.2.1 (ratio f: dc), and Table 4.2.2 (anterior wing length). Posterior wing length measurements showed a similar pattern of distribution to anterior wing lengths, and as measurement of the anterior wing is easier and therefore more practically applicable, posterior wing measurements were not further analysed.

Table 4.2.1. Results of the measurement of the ratio of posterior wing fork 1 footstalk length f to discoidal cell upper margin length dc (f:dc), for *C. adiastolus* sp. n., *C. nepotulus* and *C. brontensis* males and females.

n= number of specimens measured; µ= mean; SD= standard deviation; R= range measured

Specimen	n	µ	SD	R
C. adiastolus ♂	11	O.241	0.078	0.08-0.40
C. adiastolus ♀	10	0.20	0.086	0.07-0.35
C. nepotulus ♂	9	0.404	0.087	0.31-0.55
C. nepotulus ♀	10	0.34	0.133	0.15-0.55
C. brontensis ♂	10	0.105	0.084	0-0.24
C. brontensis ♀	10	0.04	0.113	0-0.36

Table 4.2.2. Results of the measurement of anterior wing length for *C. adiastolus*, *C. nepotulus* and *C. brontensis* males and females.

n= number of specimens measured; µ= mean; SD= standard deviation; R= range measured.

Specimen	n	µ (mm)	SD	R (mm)
C. adiastolus ♂	12	6.46	0.526	5.2-7.2
C. adiastolus ♀	10	8.032	0.448	7.3-8.9
C. nepotulus ♂	11	5.618	0.405	5-6.3
C. nepotulus ♀	11	7.458	0.418	6.5-7.9
C. brontensis ♂	10	7.236	0.307	6.8-7.9
C. brontensis ♀	10	9.300	0.527	8.4-10.2

The measured ranges of f:dc and anterior wing length values for each species are shown in Fig. 4.2.2a-d.

The range of both f:dc and anterior wing length measured in *C. adiastolus* sp.n. males and females overlapped considerably with measurements from both *C. brontensis* and *C. nepotulus*.

For *C. brontensis* and *C. nepotulus*, observed ranges of f:dc in males and anterior wing length in males and females did not overlap. The probability of overlap of these characters, predicted from the normal curve, was analysed to test their value as diagnostic characters.

Measurements of f:dc were normally distributed, and results of analysis of proportion overlap of the predicted distribution for males of these two species (summarised in Table 4.2.3 (first column)) showed that:

1. The two species overlapped at f:dc values between 0.1795 and 0.3295, i.e. specimens with f:dc> 0.3295 were *C. nepotulus* (with < 0.5% probability of being *C. brontensis*); specimens with f:dc < 0.1795 were *C. brontensis* (with <0.5% chance of being *C. nepotulus*).

2. The proportion of *C. brontensis* population with f:dc in the overlap zone was 0.1817.

3. The proportion of *C. nepotulus* population in the overlap zone was 0.1610.

4. Thus, for an unknown specimen with f:dc in the overlap zone, the probability of it being *C. nepotulus* was 46.98%, and 53.02% of being *C. brontensis*.

5. The probability of picking a *C. nepotulus* male with f:dc =0 (i.e. footstalk absent) was < 0.0001.

Anterior wing length measurements were normally distributed. The ranges measured for *C. brontensis* and *C. nepotulus* were separate for both males and females (Fig. 4.2.2c,d). Results of analysis of normal distributions are given in Table 4.2.3 (columns 2 and 3).

Maxillary palps

Measurement of male maxillary palps showed that they were different for each of the three species (Figs 4.2.3a-d). In all species palps were densely setose with golden and dark setae; segment 3 had very dense black setae. For *C. adiastolus* (Fig. 4.2.3a), the third segment was always very nearly equal in length to segment 2. The base of segment 3 (about 1/3-1/2 of segment length) was sclerotised and pigmented golden.

For *C. brontensis* (Fig. 4.2.3b), the length of segment 2 was 0.30-0.35 mm; segment 3 was much longer, about 3x length of segment 2, although often curved and thus difficult to measure accurately. The base of segment 3 was sclerotized and usually golden although in a few specimens this was unpigmented. There was little variation in length of segment 3, unlike *C. nepotulus*.

Palps of *C. nepotulus* (Figs 4.2.3c,d) had segment 2 length from 0.18-0.22
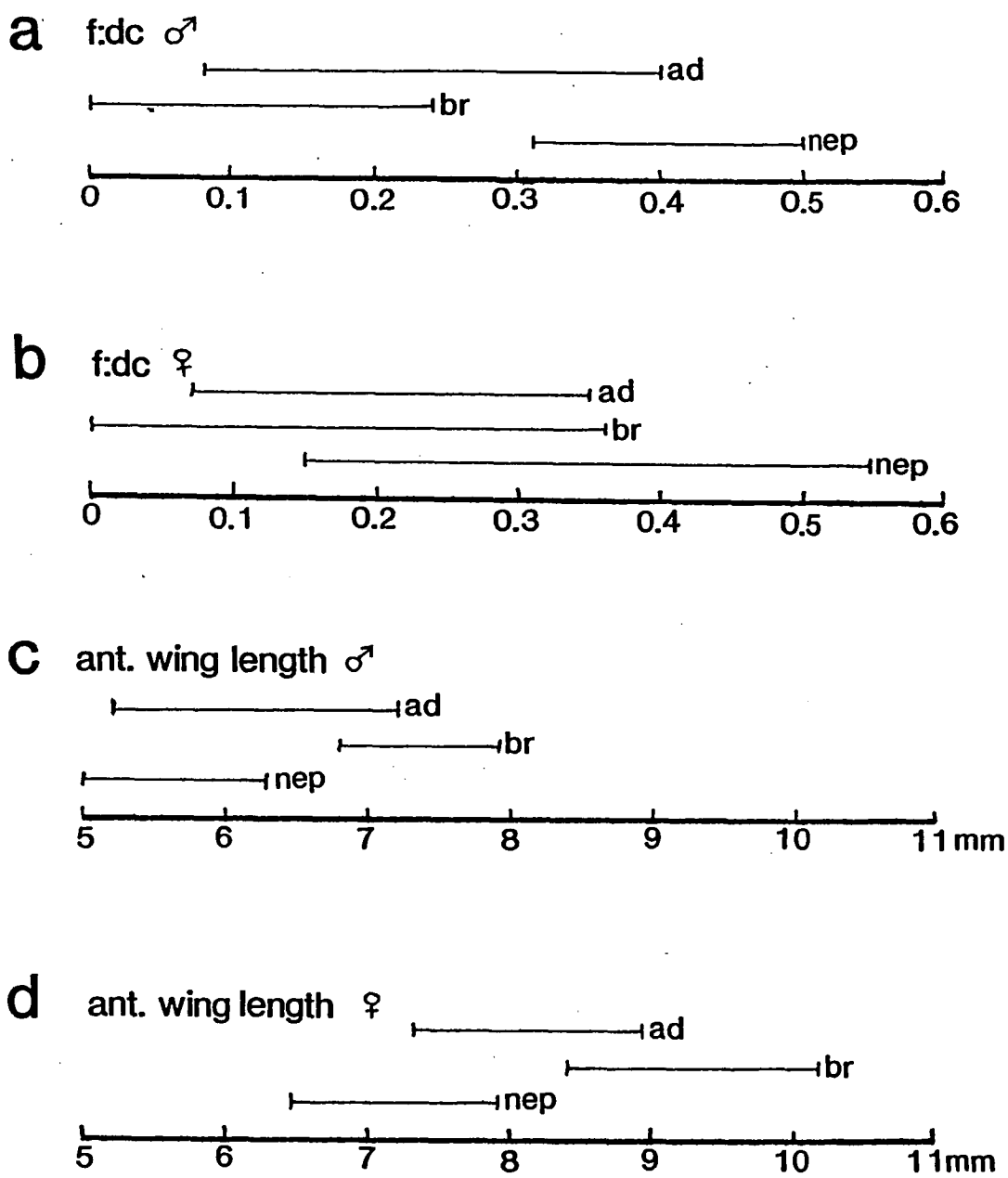
Figure 4.2.2. Ranges of f:dc measured for **a)** males and **b)** females of *C. adiastolus, C. brontensis, C. nepotulus*; ranges of anterior wing length measured for **c)** males and **d)** females.

Table 4.2.3. Results of analysis of normal distributions of anterior wing length and posterior wing fork 1 f:dc ratio for *Conoesucus brontensis* and *C. nepotulus*. l = length; P = the proportion of the population.

	Character f:dc ♂	ant. wing l ♂ (mm)	ant. wing l ♀ (mm)
zone of overlap	0.1795-0.3295	6.44-6.66	7.94-8.54
P(*C. brontensis* within overlap)	0.1817	0.0251	0.0685
P(*C. nepotulus* within overlap)	0.1610	0.0162	0.058
Probability specimen in overlap=*C. nepotulus*	46.48%	39%	45.8%
Probability specimen in overlap=*C. brontensis*	53.02%	61%	54.2%
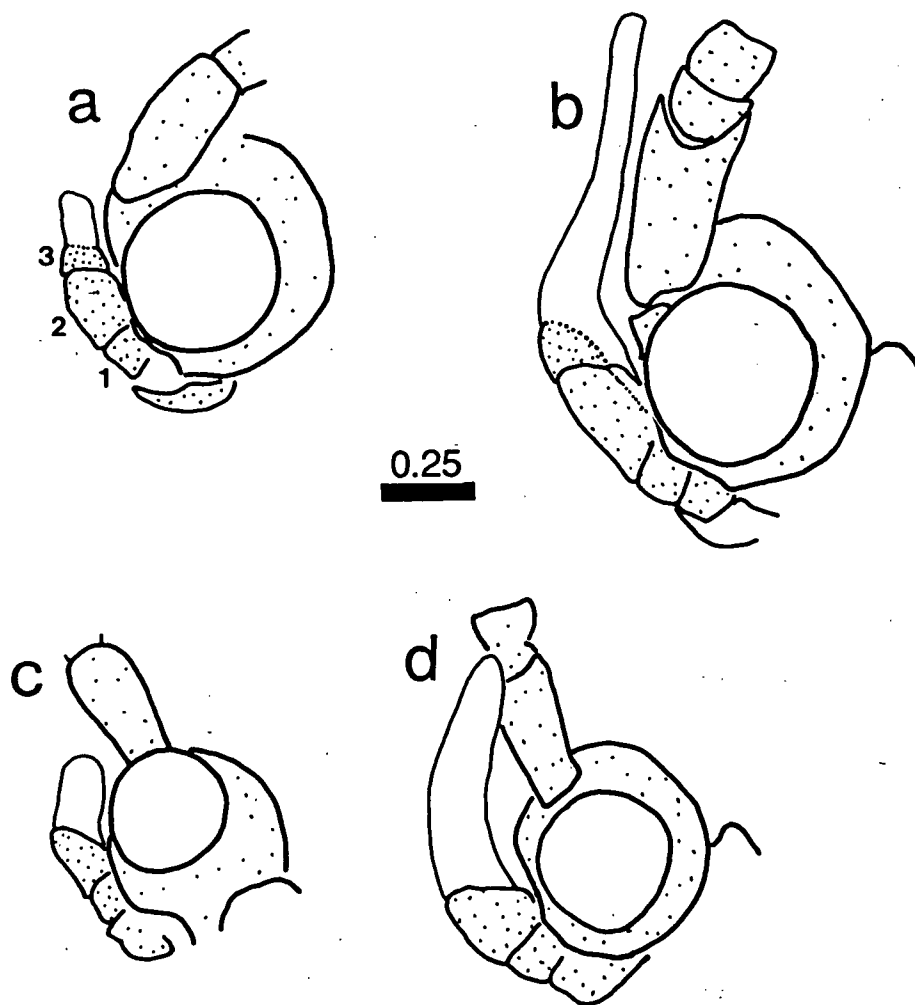
Figure 4.2.3. Male maxillary palps, lateral view, showing diagnostic characters (see text): **a)** *Conoesucus adiastolus* sp. n., segments numbered; **b)** *C. brontensis*; **c)** and **d)** *C. nepotulus*.

mm, about the same as *C. adiastolus*. The length of segment 3 was quite variable, ranging from less than the length of segment 2 to 3x its length: segment 3 is apparently expandable. There was no sclerotisation or pigmentation of segment 3.

There are some differences in general appearance of male genitalia of the three species, which may be useful when comparing different specimens but do not enable diagnosis. *C. adiastolus* has very rounded superior appendages, segment 9 dorsal hump is pointed slightly, inferior appendages mesal projections have slightly extended base, segment 10 is fairly broad and not sharply upturned, segment 9 projections are curved downwards. *C. brontensis* genitalia are generally stouter and darker, there are fingerlike projections from the inside of inferior appendages, inferior mesal projections have extended base, segment 10 is stout with sclerotized band and sharply upturned, dorsal hump of segment 9 is rounded, segment 9 dorsal projections are relatively shorter, superior appendages are fairly long. *C. nepotulus* segment 9 dorsal hump is small and may be pointy, segment 10 is relatively slender, inferior appendages are not extended at base from which mesal projections arise, inferior appendages lack fingerlike projections, segment 9 projections are relatively long, superior appendages are fairly small.

Identification of specimens from the Victoria Museum (listed in Appendix 2), including paratypes of *C. brontensis* and *C. nepotulus*, could be made with confidence on the basis of maxillary palp characters, and general appearance (including size); measurement of wing characters was not necessary. Specimens which had previously been incorrectly determined as *C. nepotulus* were: 2 of the 4 *C. nepotulus* ♂ paratypes (Dip River Falls (site 7) 1.xii.1974 A. Neboiss), which were identified as *C. brontensis*; 1♂, Flowerdale River Meunna (site 12) 4.xi.1972 A. Neboiss (=*C. brontensis*); 1♂, Leven River near Heka (site 28)17.xi.1972 A. Neboiss (=*C. brontensis*); 3♂, Sir John Falls Cataract Ck Gordon River trib. (site 156) 9.i.1977 Neboiss, Coleman, Allbrook (=*C. adiastolus*); 3♂, Ropeway Ck 400m below Smith and Gordon River junction 2.ii.1977 Coleman Richardson, Edgar (=*C. adiastolus*); 4♂, small creek Gordon River 0.5km upstream Olga River 23.ii.1976 Coleman & Allbrook (=*C. adiastolus*). A male labelled as *Conoesucus* sp. from Franklin River-Roaring Ck junction (site 157) 8.i.1977 Coleman, Neboiss, Allbrook was determined as *C. adiastolus*. All the Museum specimens determined as *C. brontensis* had been correctly identified.

4.2.4 DISCUSSION

Neither anterior wing length nor f:dc of posterior wing fork 1 were found to absolutely diagnose *C. adiastolus* sp.n., *C. nepotulus* and *C. brontensis*. The high degree of overlap of *C. adiastolus* with *C. nepotulus* and *C. brontensis* in both of the wing characters measured indicates that neither can be used to distinguish males nor females of this species from either *C. nepotulus* or *C. brontensis*.

For distinguishing male *C. nepotulus* from *C. brontensis*, both f:dc and

anterior wing length were shown to give a high probability of correct identification. Although there was some overlap between the two species, only a small proportion of the predicted total population fell within the zone of overlap.

The proportion of the population of each species within the overlap zone was greater for f:dc than for anterior wing length, therefore there is a higher probability of correct identification on the basis of wing length than on the basis of f:dc. Also, anterior wing length is more easily measured than f:dc, as it doesn't require removal of wings or visualization of venation, although measurement may be slightly less accurate due to the poorly defined proximal end of the wing.

Anterior wing length was also found to be a useful diagnostic character for females of *C. brontensis* and *C. nepotulus*; however, females are difficult to distinguish from other species on the basis of genitalia, so such a diagnostic character will only be useful when specimens are known to be either *C. nepotulus* or *C. brontensis* which is an unlikely situation.

A priori, size (as measured by wing length in this study) may be considered unlikely to be reliable for species diagnosis due to a possible high level of variation. However, *C. nepotulus* and *C. brontensis* were shown to be separable with a high level of probability on the basis of wing length, although wider geographic sampling may reveal a higher degree of overlap in wing length between the species.

In comparison to the wing characters measured, the male maxillary palps were found to provide reliable diagnostic characters. *C. nepotulus* can be distinguished by the lack of sclerotization of segment 3. *C. brontensis* and *C. adiastolus* , in which the base of segment 3 is sclerotized, can be distinguished by the long segment 3 in *C. brontensis*, compared to *C. adiastolus* in which segment 3 is about equal in length to segment 2. These characters were used to correctly identify specimens from the Southern Ranges (sites 194) and Old River (site 189), which had been determined as either *C. nepotulus* or *C. brontensis* by Neboiss.

This study demonstrates the need to describe species on the basis of more than one life stage if possible. Although larvae of all three species are distinct, *Conoesucus adiastolus* males can be reliably distinguished from *C. nepotulus* and *C. brontensis* only on the basis of maxillary palp characteristics. *C. brontensis* and *C. nepotulus* are distinguished on the basis of maxillary palp characters, and wing characters in which there is some overlap between the two species.

CHAPTER 5. TAXONOMY AND DISTRIBUTION

5.1 INTRODUCTION

There are no published descriptions or keys for larvae and pupae of Australian Conoesucidae, and immatures have previously been described for only one species each in the Calocidae and Helicophidae. Such information is essential to enable accurate identification of immature stages in biological and ecological studies of freshwater systems, and for a comprehensive data set for phylogenetic analysis.

Descriptions and figures of larvae and pupae are given for the 17 Tasmanian species of Conoesucidae, two species of Helicophidae and two species of Calocidae for which larvae have been associated with adults (refer to Table 1.1). Larvae and pupae of *Alloecella grisea* (Helicophidae) and *Caloca saneva* (Calocidae) have been previously described, by Drecktrah (1984) and Neboiss (1979) respectively. New Zealand species have been described by Cowley (1978).

In addition, adults of two new *Conoesucus* species are described and figured here, and females of *Costora luxata, C. seposita* and *C. krene/ramosa* are described and figured for the first time. (As larvae of *Costora krene* and *C. ramosa* could not be distinguished from each other, females could not be identified to species by rearing).

Keys are given to families, genera and species of larvae and pupae, and existing keys to adults are improved. Keys to immatures do not rely on case characters, although some are characteristic of taxa, since cases can be lost during preservation, and some characters may be variable (e.g. the proportion of sand:silk in *Matasia, · Lingora, Conoesucus norelus* and *C. nepotulus*).

Changes made to the existing taxonomy are the synonymy of *Lingora vesca* with *L. aurata* (ch. 4.1), and description of two new *Conoesucus* species. In addition, there is evidence from immatures that *Lingora, Hampa* and *Matasia* are congeneric; however, this conflicts with adult characters (male maxillary palps are 2-segmented and a bilobed process is present on the face in *Costora, Hampa* and *Matasia; Lingora* male maxillary palps are 1-segmented and process is absent (A. Neboiss pers. comm.)). On the basis of relationships suggested by immatures, a "generic" description is given for immatures of *Lingora, Hampa* and *Matasia*.

Distribution maps are given for all the described species, and several species for which larvae were not associated with adults but for which the known range has been significantly expanded. Data on adult distributions (Neboiss 1977, Neboiss *et al.* 1989) are included on the maps. Detailed zoogeographic analysis was not possible due to the lack of a representative sample of species (with ecological, phylogenetic and distributional data) from all the areas in which they occur (mainland Australia, New Zealand, Chilean South America).

5.2 MATERIALS AND METHODS
Preparation and drawing

Larvae and pupae were identified by rearing them to the adult stage. Whole

larvae or adult abdomens were prepared for microscopic examination by maceration of soft parts in hot 5% KOH for about 10 minutes (larval abdomens were punctured first), rinsing in glacial acetic acid, then clearing in glycerol. Specimens were then dissected and mounted in glycerol; material was subsequently stored in glycerol. A few specimens of each series were stained by adding a few drops of acid fuchsin to the acetic acid rinse, to clarify the structure of the genitalia and make the larval abdominal cuticle visible.

Wings to be drawn were removed from the body, denuded with a fine paintbrush, and stained in acid fuschin to visualise venation. They were mounted on a flat slide in glycerol or alcohol, under a coverslip.

Pupae were drawn from exuviae of reared specimens; whole specimens were also examined.

Drawings were made with the aid of a drawing tube on a Wild M20 compound microscope and a drawing mirror on a Wild M5 stereomicroscope. Untreated material was also examined, and larval sclerites from pupal cases often showed setal and scar patterns more clearly than other material. Manipulation of lighting and angle of specimen was often required to visualize fine setae.

All material examined is lodged at the Museum of Victoria.

Notes on the descriptions and figures

Morphological terminology of immatures (Figs 5.1-5.3) is based on Wiggins (1977); adult morphology is given in Neboiss (1981b).

Descriptions and figures are of late instar larvae, although they may not be the final instar, as instar could not be determined from head width.

Localities of material examined are given as a site number; for details of the localities refer to Appendix 3. Unless otherwise stated, all material was collected by the author, in Tasmania.

Abbreviations: AN= Arturs Neboiss; JD= John Dean; IFC= Inland Fisheries Commission; L= larvae; P= pupae; em.= date of emergence in laboratory; SA = setal area; on the maps E = endemic to Tasmania.

The drawings attempt to represent the organism as closely as possible, showing important taxonomic characters. However, there are limits to the accuracy of representation, e.g. fine pale setae (such as mesonotal setae) are shown clearly on the drawings although they may be difficult to see on specimens.
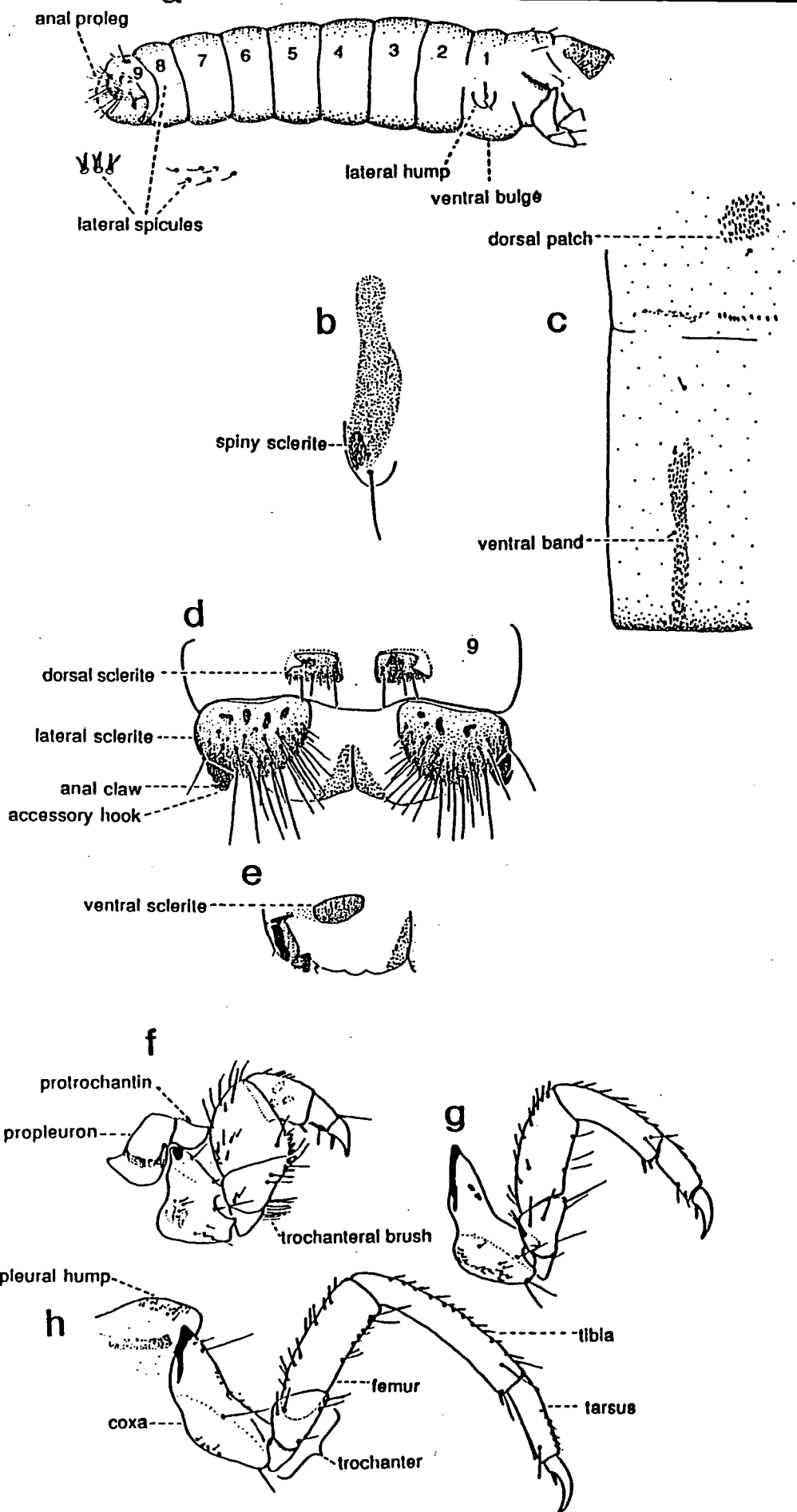
Figure 5.1. Morphological terminology, larva. **a:** abdomen, lateral; **b:** segment 1 lateral hump enlarged; **c:** abdominal segment enlarged; **d:** tergite 9 and anal prolegs, dorsal; **e:** anal proleg, ventral; **f, g, h:** fore-, mid- and hindleg.
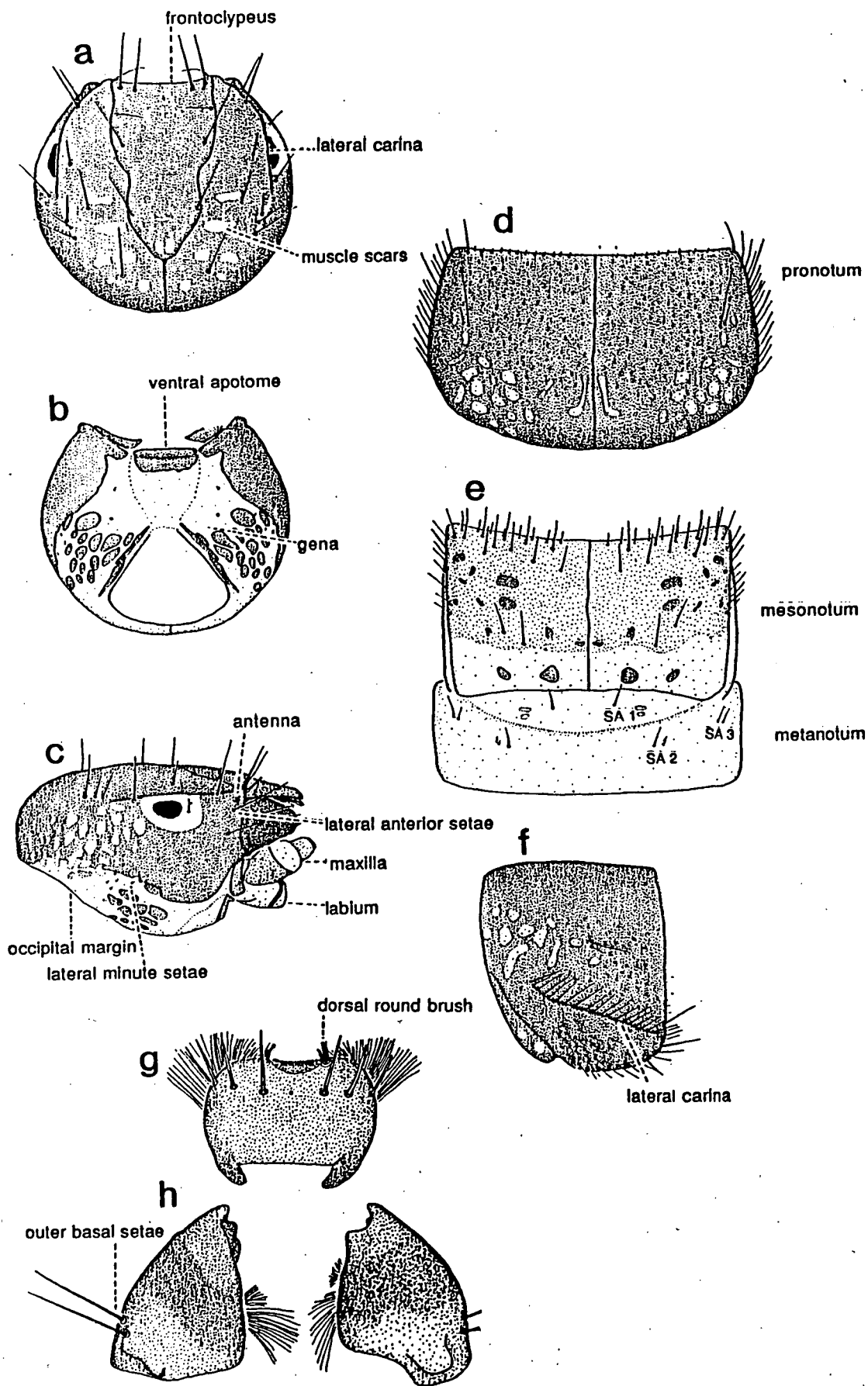
Figure 5.2. Morphological terminology, larva. **a, b, c:** head, dorsal, ventral and lateral; **d:** pronotum, dorsal; **e:** meso- and metanotum, dorsal; **f:** pronotum, lateral; **g:** labrum; **h:** mandibles.
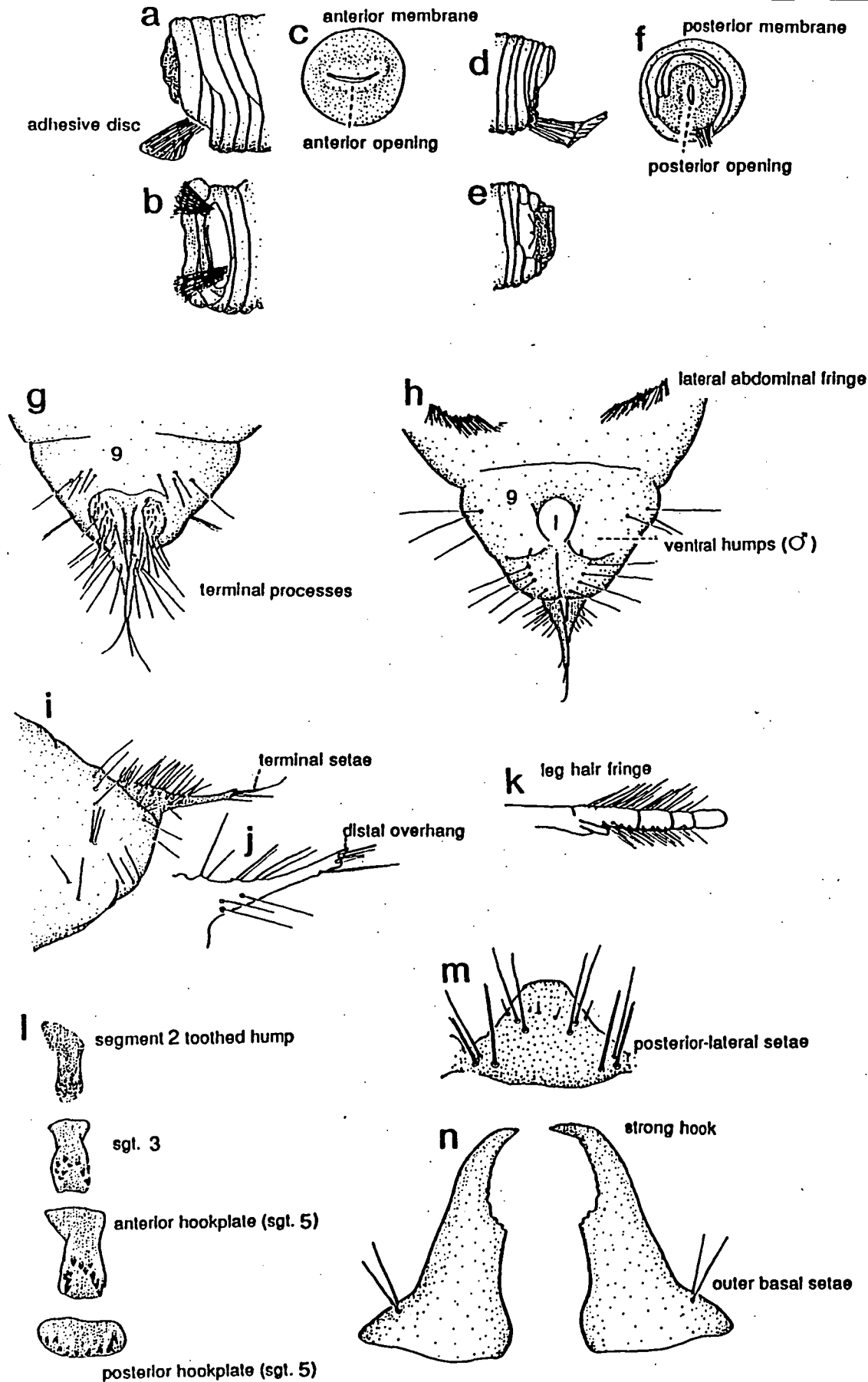
Figure 5.3. Morphological terminology, pupa. **a, b:** anterior end of case, lateral and ventral; **c:** anterior membrane; **d, e:** posterior end of case lateral and ventral; **f:** posterior membrane; **g, h, i:** terminalia dorsal, ventral and lateral; **j:** terminal process lateral, enlarged; **k:** tarsus; **l:** dorsal abdominal hookplates; **m:** labrum; **n:** mandibles.

5.3 DESCRIPTIONS, KEYS AND DISTRIBUTION MAPS.

Key to family for adults of Conoesucidae, Calocidae and Helicophidae is given in Neboiss (1986).

Key to family for larvae of Australian Conoesucidae, Calocidae and Helicophidae (based on J. Dean & D. Cartwright pers. comm., presented at Trichoptera workshop, MDFRC, Albury, Feb 1991).

> 1.-Ventral surface of head capsule with genae widely separated at occipital foramen...**Conoesucidae**
> -Ventral surface of head capsule with genae close together and almost abutting at occipital foramen.................................2

> 2.-Antennae situated very close to eyes; protrochantin fused to propleuron; segment 1 lateral hump with oval area of spines only, no additional sclerites; metanotum SA1 with row of≥ 4 setae on each side
> ....**Calocidae**
> -Antennae situated about 1/2 way between eyes and anterior margin of head capsule; protrochantin not fused to propleuron; segment 1 lateral hump with a narrow longitudinal sclerite in addition to oval spiny area; metanotum SA 1 with only 1 seta on each side (Aust.) or group of up to 5 setae (New Zealand species)...**Helicophidae**

Key to family for pupae of the Conoesucidae, Helicophidae and Calocidae studied.

> 1.-Foreleg hair fringe present........................*Alloecella*
> **(Helicophidae)**
> -Foreleg hair fringe absent......................... 2

> 2.-Segment 2 toothed hump present.................**Conoesucidae**
> -   "   "   "   "   absent............... **Calocidae**
> (*Tamasia + Caenota*)

5.3.1

Family CONOESUCIDAE Ross
1967 stat. nov.

Larva.

Case cylindrical.

Abdomen cylindrical; lateral hair fringe absent; lateral line of minute bifid and/or single spicules. Anal claw with single dorsal accessory hook, sometimes notched and

appearing double; claw with several short and minute setae; area between anal prolegs with minute spicules. Segment 1 lateral hump with small oval sclerite of spines.

Head round or almost round in dorsal view; 2-3 muscle scars on each side of posterior half of dorsum, posterior scars smaller and rounded; long seta on edge of dorsum between eye and anterior margin, group of setae behind eye on dorsum. Eye smooth or slightly bulging, surrounded by pale area. Frontoclypeus with pair of irregular apical scars and row of 3 just anterior to apex; 3 pairs of lateral setae; each anterolateral corner with single clear curved seta and pair of long brown setae, additional setae present in some species.

Antennae small, very close to anterior margin of head capsule, below carina (if present).

Laterally, head with 2 long setae near anterior margin; many scars posterior to eye. Ventrally, head largely unpigmented in last instars, with dark scars in posterior area, non-setose pit and short clear seta anterior to scars on each side; ventral apotome subquadrate, pigmented anteriorly, anterior margin generally straight or slightly curved outwards, sutures indistinct; genae widely separated.

Mandibles short and stout, about as long as wide or slightly longer, smooth or with blunt apical teeth; each mandible with 2 large outer basal setae, additional setae present in some species; mesal brushes of long hairs.

Labrum quadrate-oval, with mid row of 3 pairs of pale stout setae and central non-setose pit, 2 clear stout setae on each anterolateral margin; anterior margin with slight indentation and brush of straight short hairs, small round dorsal brush each side of indentation; ventral long brushes.

Pronotum heavily sclerotized, polygonal reticulation texture; muscle scars median and posterolateral; dorsum anterior to scars scattered with minute fine setae; anterior margin smooth, with regular row of minute setae, large setae present in some species.

Mesonotum weakly sclerotized, posterior 1/3 unpigmented in all species except *Costora ebenina*; anterior row or band of medium-long setae, anterolateral area setose. Metanotum largely or entirely membranous and unpigmented; curved transverse fold between SA 1 and 2; pair of minute setae anteriorly.

Protrochantin well-developed. Legs even brown, increasing in length and slenderness posteriorly, midleg about 2x length of foreleg and 3/4 length of hindleg; hindleg femur cylindrical, straight. Fleshy, setose pleural humps basal to mid- and hindleg.

Pupa.

Case constructed from larval case by shortening and adding anterior and posterior closure membranes; anterior opening transverse slit, posterior vertical slit or oval.

Gills absent; lateral fringe extending from posterior of segment 6, 2/3 along segment 8. Lateroventral elongate brown sclerites on segments 2-8. Dorsal hookplates on anterior of segments 3-6, posterior of segment 5; toothed hump on segment 2; additional sclerites may occur.

Mandibles broad basally, distal 1/2-1/3 tapered and curved, inner curved margin serrated; in some species right mandible more strongly hooked than left; each with 2 large outer basal setae, additional setae in some species. Labrum broader at base, truncate cone or hemispherical; anterior margin papillate.

Terminalia: segment 9 ventrally in M with 2 low lateral humps and central round hump (genitalia sheaths); terminal processes elongate, with 2 clear terminal setae arising subapically.

Midleg with hair fringe, either dense on both sides, very sparse on one side or absent; fore- and hindlegs lacking fringe.

Key to adults of Australian genera of the family Conoesucidae (modified from Neboiss 1977 p. 100 and Neboiss 1991; couplets 1-4 as in Neboiss 1977).

5.-Male with bilobed hinged process on frons; female terminalia with pair of more-or-less distinct dorsolateral processes; female with distinct setae on sternite 8 only... *Costora*

-Male without bilobed process; female without dorsolateral processes; female with distinct setae on all sternites................... *Conoesucus*

Key to genera of Tasmanian Conoesucidae larvae.

1.-Protrochantin fused to propleuron; tergite 9 single sclerite, or unpigmented [unknown for *Hampa*].............. 2

-Protrochantin separated from propleuron by suture; tergite 9 consisting of two pigmented sclerites; (case slightly curved and tapered, just longer than larva)..................................... *Conoesucus*

2.-Frontoclypeus anterolateral setae 2 long one clear curved; pronotum smooth texture, not spiny; mandibles with 2 outer basal setae; anal leg lateral sclerite faces dorsally; anal leg ventral sclerite brown oval; (case curved and tapered, elongate, much longer than larva, except in ebenina in which the case is just longer)...*Costora*

-Frontoclypeus with many anterolateral setae; pronotum with minute spines, either anterior band or anterior 2/3; mandibles with many outer basal setae; anal leg lateral sclerite facing posteriorly; anal leg ventral sclerite a thin bar (unknown for *Hampa*); (case straight or almost straight, only slightly longer than larva)...*Lingora, Hampa, Matasia*

Partial key to genera for pupae of Conoesucidae studied.

1.-Midleg hair fringe on both sides................... *Costora*
Lingora, Hampa,
Matasia

-Midleg hair fringe on one side/absent............. *Conoesucus*

5.3.1.1

Genus **Conoesucus** Mosely

Mosely, 1936, p. 408; Mosely and Kimmins, 1953, p. 87; Neboiss, 1977, p. 109.

Type species: *Conoesucus fromus* Mosely

Larva.

Case slightly curved and tapered, length just longer than larva; anterior and posterior margins straight or slightly oblique; constructed from sandgrains and/or circularly arranged bands of plant material or entirely of silk. Posterior membrane flat or projecting, with central circular or slightly oval opening.

Abdomen with branched gills present on segments 1-3 in some species; lateral row of bifid and/or single spicules on segment 8 (may be visible only on cleared specimens at high magnification), segments 2/3-7 with row or band of single spines and anterior bifid spicules; segments 2-7 with dorsal patches and a ventral band of minute elongate spicules.

Tergite 9 with 2 irregularly pigmented oval-rectangular sclerites (borders visible only in stained specimens); each with 4-7 setae on posterior margin, of which 1 pair is long.

Lateral sclerites of anal prolegs brown-gold, pigmentation varying with species, 3-4 kidney-shaped scars in anterior unpigmented area; densely setose posteriorly, with long black setae decreasing in size antero-medially, antero-median area bearing short fine setae. Ventral sclerites of anal prolegs brown, oval; width about 2x length.

Head round in dorsal view, tapering slightly anteriorly in some species, colour golden to very dark brown, polygonal reticulation texture, sometimes with smoother texturing on frontoclypeus. Strong carina extending from anterior margin of head capsule to posteriad of eye. Several long setae on dorsum. Scar width 3-5x length. Frontoclypeus somewhat variable in shape, broadest anteriorly, apex pointed. Anterior pair of lateral setae pale, recumbent; mid pair dark and upright, posterior pair either upright or recumbent (possibly depending on instar).

Ventral mandibular articulation not prominent. In some species, lateral head capsule with short fine setae in scar-free area between lateral and ventral scars.

Mandibles: right shorter than left, ventral margins undercut relative to dorsal, each with 2-4 blunt apical teeth, right with broad dorsal thumb-like tooth, left with straight dorsal margin; short distal and longer proximal mesal brushes; 2 outer basal setae.

47

Pronotum dark brown, with median elongate scar and scars in posterolateral area. Dorsal long setae varying with species. Anterolateral corner shape varying with species from round to pointed; strong lateral carina extending posteriorly from corner or just posterior to it, more or less straight, curving slightly dorsad posteriorly; row of setae along carina. Lateral face setose, same colour as dorsum.

Mesonotum about as wide as long, anterior 2/3 pigmented, posterior 1/3 mostly unpigmented, pair of long dark setae about 2/3 from anterior margin (usually near posterior margin of pigmentation, in unpigmented area in some species). Scars darker, two pairs on posterior unpigmented area, central pair, group of about 5 smaller in anterolateral area. Metanotum SA 1, 2 and 3 with up to 4 setae and sometimes pigmented area; or SAs with numerous minute clear spines (*norelus*).

Protrochantin not fused to propleuron; shape slightly variable within species, broadly cow-horn shaped, rectangular with extended corner, or narrow and tapering to apex, tip slightly pointed and upturned; upper margin with few short setae. Pleural humps with many minute setae, with additional long seta in some species.

Gonads: each testis with four round lobes.

Pupa.

Case: anterior membrane domed or flat, set in from margin in some species, with upwardly curved transverse slit at or below centre; posterior membrane flat or domed, with vertical central narrow slit about 1/2 the length of membrane diameter, or opening oval in some species.

Midleg hair fringe on one side only, very sparse or lacking in some species. Anterior hookplates roughly oval, anterior margins sometimes indistinct, hooks scattered or in row; posterior plates rounded-quadrate or about 2x as wide as long.

Labrum with anterior pair of median setae, 2 large pairs in mid-transverse row and single medium seta on each lateral margin, 3 large setae in each posterolateral corner (2 large, 1 smaller).

Terminalia: dorsum of segment 9 with tranverse row of 3-6 setae each side, more setae laterally. Processes broad basally, tapering to cylinder; setose dorsally.

Key to Tasmanian species of *Conoesucus* adult males (modified from Neboiss 1977 p. 109; couplets 1-2 as in Neboiss).

3.-Segment 10 in lateral view very slightly curved upwards, margins parallel, apex broad and rounded (dark coloured) .... *C. digitiferus*
-Segment 10 in lateral view with margins not parallel, broadening then tapering to apex.................................... 4

4.-Segment 10 turned upwards almost at right angle, tapering to somewhat triangular apex.................................5

-Segment 10 turned only slightly upwards, apex triangular/pointed, segment 9 dorsal processes stout............................... *C. notialis sp. n.*

5.-Maxillary palp segment 3 completely lacking sclerotization

.... *C. nepotulus*

-Maxillary palp segment 3 sclerotized at base..... 6

6.-Segment 3 about three times length of segment 2

.... *C. brontensis*

-Segment 3 about equal in length to segment 2....*C. adiastolus* **sp. n.**

Key to larvae of Tasmanian *Conoesucus* species.

1.-Pronotum anterolateral corner pointed; gills present.

.... 2

-Pronotum corner not pointed; gills absent........ 4

2.-Pronotum anterior margin with several long setae.

.... 3

-Pronotum anterior margin without long setae.... .*C. notialis* **sp. n.**

[silk case]

3.-Metanotum all setal areas (SA) with many small spine-like setae

.....................*C. norelus* [sand case]

-Metanotum all SAs with 1-3 longer and 2-3 small setae.

.....................*C. fromus* [plant case]

4.-Pronotum anterior margin with about 4 long dark setae

.... *C. digitiferus* [plant

case]

-Pronotum anterior margin lacks long setae....... 5

5.-Pronotum anterolateral corner square; carina begins mesad of corner

.........................*C. nepotulus* [sand case]

-Pronotum anterolateral corner rounded; carina begins at anterolateral angle

.........................6

6.-Mesonotum with dense anterior band of long setae 3-4 wide; pronotum anterolateral corner very round.....................*C. adiastolus* **sp. n.**

[plant case]

-Mesonotum anterior band of setae sparse, 1-2 wide; pronotum anterolateral

corner with definite angle............................ *C.brontensis* [silk case]

Key to pupae of *Conoesucus* species studied.

1.- Right mandible more strongly hooked........... 2
  -Mandibles equally hooked......................... 5

2.-Posterior hookplates about as wide as long...   3
  -Posterior hookplates much wider than long....   4

3.-Terminal processes pointed; distal overhang
  short... *C. norelus*
  -Terminal processes rounded; no distal
  overhang.. *C. fromus*

4.-Posterior hookplate with 8-15 hooks; terminal processes pointed,
  overhang short..................................... *C.adiastolus* **sp.n.**
  -Posterior hookplates with 3-7 hooks; terminal processes rounded, no
  overhang.. *C. digitiferus*

5.-Terminal processes with upturned apex, pointed
  .... *C. nepotulus*
  -Terminal processes straight, apex rounded....... 6

6.-Terminal processes with no distal overhang; processes
  smooth.. *C. brontensis*
  -Terminal processes with short distal overhang; processes
  toothed... *C. notialis* **sp. n.**

Conoesucus adiastolus **sp. n.**
(Figs 5.4-5.9)

Etymology: *adiastolus* from the Greek *adiastolos*: not separated, confused; refers to the similarity of adults of this species to *C. nepotulus* and *C. brontensis*.

Adults.

Dark coloured. Male anterior wings without specialised hairs or fold; posterior wing with row of bristles/long hairs on Cu and Cu_2. Cu_2 ending at margin in both sexes, connecting to Cu_{1b} by cross vein. Posterior wing: Sc and R running separately to margin; f1 with footstalk of varying length; 2A not reaching margin in either sex. Anterior wing length ♂ 5.25-7.25mm, ♀ 7.25-9.0mm.

Male maxillary palps with long golden and brown hairs; segment 1 short, segment 2 about 2x length of 1, broad; segment 3 short, about length of 2, base of

igure 5.4. *Conoesucus adiastolus* sp. n. larva. **a**: case, lateral; **b**:
osterior membrane; **c**: larva lateral; **d**: lateral spicules, enlarged; **e**:
bdominal segment, lateral; **f**: segment 1 lateral hump; **g**: tergite 9 and anal
gs, dorsal; **h**: anal leg, ventral.

a

b

1

c

d

0.05

e

f

0.1

0.2

g

h

0.2

0.2
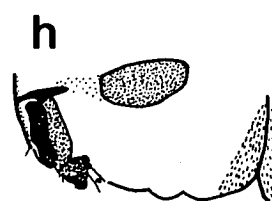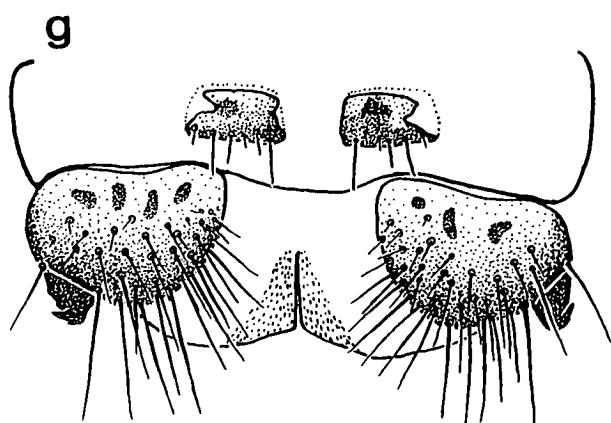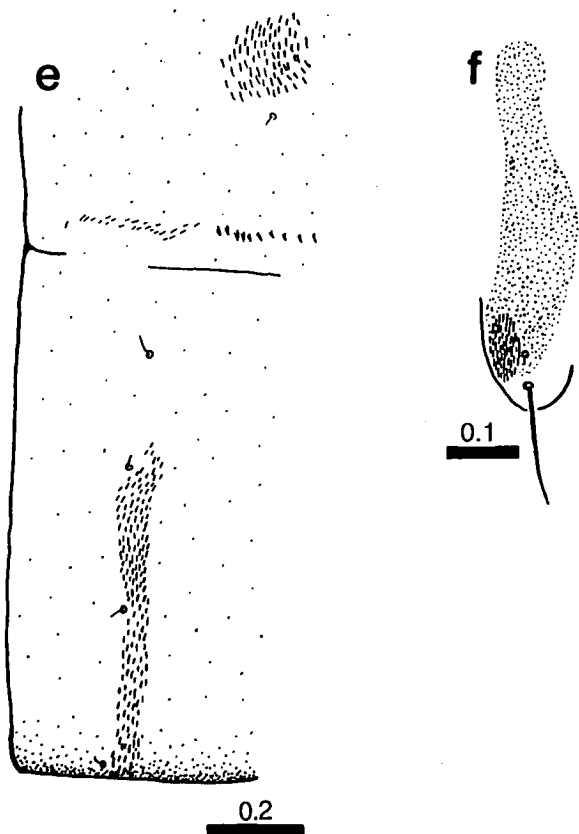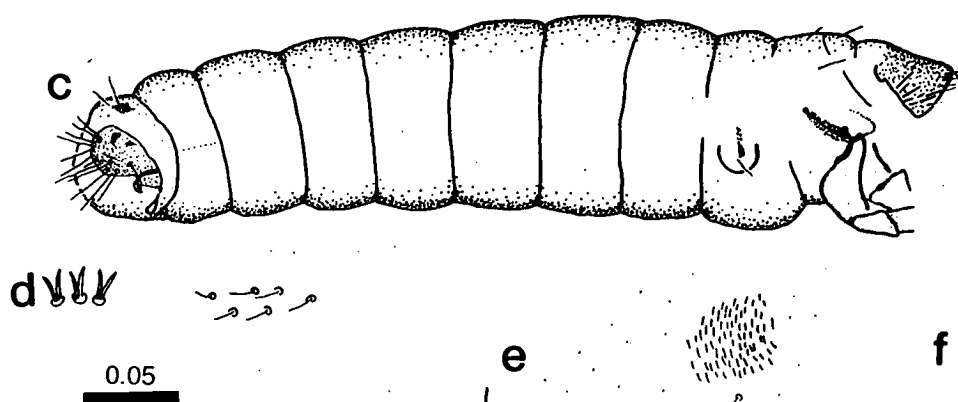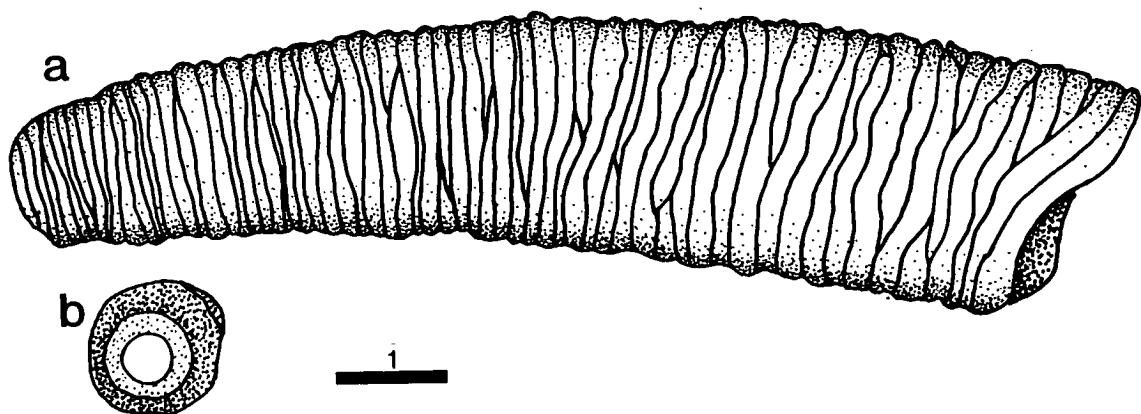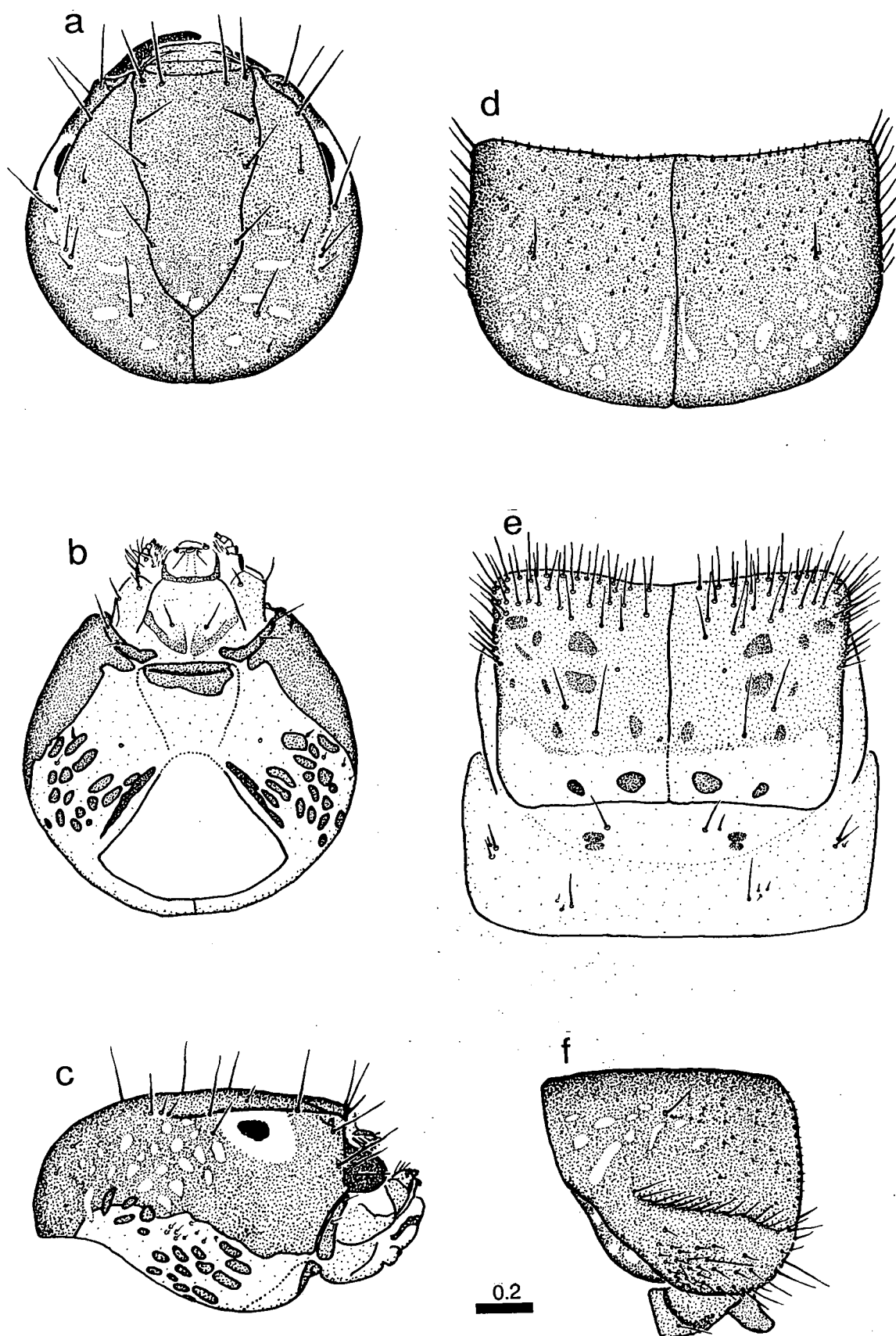
Figure 5.5. *Conoesucus adiastolus* sp. n. larva. **a, b, c**: head, dorsal, ventral, lateral; **d, e**: pronotum, meso- and metanotum; **f**: pronotum and protrochantin, lateral.
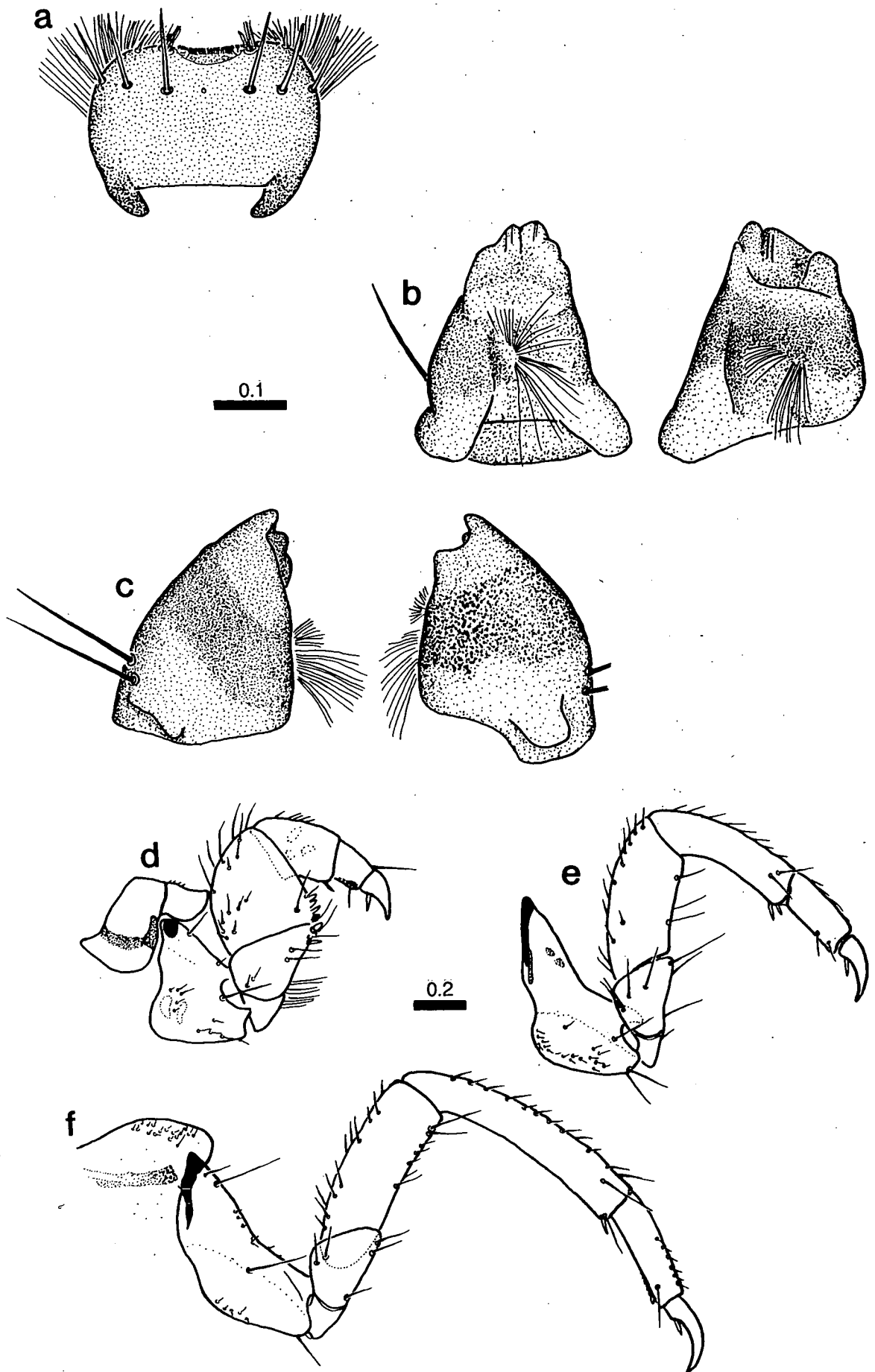
Figure 5.6. *Conoesucus adiastolus* sp. n. larva. **a:** labrum; **b:** mandibles L & R, inner face; **c:** mandibles, dorsal; **d:** foreleg (R) and protrochantin; **e:** midleg; **f:** hindleg.

Figure 5.7. *Conoesucus adiastolus* sp. n. pupa. **a:** case anterior, lateral; **b:** anterior , ventral; **c:** anterior membrane; **d:** posterior, lateral; **e:** posterior, ventral; **f:** posterior membrane; **g, h, i:** ♂ terminalia dorsal, ventral, lateral; **j:** terminal process, lateral; **k:** hookplates; **l:** mandibles, ventral; **m:** labrum.

a c d f

b e

1

g h

i

k

2

0.1

5a

5p

0.2

j 0.05

6 l m

0.1
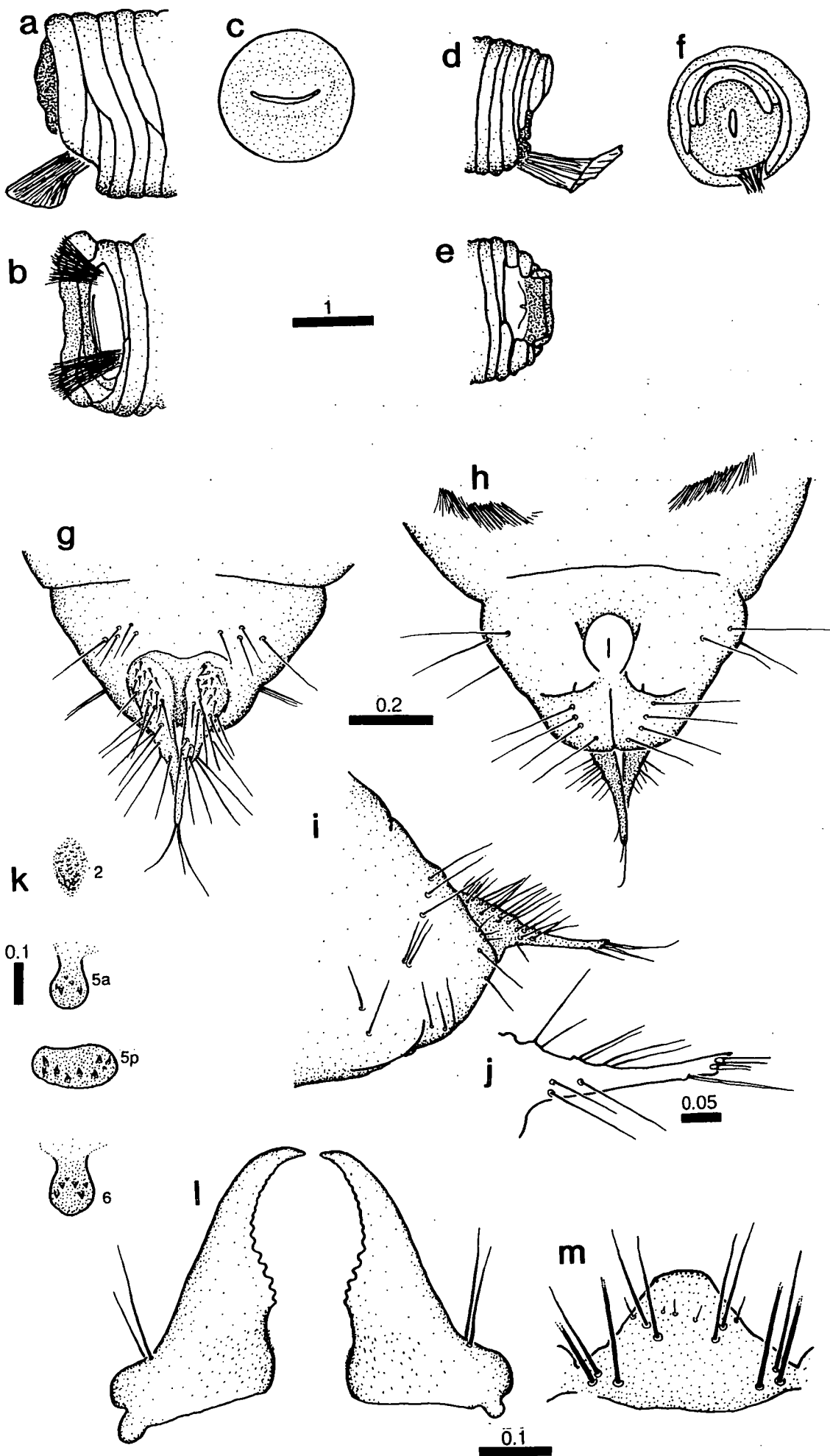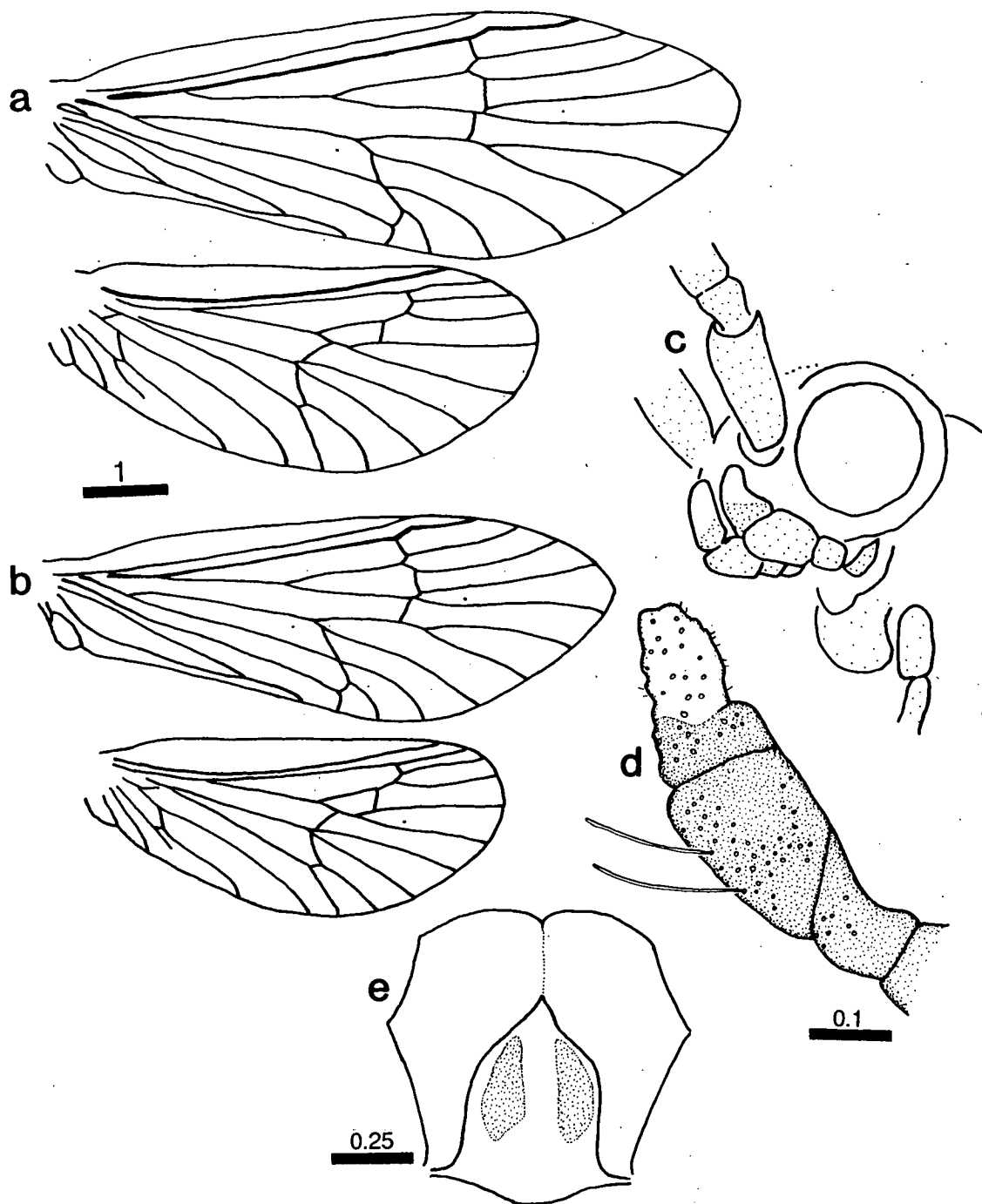
Figure 5.8. *Conoesucus adiastolus* sp. n. adults. **a, b:** ♀ , ♂ wings; **c:** ♂ head lateral; **d:** ♂ maxillary palp; **e:** mesothorax and scutellum.

Figure 5.9. *Conoesucus adiastolus* sp. n. adults. **a, b, c:** ♂ genitalia dorsal, ventral, lateral; **d, e:** ♀ genitalia dorsal, ventral.

a

b

c

d

e
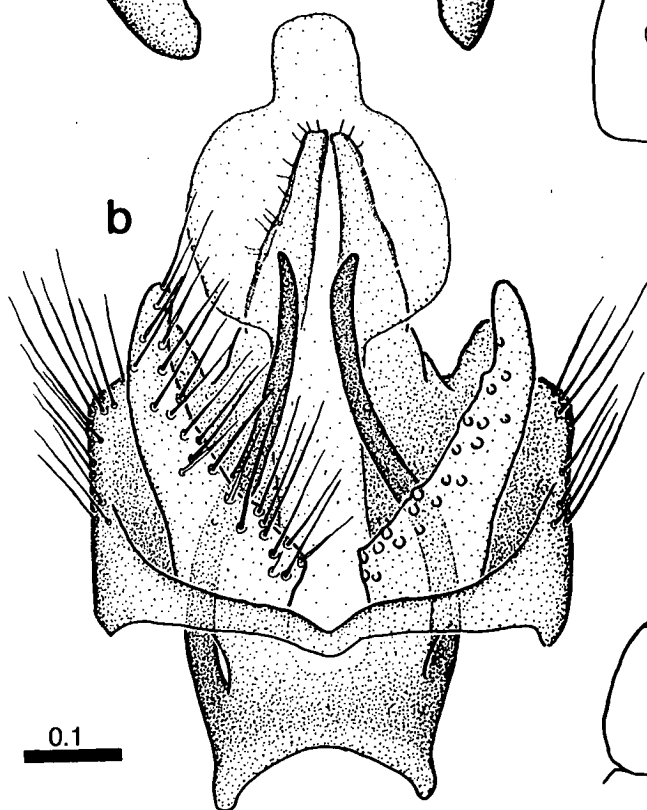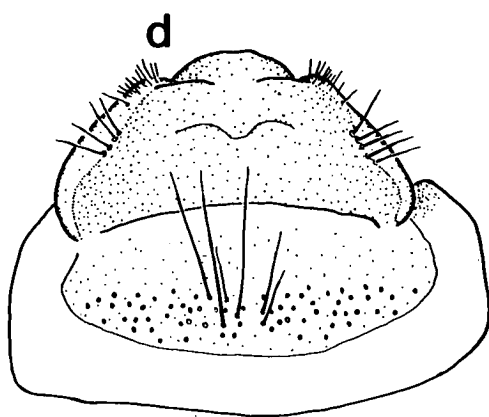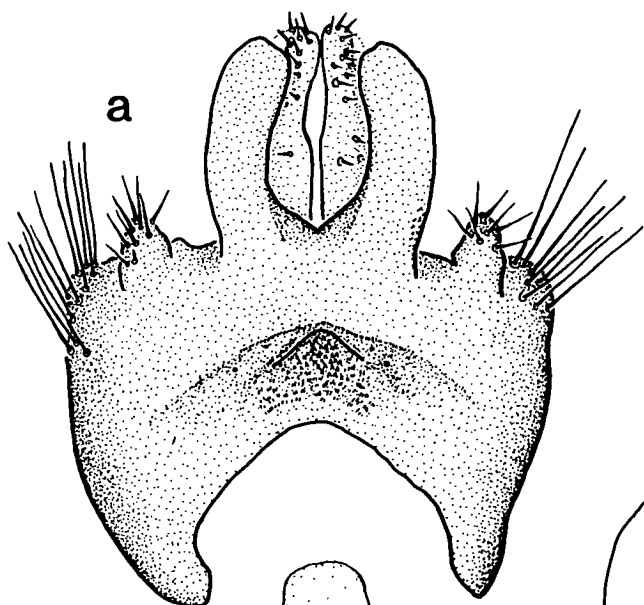
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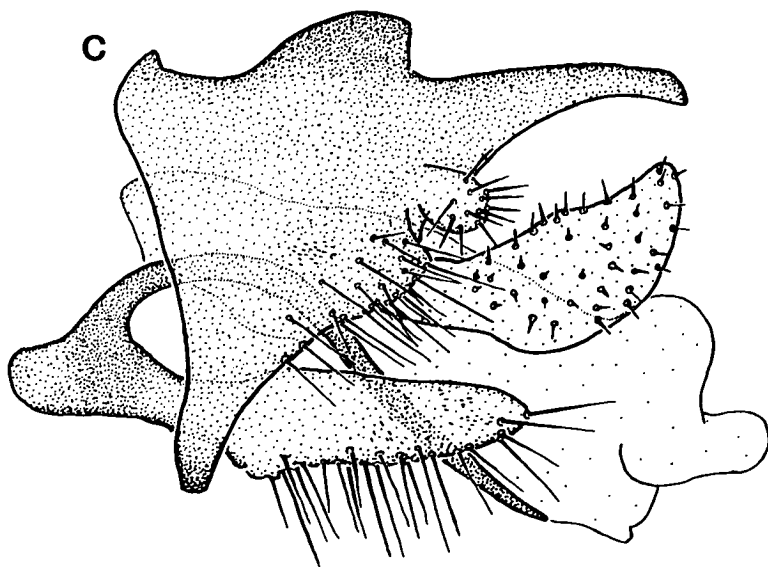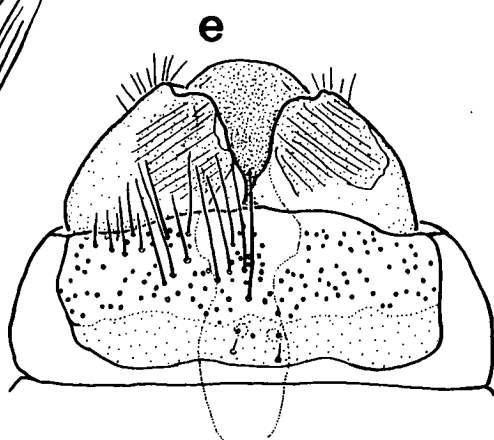
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segment 3 pigmented. Scutellum scars about 2/3 of its length, usually widely separated.

Male genitalia very similar to *C. brontensis*; tergite 9 extended distally into two curved processes, produced upwards between these into prominent ridge or hump; laterally produced into rounded process with setae extending almost to ventral surface. Superior appendages small round setose lobes; inferior appendages tapering and curving slightly, inner (concave) margin setose, but setal sockets not produced into fingerlike projections (cf. *C. brontensis*); phallus expanded laterally near apex. Segment 10 laterally flattened broad processes, setose, broadening then tapering, curving evenly upwards so that apices point dorsad, tapering to rounded apex, with slight convexity on upper margin. Distal margin of sternite 7 with broad extension but no free process.

Female terminalia: tergite 9 median process prominent, without median concavity, dorsolateral areas setose distally. Ventral plates about as wide as long; ventral incision widening distally, margins approximately straight. Sternite 8 distal 2/3 with dense broad band of dark stout setae, other sternites with sparse dark setae; no process on sternite 7. Tergite 8 with 2 close groups of dark setae, other tergites also setose.

Larva.

Case of plant material, rarely including sand grains; anterior margin oblique, with slight dorsal overhang; posterior membrane narrow, opening circular .

Abdominal gills absent; lateral spicules visible only at high magnification: segment 8 with row of 20-40 bifid, segments 3-7 with anterior row of 3-30 bifid (number decreases anteriorly) and band of many (20-35) single, segment 2 without lateral spicules.

Head brown, scars paler not very distinct. Frontoclypeus usually constricted near anterior margin as well as mesally. Group of about 9 minute setae laterally, between border of pigmentation and ventral muscle scars.

Pronotum anterolateral corner round, with few short pale setae then long dark setae alternating with pale towards lateral margin. Carina extending from just behind corner; lateral face between carina and margin broad, with many medium length fine hairs. Mesonotum with dense anterior band of medium length setae 2-4 deep. Metanotum: each SA with 1-2 easily visible setae and 1-3 small; SA 1 sometimes with pigmented area.

Protrochantin tip slightly pointed and upturned slightly, broadly horn-shaped or rectangular with extended corner. Pleural humps with many minute setae.

Pupa.

Case: anterior opening broad, width about 1/2 membrane diameter, central, slightly raised, under small dorsal hood. Posterior membrane with slit, raised slightly in membrane, small dorsal hood. Adhesive stalked discs at both ends.

Midleg hairs very sparse.

Anterior hookplates with 6-8 hooks scattered or in semicircle; posterior plates oval, wider than long, with 8-14 small hooks. Rarely additional hookplates present.
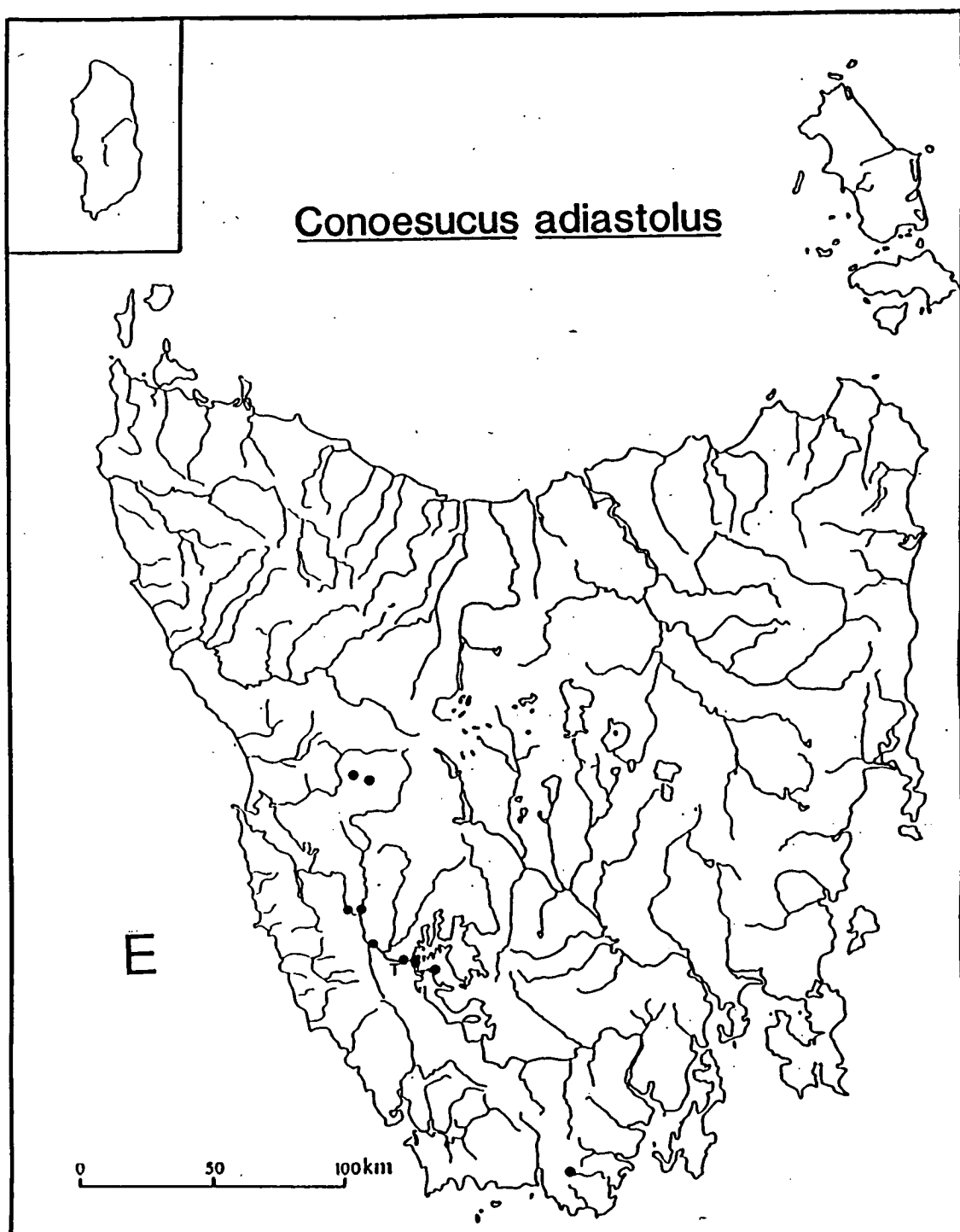
Figure 5.10. Distribution of *Conoesucus adiastolus* sp. n.

Apices of terminal processes pointed, dorsal surface smooth except for setal sockets; clear setae arise very close to apex. Mandibles equally hooked.

Remarks.

Found in rocky streams with moss or algae. Pupates singly, attached at both ends under rocks. Predation on pupae by larvae observed in captivity, and damaged pupal cases found in field.

Type material: HOLOTYPE ♂: Gordon River 2km downstream of Serpentine junction (site 163), 12.i.77, AN; ALLOTYPE ♀: site 164, 29.xii.88 em. 2.i.89; PARATYPES: 3♂ cleared 163, 12.i.77, AN; 1♂ 1♀, 164, 29.xii.88 em. 2.i.89; 5L 163, 12.i.77; 5L 164 29.xii.88.

Material examined: adults: 2♂, pharate ♀ 163, 12.i.77, AN; 20♂ reared, 7♀ reared, 2♂ netted 164, 29.xii.88; 2♂ reared 2♀ reared same locality 11.xi.88 ; 1♀ reared 133, 31.x.88; 2♂ reared 6♀ reared same locality 12.i.89; 2♂ reared 166, 29.xii.88. Drawings based on specimens: 1♂ 164, 29.xii.88 em. 8.i.89; 1♀ 133, 31.x.88 em. 18.xii.88.

Larvae and pupae: cleared: 5L 163T, 12.xii.77, AN; 3L 133, 12.i.89; 3L 164, 11.xi.88; 4P 164, 29.xii.88 em.8.i.89; 2P 133, 31.x.88 em.25.xii.88; other: 33L 164, 29.xii.88, 1.ix.88,14.x.87,11.xi.88; 15L 163T,12.i.77, AN; 3L 166, 29.xii.88, 11.xi.88; 5L 137, 31.x.88;1L 135, 19.ix.88; 40L 133, 19.ix.88, 12.i.89; 6L 139, 19.ix.88; 1L 126, 20.ix.88; 6L 129, 20.ix.88; 5P 163T, 12.i.77, AN; 22P 164, 11.xi.88 em. 10.xii.88, 29.xi.88 em. 12.i.89, 29.xii.88 em. 16.i.89; 2P 166, 29.xii.88 em. 15.i.89; 8P 133, 12.i.89 em. 16.i.89. Drawings based on specimens: 2L 163, 12.i.77, AN; 1P 164, 29.xii.88.

Distribution (Fig. 5.10). Endemic to Tasmania; collected from a few SW sites; common where collected.

Conoesucus brontensis Neboiss
(Figs 5.11-5.13)

Conoesucus brontensis Neboiss, 1977, p. 112.

Larva.

Case almost entirely of golden silk, sometimes with bands of moss/plant material in posterior; anterior margin square, posterior membrane projecting in cone shape, opening a central circular hole, about 1/2 the diameter of membrane.

Abdominal gills absent; lateral spicules: segment 8 with row of about 40 bifid; 3-7 with band of 30-40 single, and anterior row of 15-25 bifid; segment 2 with band of about 20 single.

Tergite 9 sclerites largely unpigmented, irregular pigmented areas around posterior setae.

Anal prolegs with lateral sclerites unpigmented anteriorly.

Head dark golden, scars paler. Frontoclypeus margins turn slightly inward from anterior, mid constriction pronounced, apex not strongly pointed. Lateral setae long and thick. Between lateral and ventral scars, about 10 small setae, on pigmented and unpigmented areas.

Mandibles with low apical teeth; left mandible with bristle-like setae distal to
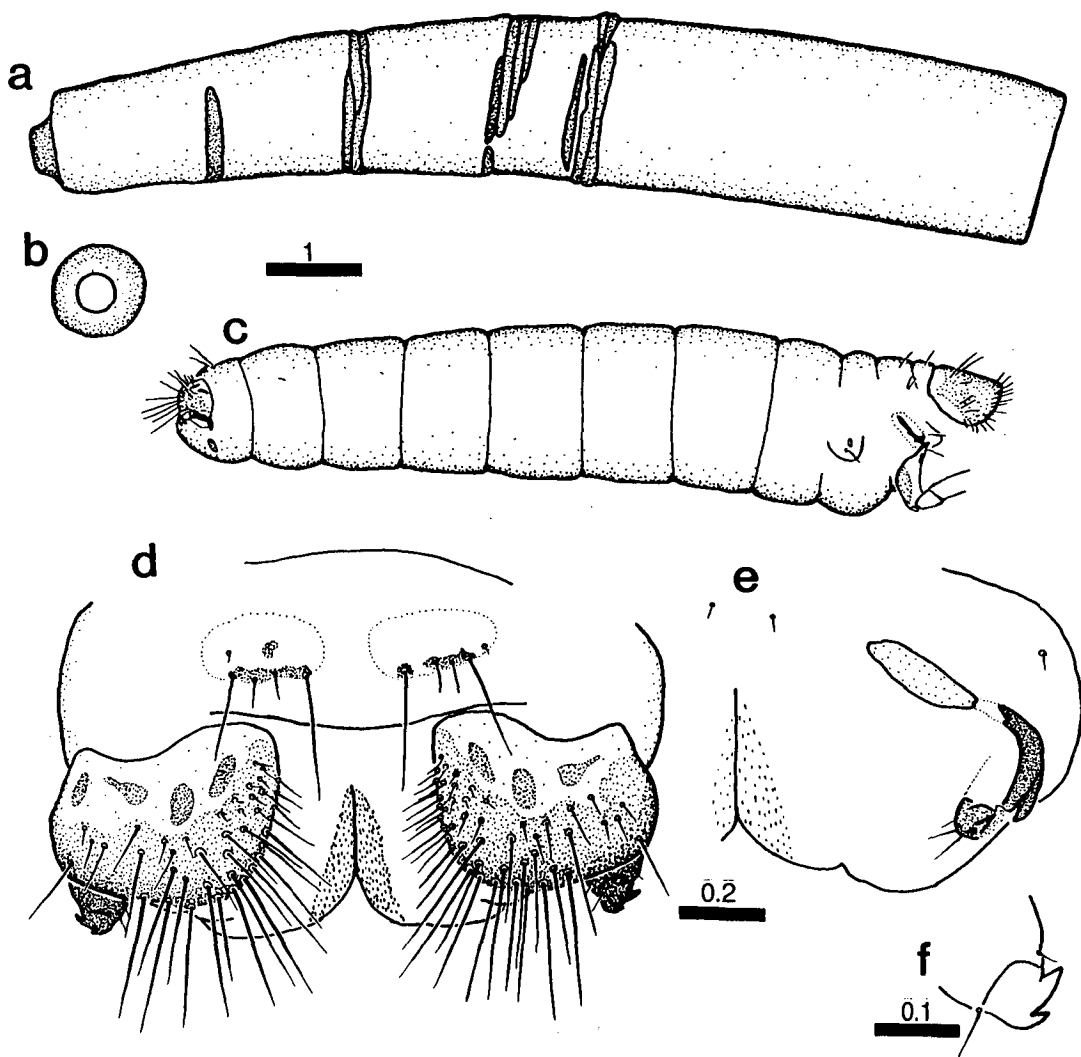
Figure 5.11. *Conoesucus brontensis* larva. **a, b:** case lateral, posterior membrane; **c:** larva, lateral; **d, e:** tergite 9 and anal legs dorsal, ventral; **f:** anal claw, ventral.

Figure 5.12. *Conoesucus brontensis* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f, g:** pronotum lateral, anterolateral corner.

a

b

c

d

e

f

g
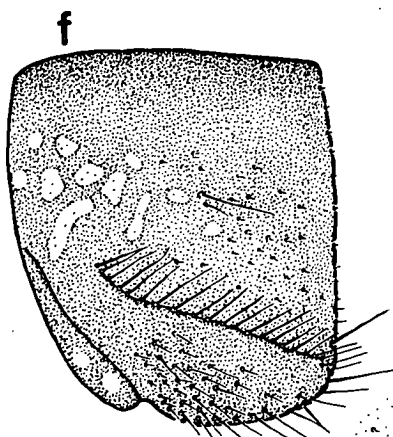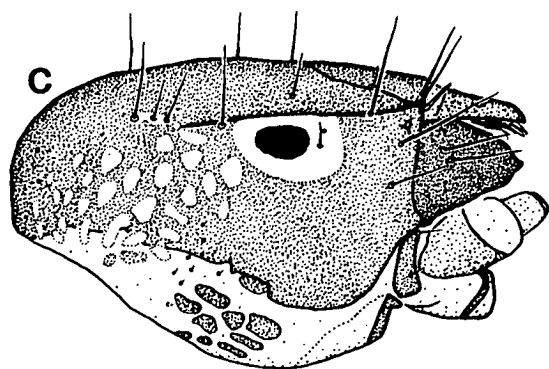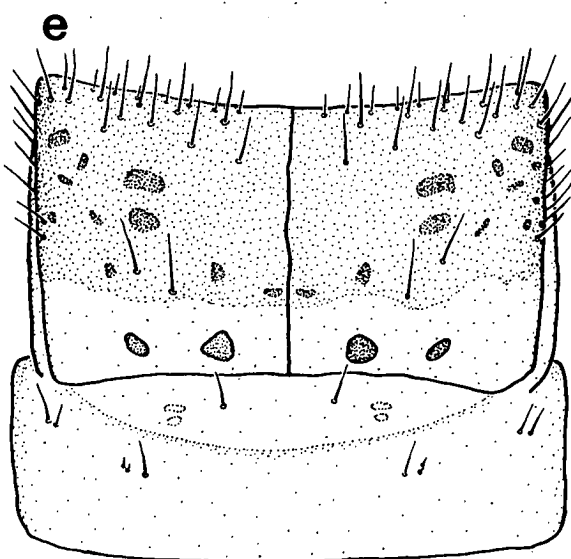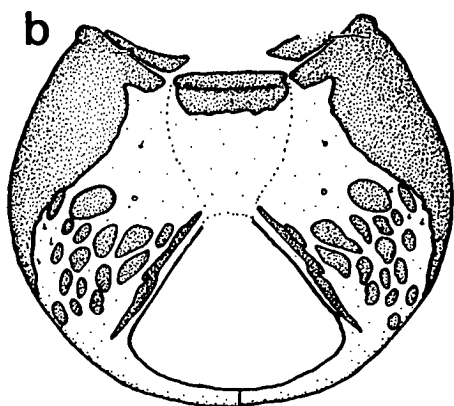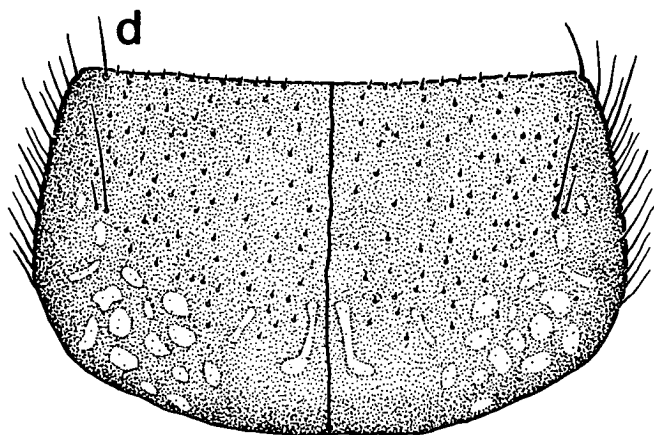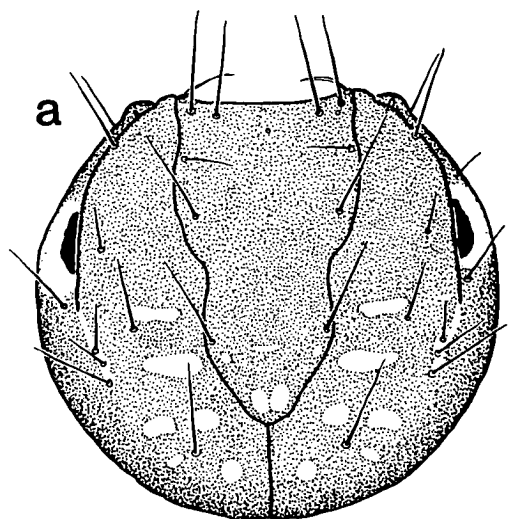
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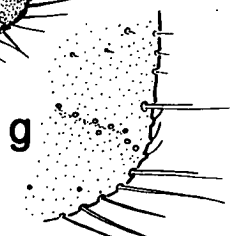
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Figure 5.13. *Conoesucus brontensis* pupa. **a, b, c:** case lateral, posterior, anterior membrane; **d, e, f, g:** ♂ terminalia ventral, dorsal, lateral, process apex lateral; **h:** mandibles, ventral; **i:** hookplates.

a

1

b

c

0.5

d

0.1

e

f

g

0.05

h

0.1

i

2

5

0.05
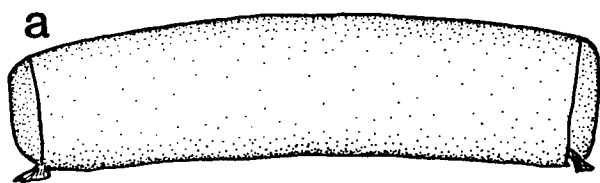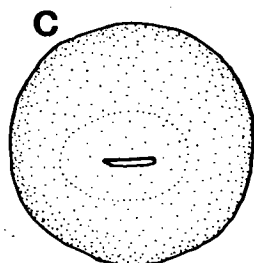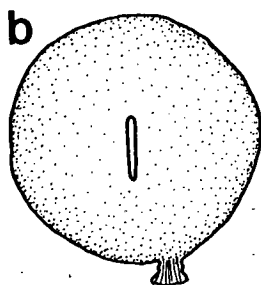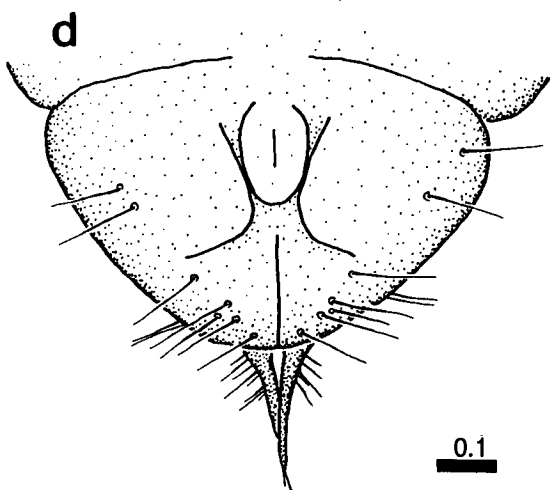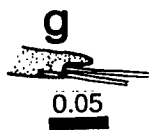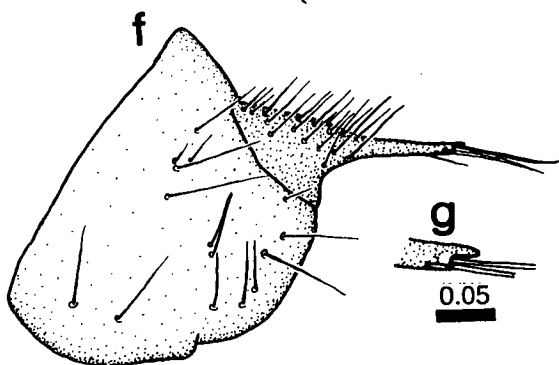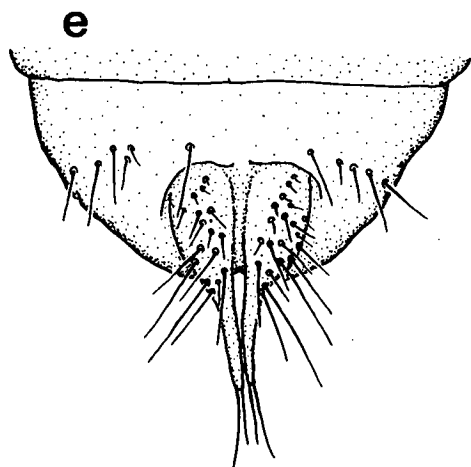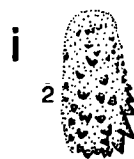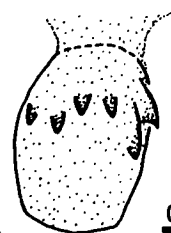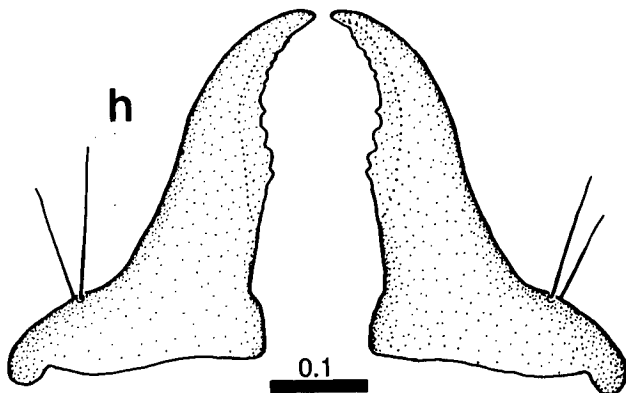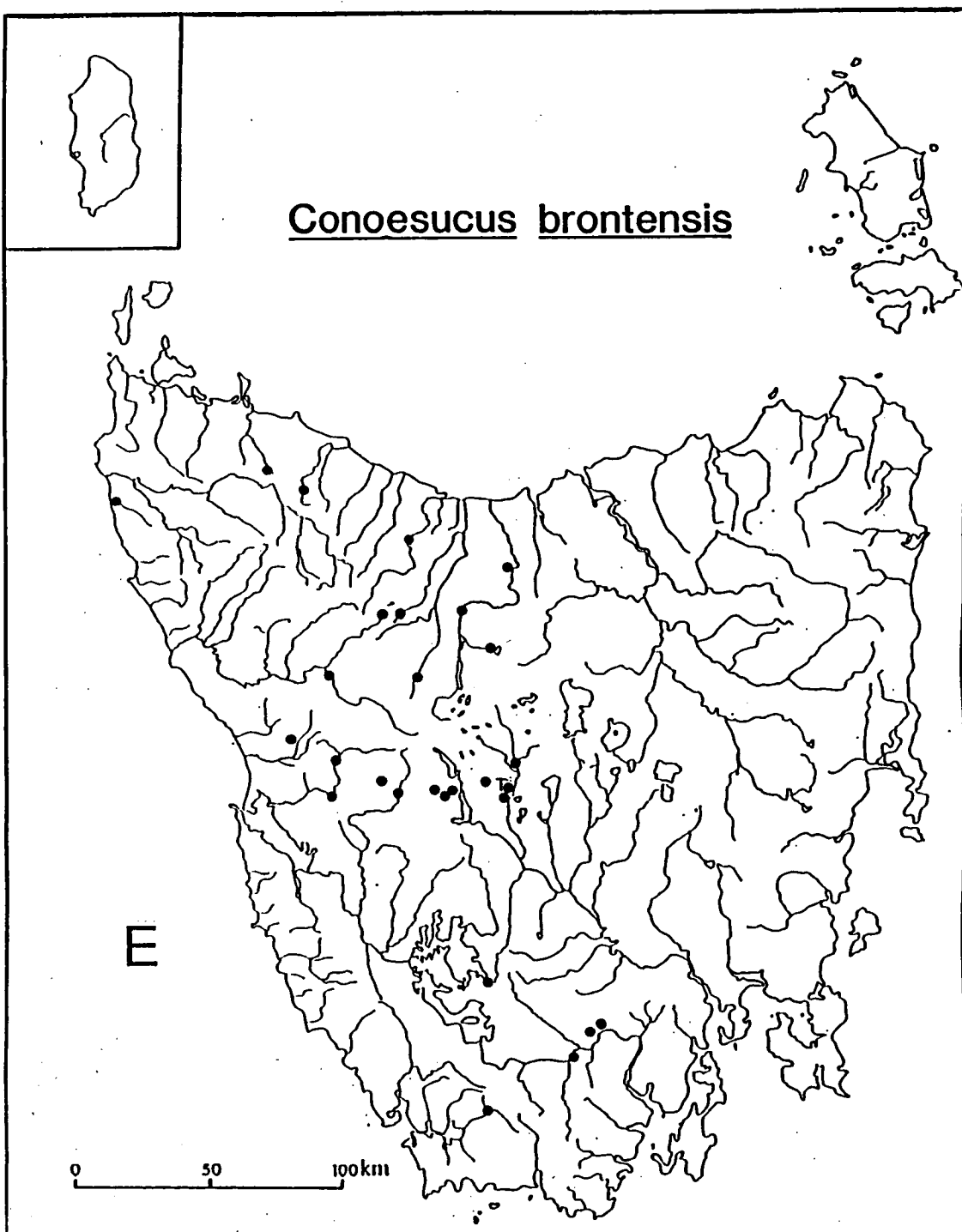
Figure 5.14. Distribution of *Conoesucus brontensis*.

brush.

Pronotum brown, scars golden, indistinct. Anterolateral corner sharply rounded, angle obtuse. Carina extending from corner, setae long and closely spaced. Mesonotum with anterior band of long setae 1-3 wide; anterolateral area not densely setose: about 10 setae along lateral margin. Each metanotal SA with 1-2 longer setae and 0-2 small; SA1 with pigmented area.

Protrochantin variable in shape, triangular or tapering and upturned, large basal seta on anterior margin. Pleural humps with many minute, and one long, dorsal setae.

Pupa.

Case almost straight; anterior membrane domed, opening slit small (about 1/4 width of membrane), just below centre. Posterior membrane domed, with slit about 1/3 height of membrane. Small adhesive stalked discs at both ends.

Midleg tarsi with sparse hairs. Apices of terminal processes projecting slightly beyond base of clear setae. Anterior hookplates with about 5-6 hooks in semicircle, posterior plates width about 2x length, 5-8 hooks. Mandibles equally hooked, serrations relatively large.

Remarks.

Larvae found amongst moss in rocky streams.

Pupates singly, attached at both ends to base of plants, or in rock crevices or moss.

Material examined: cleared: 2L 212, 11.viii.88; 1L 260, 18.viii.88;

other: 3L 212,11.viii.88; 2L 124, 20.ix.88; 4L 169, 12.ix.89; 1L 111, 20.ix.88; 3L 155, 10.xii.89; 2L 259, 25.viii.88, 18.viii.88; 2L 246, 18.viii.88; 1L 136, 19.ix.88; pupae: 1P 136, 27.x.87 em. 23.xi.87; 2P 259, 1.xi.88 em. 18.xi.88; 4P 150, 27.x.87 em. 30.x.87, 1.xi.88 em. 1.xi.88; 4P 246, 4.xi.87, 18.viii.88 em. 20.x.88; 11P 169, 1.ix.88 em. 2.xi.88, 11.xi.88. Drawings based on specimens: 1L 260, 18.viii.88; 1L sclerites 250, 4.xi.87; 1L sclerites + 1P 246, 4.xi.87; 1P 150, 27.x.87.

Distribution (Fig. 5.14). Endemic; widespread in area west of line between Geeveston in the south and Devonport in the north; rare where collected.

Conoesucus digitiferus Jacquemart
(Figs 5.15-5.17)

Conoesucus digitiferus Jacquemart, 1965, p. 9.

Larva.

Case of stout plant material (algae, moss stems, grass), anterior margin slightly oblique, posterior membrane projecting into cone shape, opening a central circle.

Abdominal gills absent. Lateral spicules on segment 8 a single row of about 35 bifid, segments 3-7 with band of 20-30 single and row of 1-15 bifid, segment 2 with row of 5 single. Anal prolegs: posterior margin of ventral sclerite sometimes extending downwards in triangular shape. Tergite 9 sclerites relatively large.

Head very dark brown, scars slightly darker. Frontoclypeus apex fairly broad. Group of about 14 minute pale stout setae amongst ventral scars, laterally.

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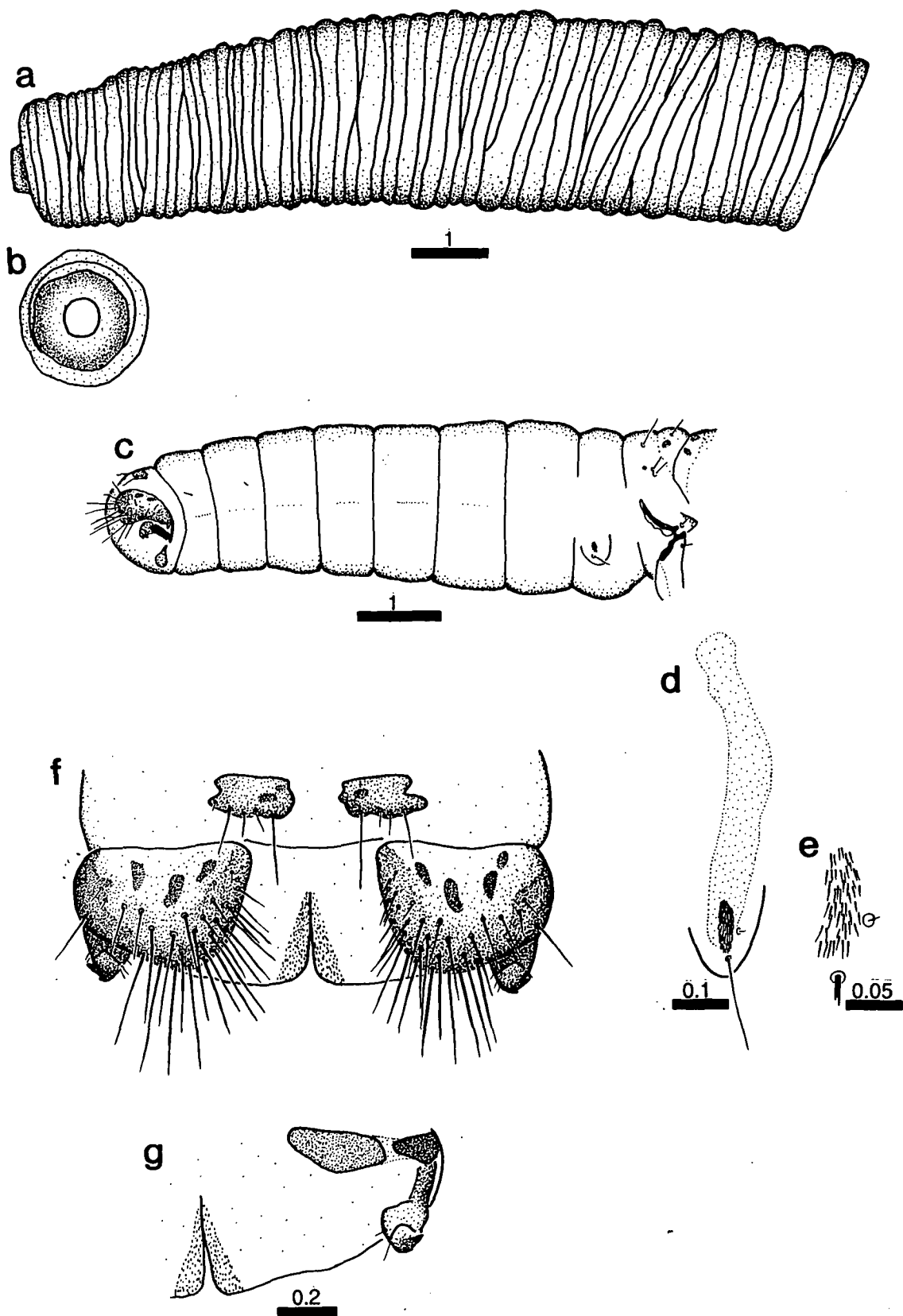
Figure 5.15. *Conoesucus digitiferus* larva. **a, b:** case lateral, posterior membrane; **c:** larva lateral; **d, e:** segment 1 lateral hump, sclerite enlarged; **f, g:** tergite 9 and anal legs dorsal, ventral.

Figure 5. 16. *Conoesucus digitiferus* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f, g:** pronotum lateral, anterolateral corner.

a

d

b

c

e

0.2

f

g
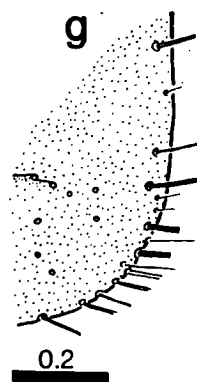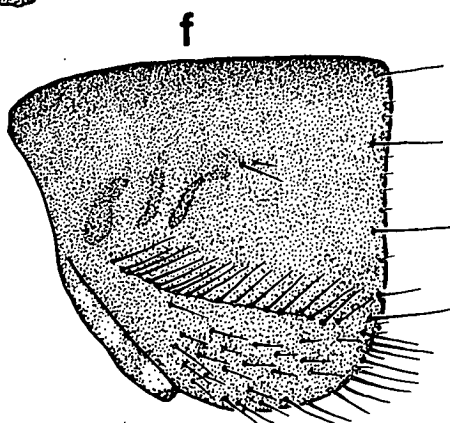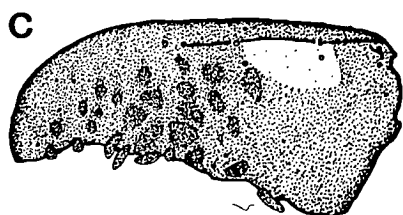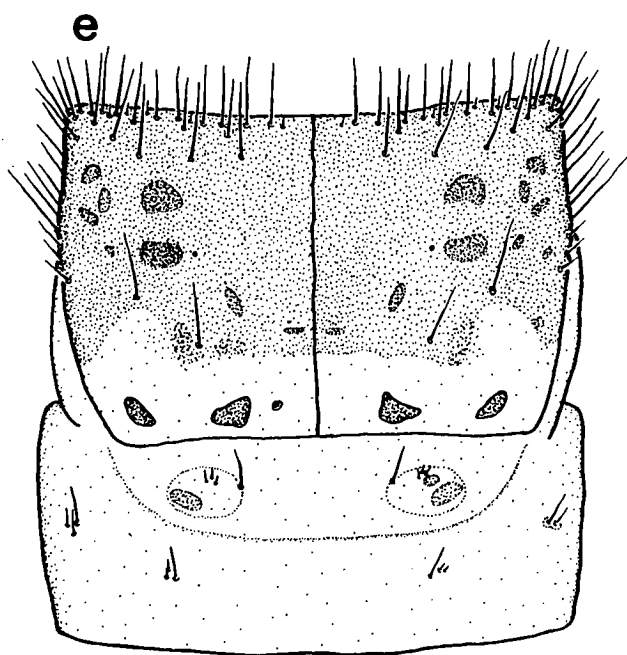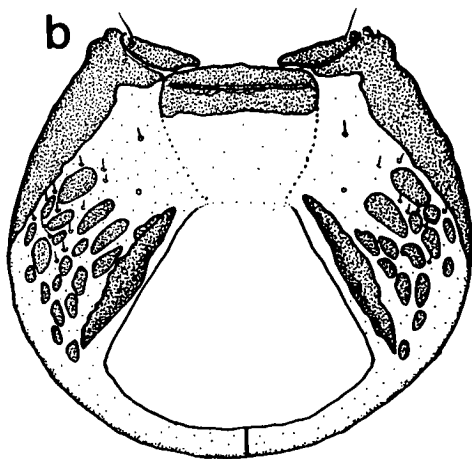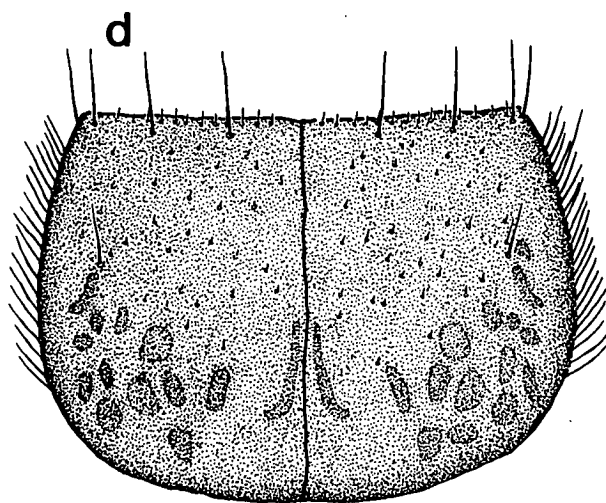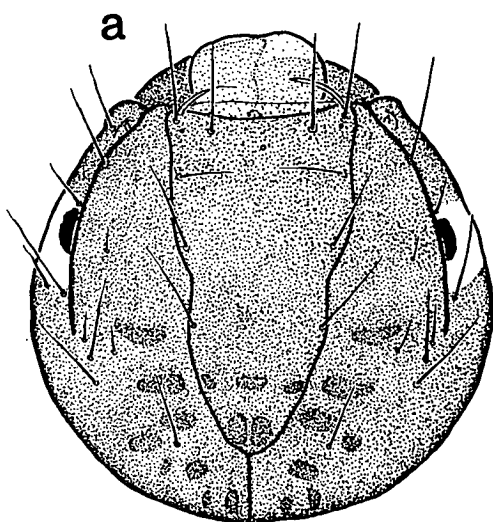
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Figure 5.17. *Conoesucus digitiferus* pupa. **a, b, c, d, e:** case lateral, posterior membrane, anterior membrane, posterior, anterior ventral; **f, g, h, i:** ♂ terminalia dorsal, ventral, lateral, process apex lateral; **j:** hookplates; **k:** mandibles, ventral.

a

b

c

2

d

e

f

0.2

g

h

j

2

3

5a

5p

0.1

i

0.1

k

0.1
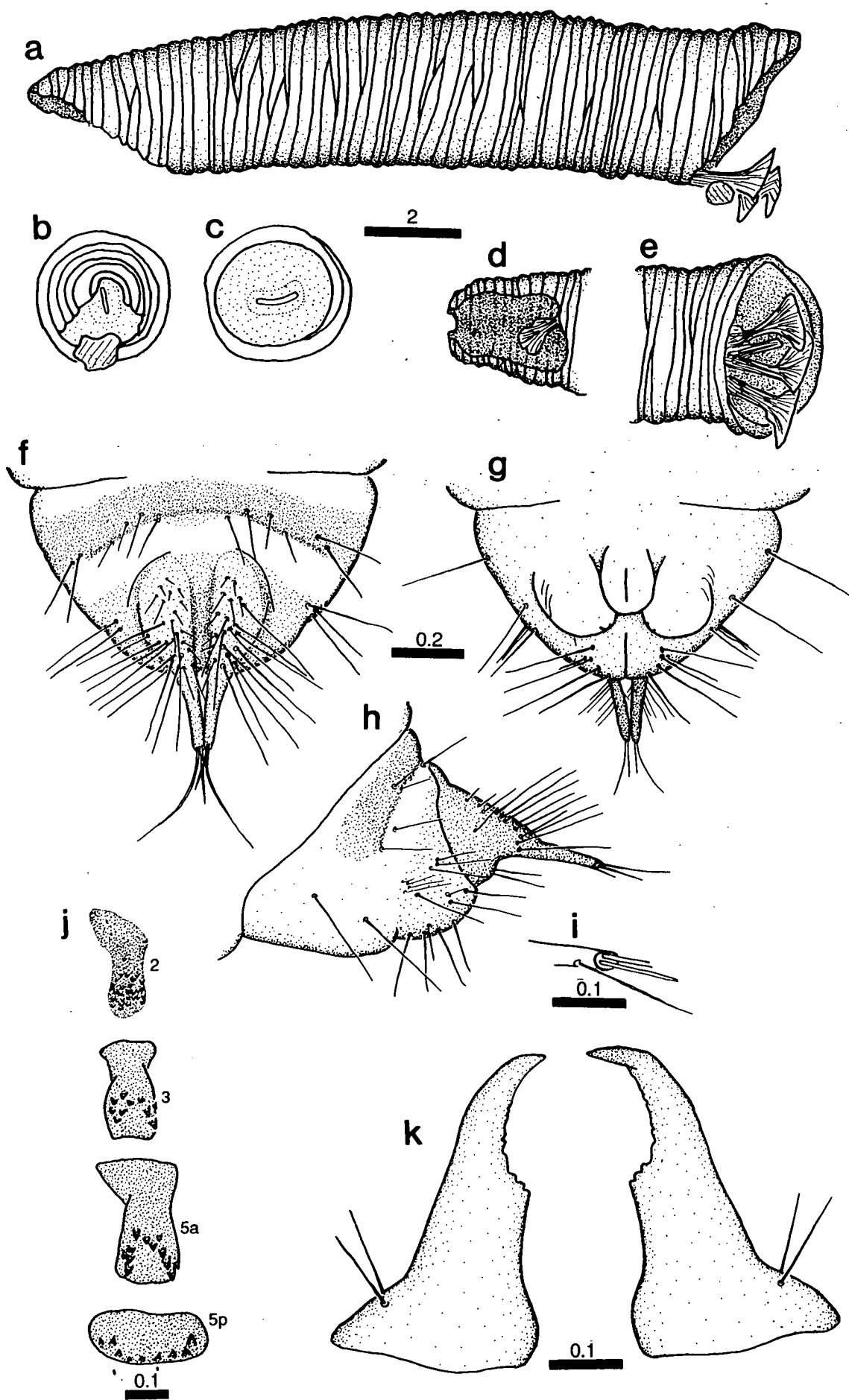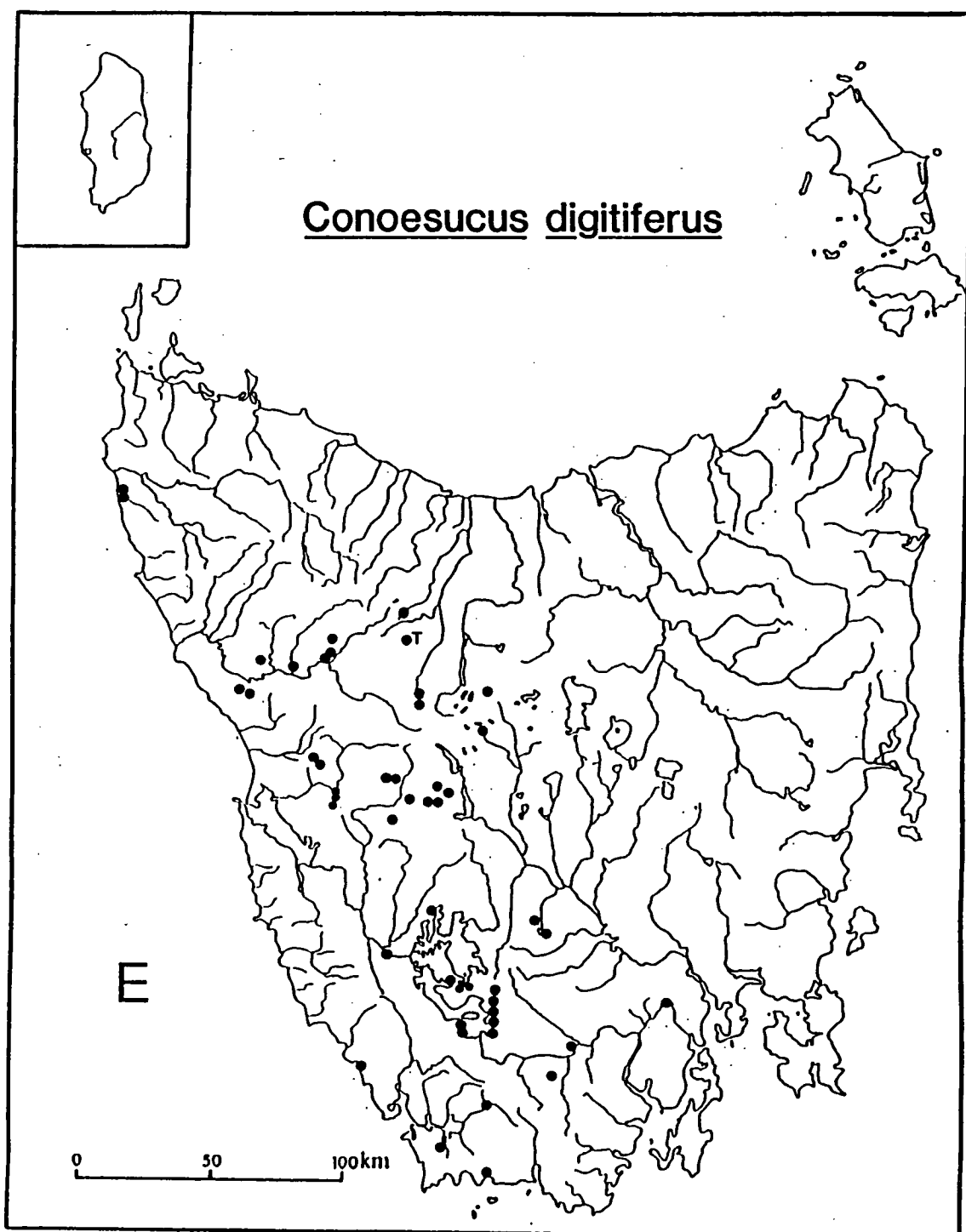
Figure 5.18. Distribution of *Conoesucus digitiferus.*

Pronotum dark brown, anterior margin with 4-5 long dark evenly spaced setae on each side. Anterolateral corner rounded; carina extending from behind corner, sometimes turning sharply dorsad at posterior end; lateral face with fairly long dark setae. Mesonotum with sparse anterior band of medium length setae,1-3 wide . Metanotum: each SA with 1-3 setae and 0-3 minute setae; areas 1 and 2 with pigmented patch.

Protrochantin relatively narrow, tapering to apex, single dorsal seta. Pleural humps pigmented dorsally.

Pupa.

Case with anterior margin sometimes flaring out slightly; anterior membrane set in from margin, opening slit curving slightly upwards, about 1/3 width of membrane; posterior end of case cut away ventrally to form large dorsal hood, posterior closure a central vertical slit. Adhesive discs ventrally at both ends.

Midleg tarsi with sparse fringe. Anterior hookplates with many (about 10) small hooks in semicircle, posterior plates width about 2x length, bearing about 8 hooks; sometimes with additional sclerites. Segment 9 with dorsal transverse brown band, setae in narrow groove, posterior part also pigmented. Processes with long dorsal setae, apices not projecting beyond bases of terminal setae. Right mandible more strongly hooked than left.

Remarks.

Pupates singly or in small groups, attached at both ends to the underside of rocks.

Material examined: 3L 204, 17.xii.87; 4L 182, 3.vii.87; 19L 41, 22.ix.88; 15L 127, 20.ix.88, 1.xi.88; 3L 108, 20.ix.88; 2L 184, 25.viii.88; 14L 168, 1.ix.88; 1L 136, 31.x.88; 3L 142, 19.ix.88; 2L 228, 18.ii.86; 1L 39, 22.ix.88; 4L 260, 18.viii.88; 4L 139, 19.ix.88; 5L 183, 25.viii.88; 4L 182, 25.viii.88; 5L 110, 20.ix.88; 3P 182, 6.x.87 em. 9.xi.87; 9P 168, 14.x.87 em. 16.xi.87, 11.xi.88 em. 10.xii.88; 6P 127, 1.xi.88 em. 17.xi-28.xi.88;1P 204, 17.xii.87 em. 24.xii.87; 3P 184, 25.viii.88 em. 22.x.88; 2P 41, 8.xii.88 em. 23.xii.88. Drawings based on specimens: 1L 182, 3.vii.87; 2L 168, 14.x.87.

Distribution (Fig. 5.18). Endemic; widespread in area west of Burnie-Hobart line (Fig.5.81); often very common where collected.

Conoesucus fromus Mosely
(Figs 5.19, 5.20)

Conoesucus fromus Mosely, 1936, p. 409; Mosely & Kimmins, 1953, p. 88; Neboiss, 1977, p.109.
Conoesucus moselyi Jacquemart, 1965, p. 12.

Larva.

Case of plant material; anterior margin square; posterior membrane projecting slightly, opening about 1/2 width of membrane.

Abdominal gills: segment 1 with single dorsal filament and branched gill posteroventrally; segments 2 and 3 with anterodorsal and anteroventral branched gills and small lateral gill. Lateral abdominal spicules on segment 8 a single row of bifid, on segment 7 a single row of mixed single and bifid, segments 4-6 a single row with 7-10

Figure 5.19. *Conoesucus fromus* larva and pupa. **a, b:** case lateral, posterior membrane; **c:** larva lateral; **d, e, f:** pupal case lateral, posterior, anterior membrane; **g:** testis; **h:** midleg fringe; **I, J:** terminalia lateral, process apex enlarged; **k, I, m:** pupal abdomen ventral, hookplates, dorsal.
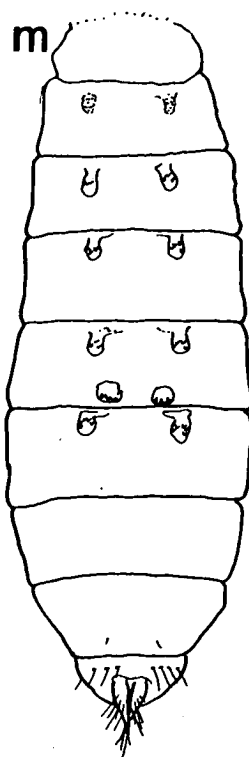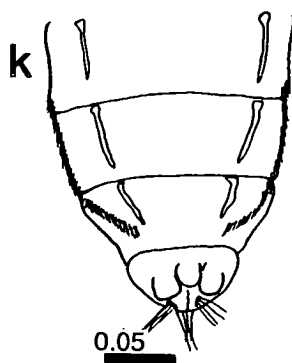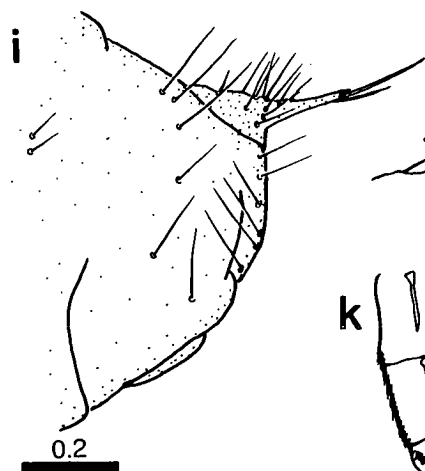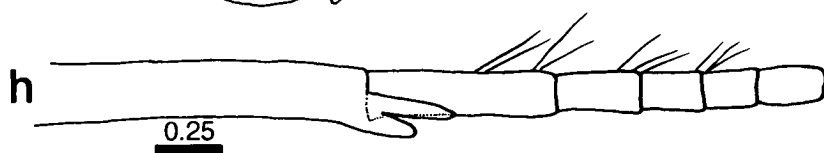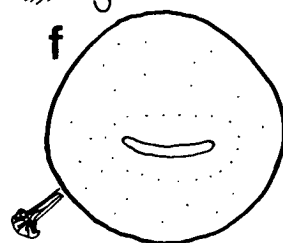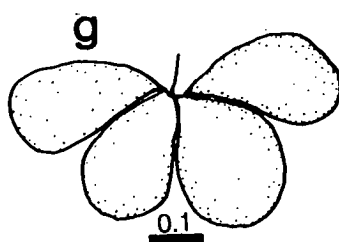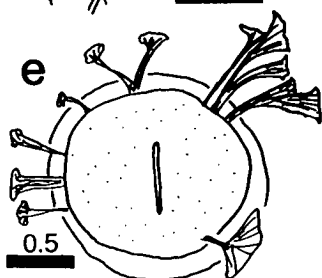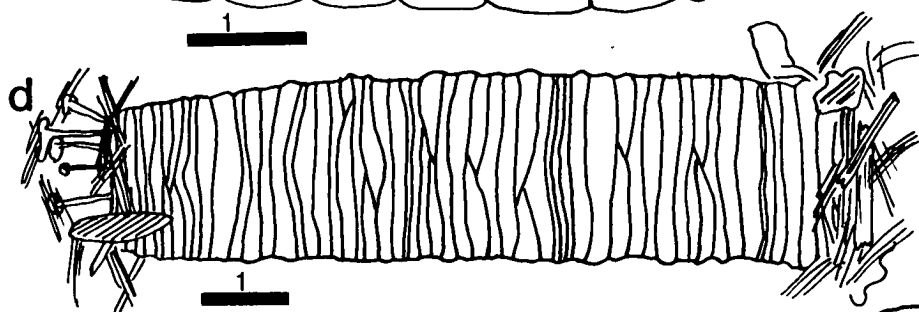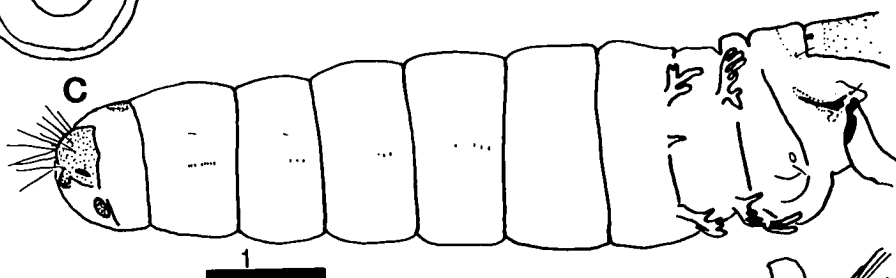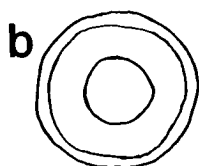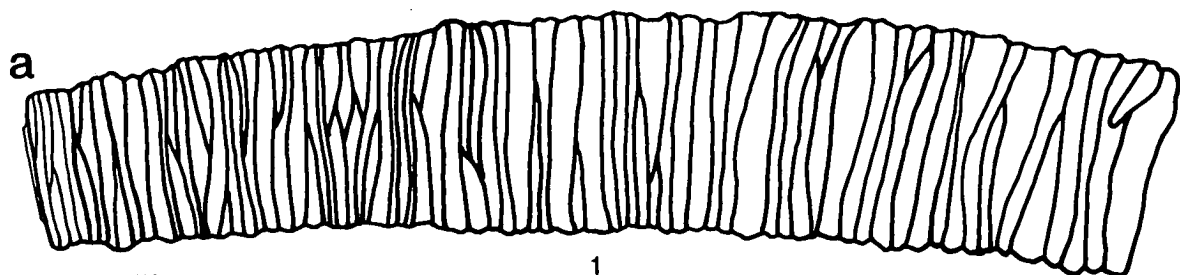
igure 5.20. *Conoesucus fromus.* **a, b, c:** head dorsal, ventral, lateral;
: pupal mandibles, ventral; **e, f:** pronotum, meso- and metanotum; **g:**
ronotum, lateral.

a

e

b

f

c

0.2

d

0.1

g
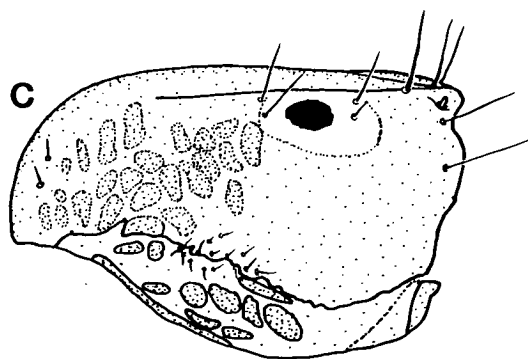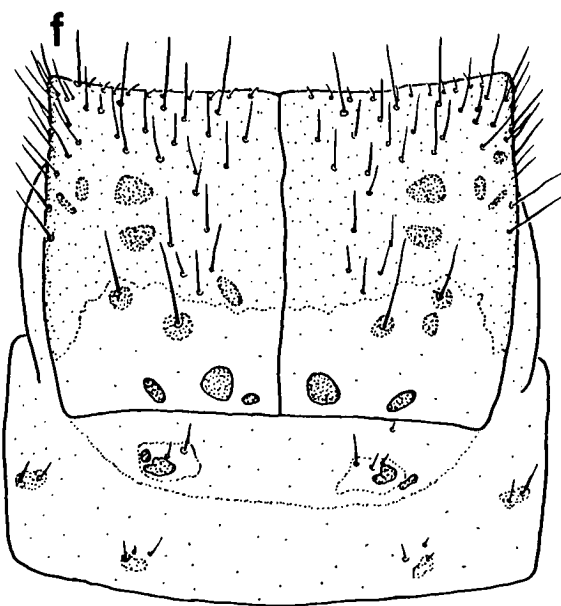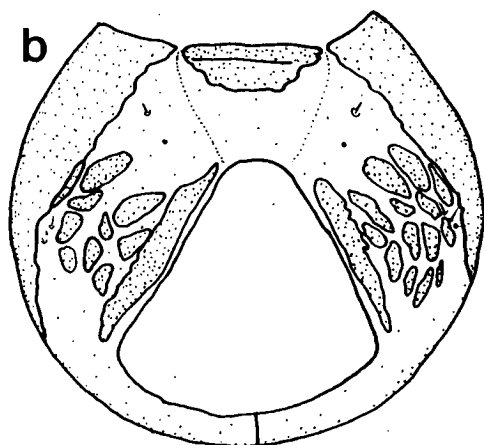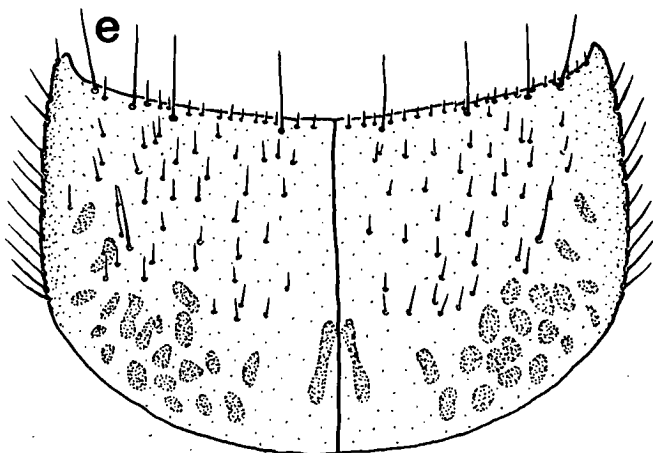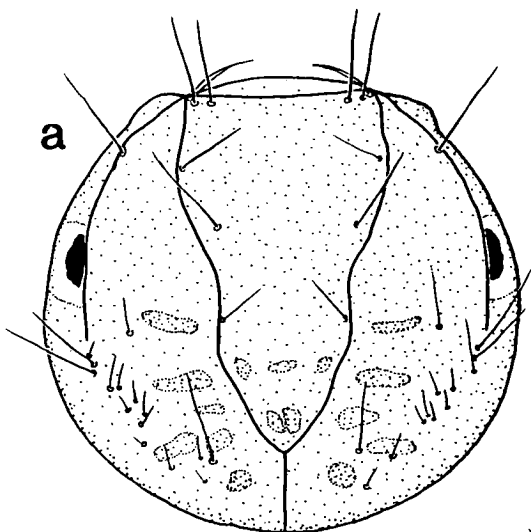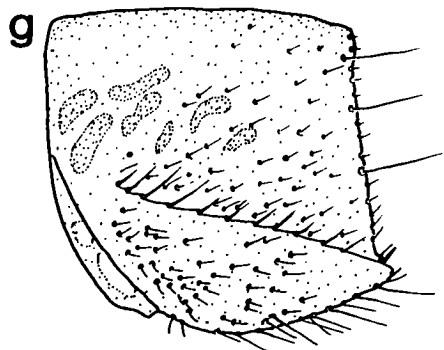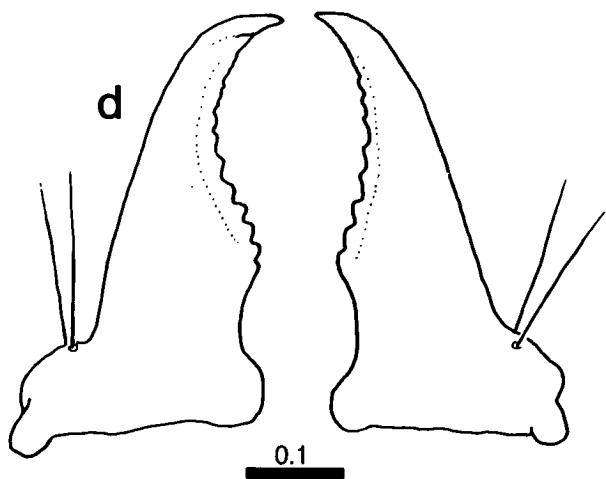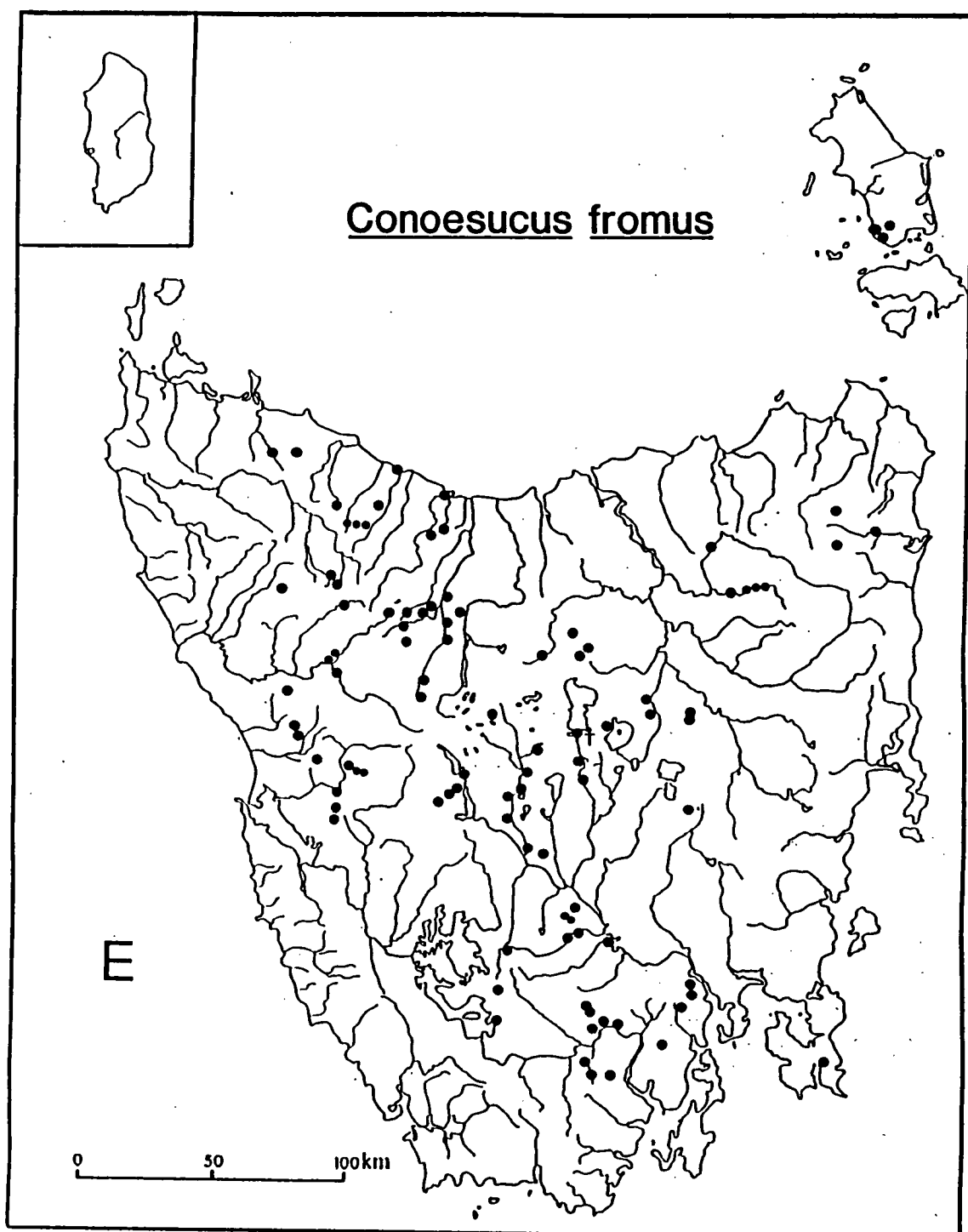
Figure 5.21. Distribution of *Conoesucus fromus*.

single and 3-6 bifid, segment 3 single spicules only. Anal prolegs with lateral sclerites evenly pigmented.

Head dark brown, scars only slightly darker, with darker borders; group of 6-8 short fine setae in posterior lateral area. Frontoclypeus distinctly broader anteriorly than posteriorly, apex pointed. Group of about 18 short fine setae between lateral and ventral scars of head.

Pronotum dark brown, scars just paler; anterior margin with row of 3-4 long dark setae each side. Anterolateral corner pointed, projecting slightly, a few clear stout setae mesally, 3 stout brown setae laterally. Carina extending from mesad of point (so that point is part of lateral face, not divided by carina), setae widely spaced, medium length. Lateral face scattered with short stout setae, lateral margin with longer setae.

Anterior margin of mesonotum with row of small fine closely spaced setae and wider spaced long setae, smaller setae scattered behind them; pigmented area with scattered fine pale setae. Metanotum: each SA with pigmented area, 1-2 longer and 1-2 minute setae.

Pleural humps with single long seta and many minute setae.

Pupa.

Case posterior membrane flat, with central narrow vertical slit; anterior membrane flat, with slightly curved slit just below centre; both ends with many (> 10) small thin stalked discs, attached to loose plant material.

Anterior hookplates with about 4 hooks, posterior plates with about 6 prominent hooks. Midleg tarsi with sparse hairs. Anal processes relatively short, apical overhang just beyond base of terminal setae.

Right mandible more hooked and strengthened than left, serrations relatively large, smooth.

Remarks.

Pupates at base of grass-like plants.

Material examined: cleared: 1L 18, 21.xi.87; 1L 229, 12.xi.88; 1L 76, 3.xi.87; 1L 127, 20.ix.88; 2L 142, 19.ix.88; 1L 30, 21.ix.88; other: 1L 246, 18.viii.88; 3L 213, 11.viii.88; 1L 183, 25.viii.88; 4L 259, 18.viii.88; 5L 212, 11.viii.88; 9L 142, 19.ix.88; 4L 252, 18.viii.88; 10L 53, 29.xi.88; 10L 48, 30.xi.88; 5L 114, 20.9.88; 1L 67, 18.xi.88; 9L 31, 21.ix.88; 1L 46, 29.xi.88; 4L 213, 11.viii.88; 2L 45, 29.xi.88; 3L 229, 25.viii.88; 10L 257, 18.viii.88; 2L 9, 21.xi.87; 10L 300, 30.xi.87; 2L 228, 18.xi.87; 1L 150, 27.x 87; 10L 180, 5.x.87; 5L 64, 22.xi.87; 10L 301, 30.xi.87; 3P 301, 4.xii.87 em. 5.xii.87; 2P 9, 20.xi.87; 1P 153, 27.x.87 em. 1.xii.87; 5P 127, 1.xi.88; 5P 53, 29.xi.88; 3P 14, 21.xi.87. Drawings based on specimens: 1L 76, 3.xi.87; 1L 127, 20.ix.88; 1P 14, 21.xi.87; 1P 53, 29.xi.88.

Distribution (Fig. 5.21). Endemic; widespread including Flinders Island, except for absence from mid-east area; usually not in very high numbers.

Conoesucus nepotulus Neboiss
(Figs 5.22, 5.23)

Conoesucus nepotulus Neboiss, 1977, p. 111.

Figure 5.22. *Conoesucus nepotulus* larva and pupa. **a, b:** larval case lateral, posterior membrane; **c, d, e, f:** pupal case lateral, anterior, posterior membrane, posterior ventral; **g:** hookplates; **h:** terminalia, lateral; **I:** mandibles, ventral.

a

b

c

0.5

d

e

f

g

2

5a

h

0.1

5p

6

i
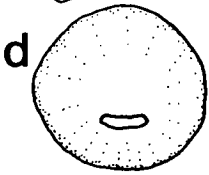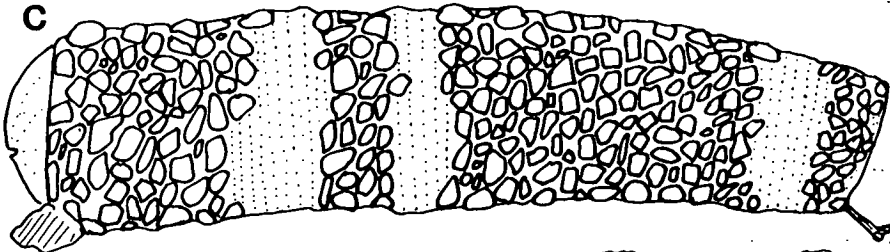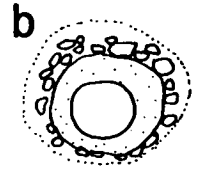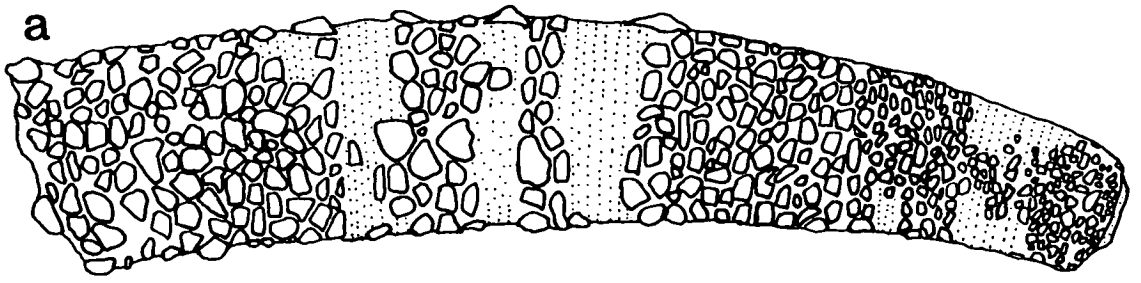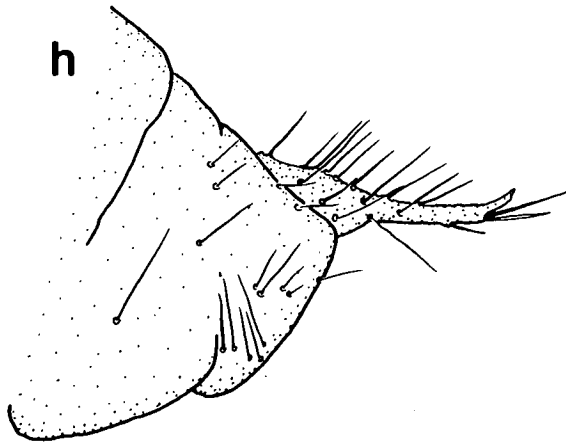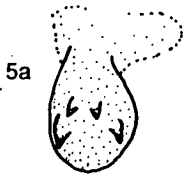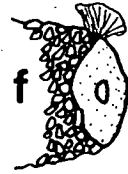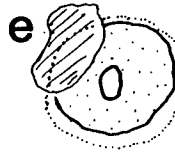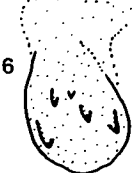
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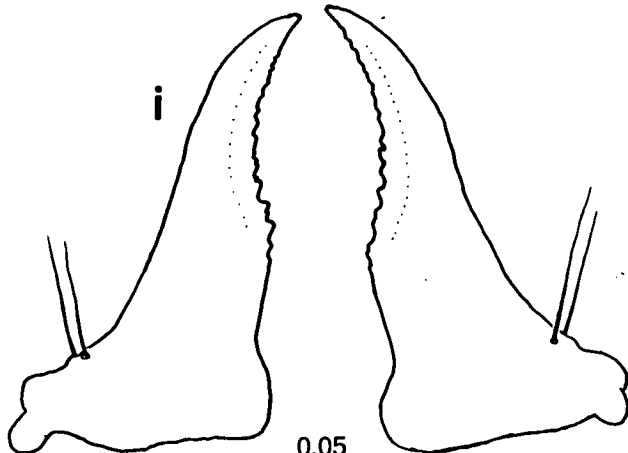
0.05

Figure 5.23. *Conoesucus nepotulus* larva. **a, b, c:** head dorsal, ventral, lateral; **d:** pleural humps, lateral; **e, f:** pronotum, pattern of texturing; **g:** meso- and metanotum; **h:** pronotum, lateral.

a

b

c

d

e

f

0.1

g

h
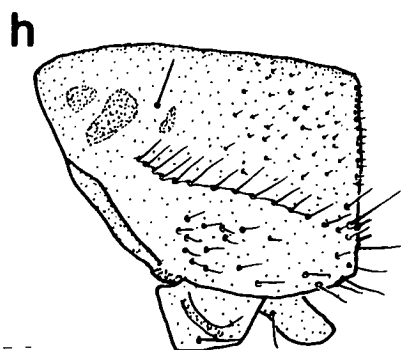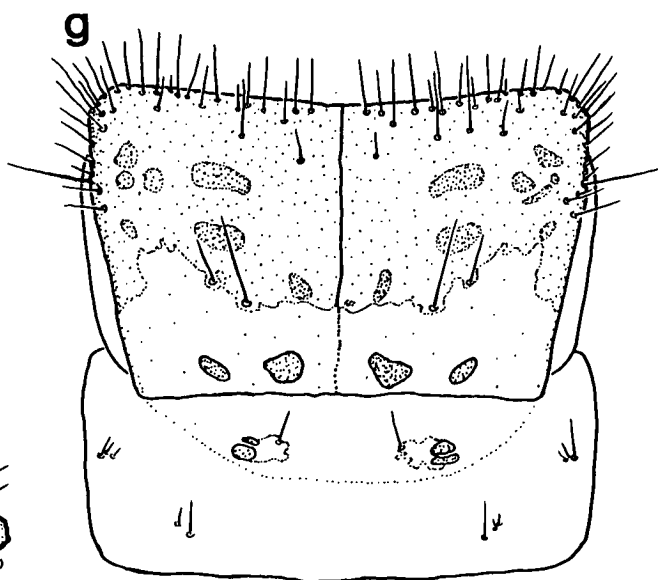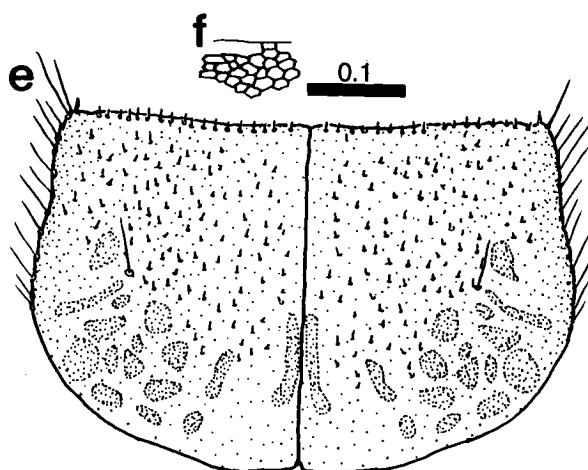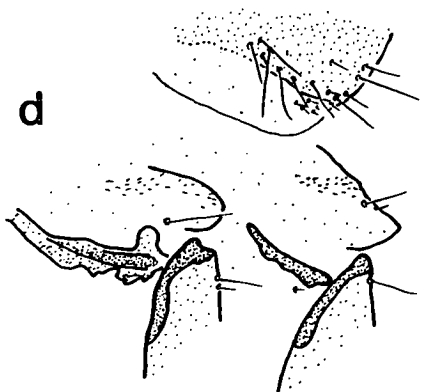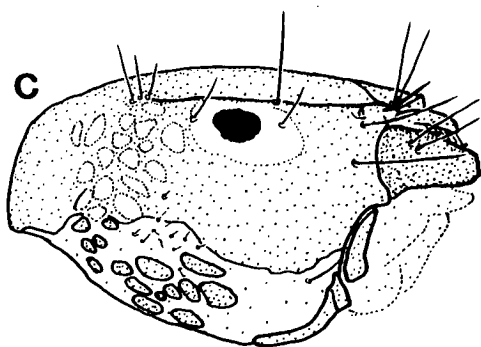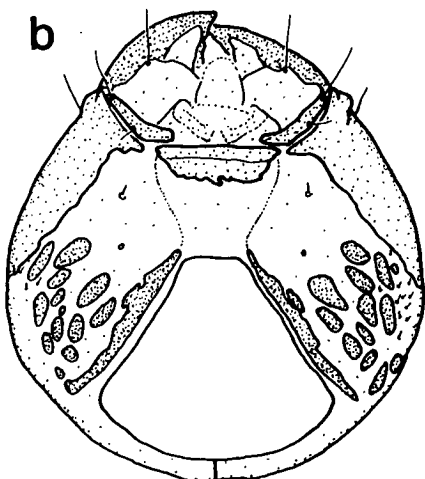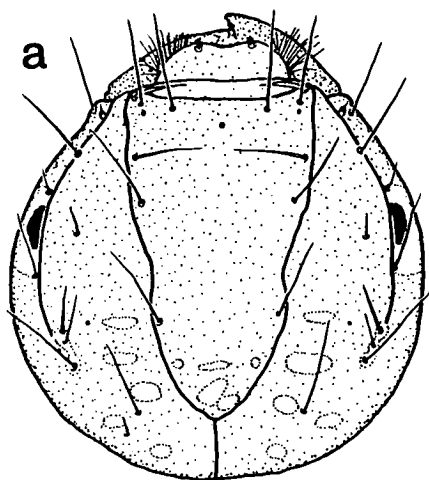
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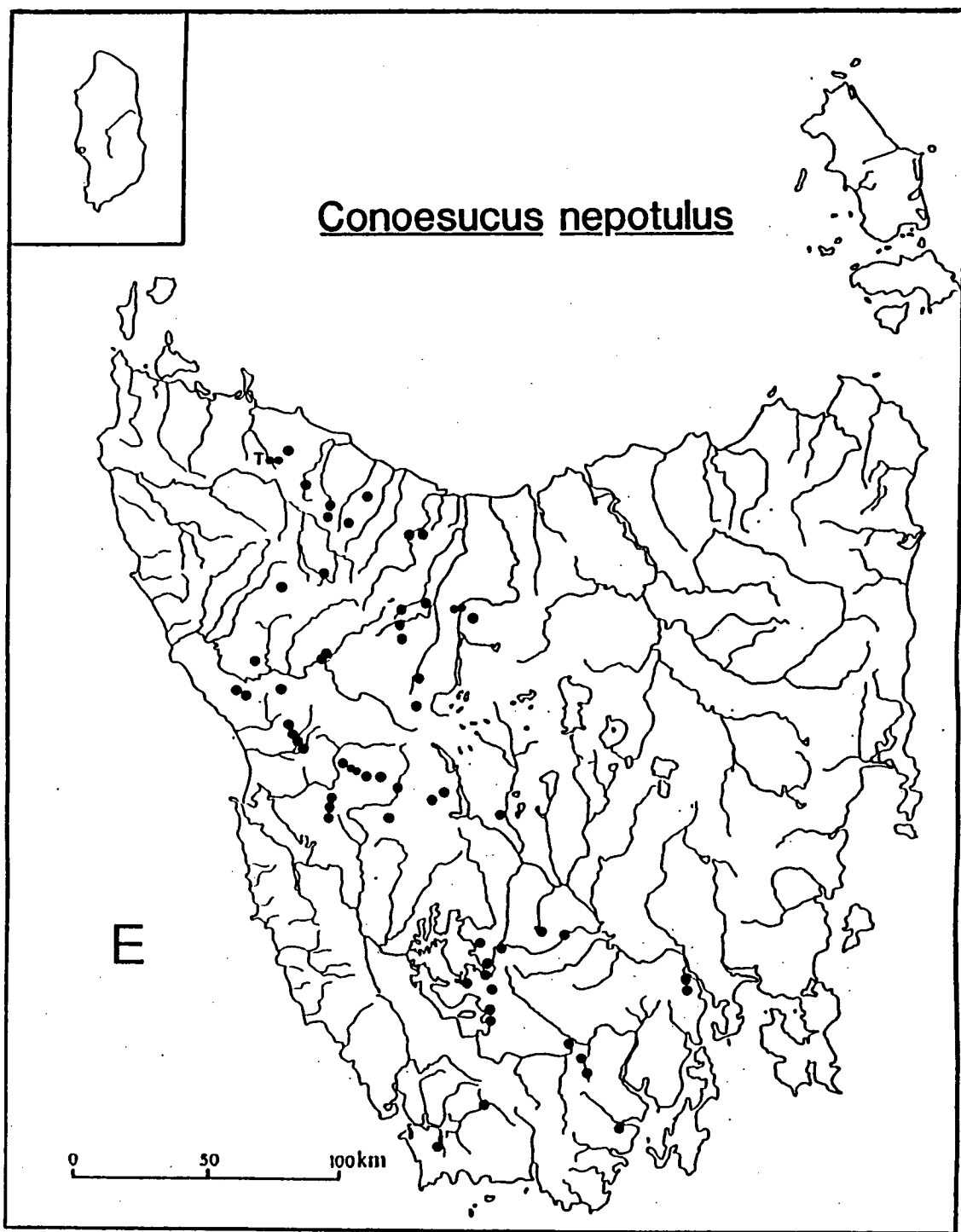
Figure 5.24. Distribution of *Conoesucus nepotulus*.

Larva.

Case of sandgrains, interstices filled with silk, some areas of silk only; anterior margin very slightly oblique; posterior opening central circular or oval hole, about 1/2 width of membrane.

Abdominal gills absent; lateral spicules on segment 8 a row of about 13-15 bifid spicules then 5 single; segment 3-7 with band of 20-30 single and anterior row of about 10 bifid.

Head in dorsal view slightly tapered anteriorly, dark brown, scars paler; dorsum raised into bump in each posterolateral area in early larvae, indistinct in late larvae. About 11 minute setae between ventral scars and border of pigmentation.

Pronotum scars slightly darker, indistinct; no large anterior setae. Anterolateral corner square but not pointed; carina beginning mesad to angle; lateral face with about 14 medium length setae in posterior area. Mesonotum with narrow anterior band of setae 1-2 wide; about 4-5 short pale setae on lateral part of anterior margin visible at high magnification. Metanotum: each SA with 1-2 setae and 0-2 minute setae; SA 1 with irregular sclerite with two dark muscle scars.

Protrochantin oblong, broadly rounded tip. Pleural hump setae minute.

Pupa.

Case anterior membrane domed, slightly curved crescent opening 2/3 below top, width about 1/3 of membrane; slight dorsal overhang posteriorly, posterior membrane slightly concave, opening oval. Adhesive stalked discs at both ends.

Midlegs lacking hair fringes. Terminal processes extending well beyond base of terminal setae. Anterior hookplates with 4 large hooks, posterior plate width about 2x length, with about 6 large scattered hooks. Mandibles equally hooked.

Remarks.

Pupates in small groups attached at both ends to firm substrate, usually in rock crevices.

Material examined: cleared: 1L 180, 9.ii.88; 1L 183, 3.vii.87; 1L 14, 21.xi.87; 2L 136, 27.x.87; 2L 233, 22.x.87; 1L 170, 14.x.87; 1L 152, 27.x.87; other: 13L 41, 4.xii.88, 10.xii.89; 15L 223, various dates; 22L 233, 12.iv.89, 25.viii.88; 2L 136, 31.x.88; 10L 171, 7.xii.87; 10L 152, 27.x.87; 9L 183, 12.xi.88, 25.viii.88; 3L 38, 21.ix.88; 5L 39, 22.ix.88; 15L 170, 11.xi.88; 6L 134, 19.9.88; 5L 126, 20.ix.88; 11L 31, 21.ix.88; 6L 230, 6.x.87; 141 19, 21.ix.88; 7L 135, 19.ix.88; 1L 129, 19.ix.88; 1L 260, 18.viii.88; 1L 30, 21.ix.88; 8L 124, 20.ix.88; 7L 169, 1.ix.88; 5P 41, 7.xii.88; 4P 136, 20.ix.88; 5P 223, 4.ix.88 em. 4.x.88; 5P 170, 14.x.87. Drawings based on specimens: 1L 152, 27.x.87; 1L 136, 27.x.87; 1P 180, 9.ii.88; 1P 223, 4.ix.87 em. 4.x.87.

Distribution (Fig. 5.24). Endemic; widespread west of Burnie-Hobart line; often very common where collected.

Conoesucus norelus Mosely
(Figs 5.25, 5.26)

Conoesucus norelus Mosely in Mosely & Kimmins, 1953, p. 90; Neboiss, 1977, p. 110.

Larva.

Case usually mostly of sand grains but proportion of sand: silk quite variable,
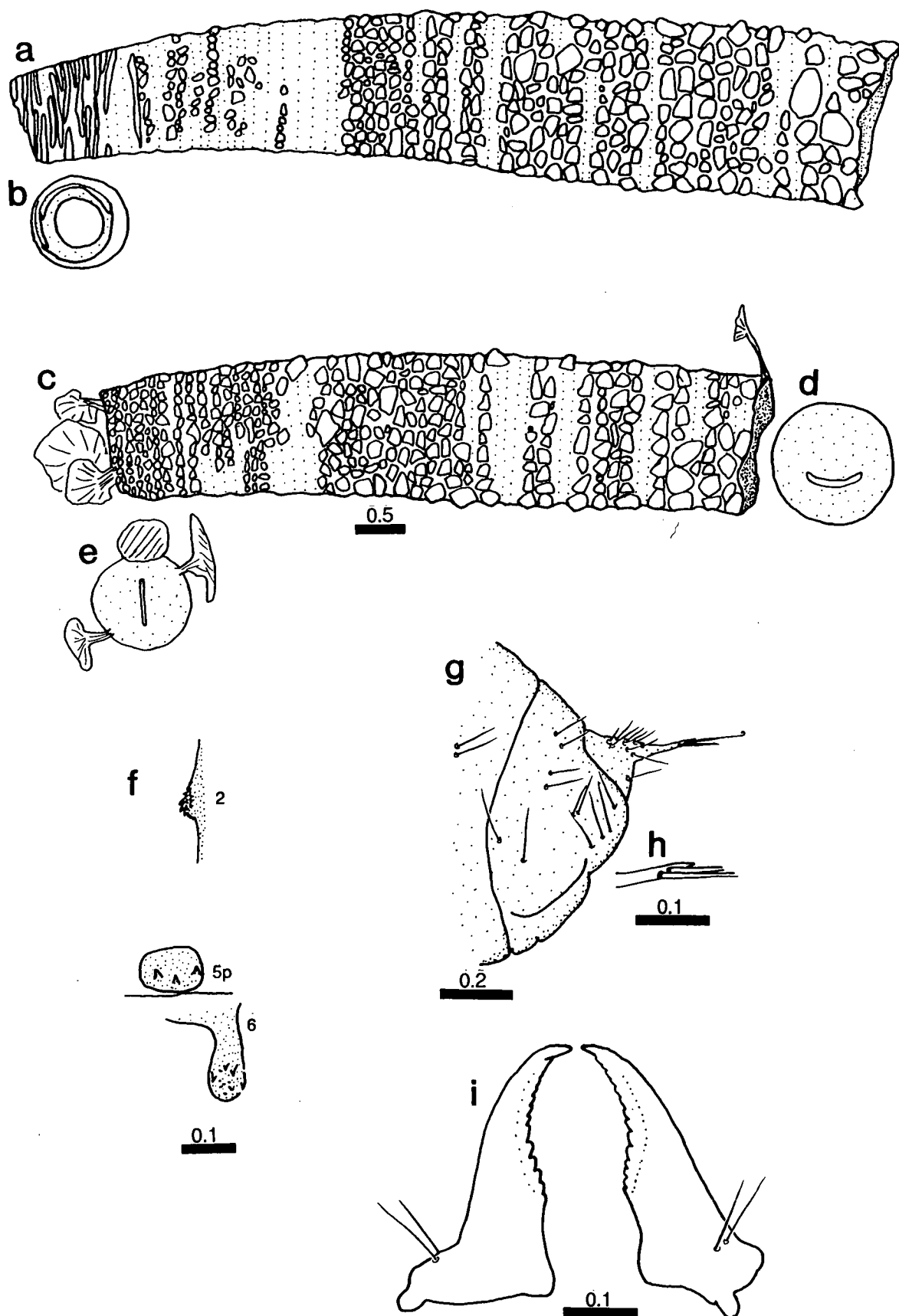
Figure 5.25. *Conoesucus norelus* larva and pupa. **a, b:** larval case lateral, posterior membrane; **c, d, e:** pupal case lateral, anterior, posterior membrane; **f:** hookplates; **g, h:** ♂ terminalia lateral, process apex; **i:** pupal mandibles, ventral.
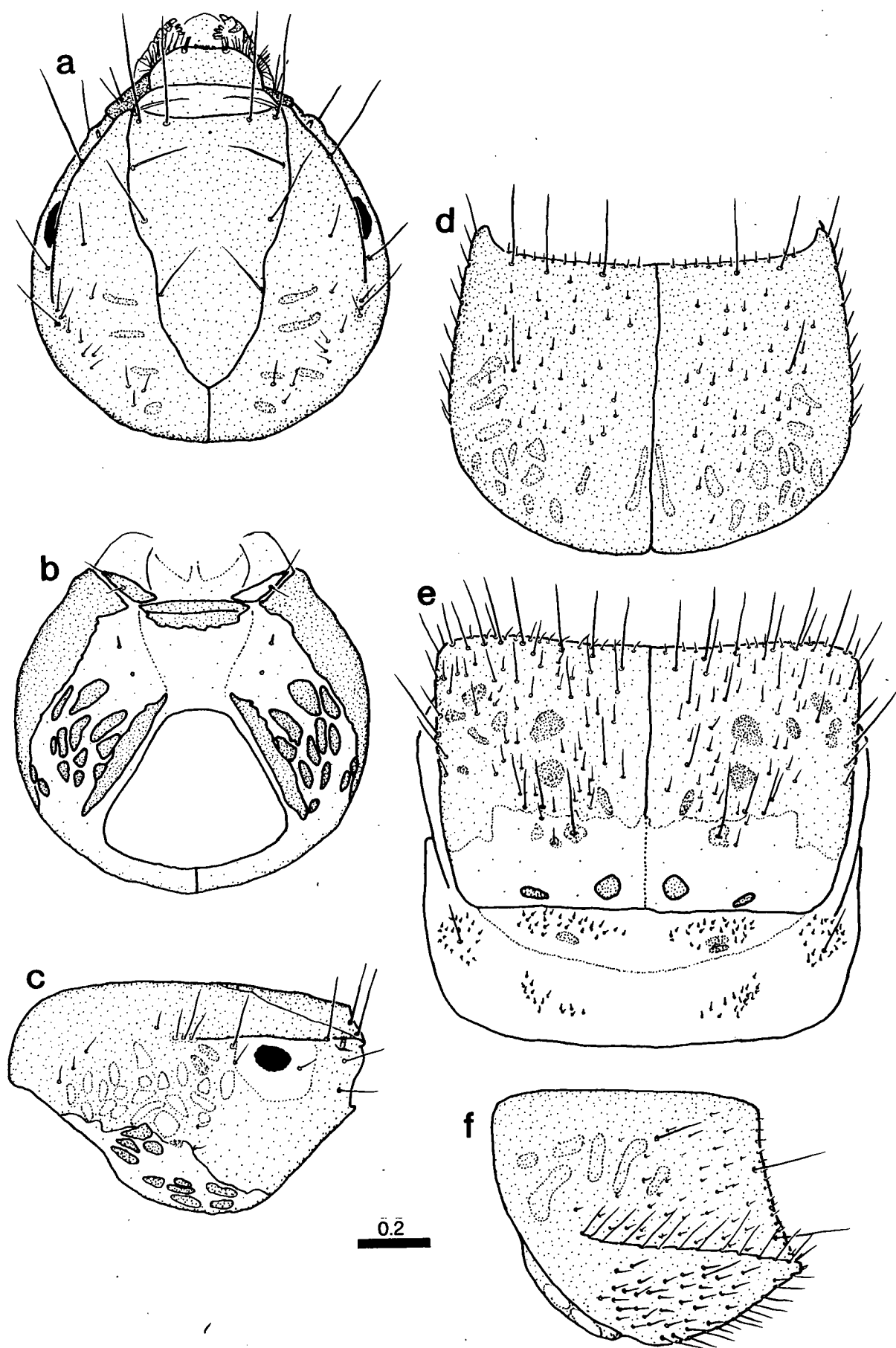
Figure 5.26. *Conoesucus norelus* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f:** pronotum, lateral.

sometimes including plant material at posterior end. Anterior and posterior margins slightly oblique; posterior membrane flat, with large circular hole.

Gills present: segment 1 posterodorsal and ventral, segment 2 anterodorsal, ventral and lateral, segment 3 anterodorsal. Lateral abdominal spicules on segment 8 alternating single spines and bifid spicules, segments 3-7 each with band of about 33-38 single and anterior row of 1-7 bifid spicules. Segment 3 lacking dorsal patches of minute spicules.

Head in dorsal view narrowing slightly anteriorly; colour dark golden, scars same colour and indistinct, small and thin. Group of several fine setae in each posterolateral area. Laterally, two short setae above margin of pigmentation.

Pronotum scars indistinct, same colour or slightly paler than background. Anterior row of about 3 long dark setae on each side just behind margin. Anterolateral corner pointed, not really projected, angle almost square, one or two stout setae at apex. Carina extending from just mesad of corner; lateral margin with scattered fairly short setae.

Mesonotum with anterior row of small fine setae, even row of long setae just behind anterior margin; fine setae scattered over pigmented area of dorsum. Metanotum: each SA with numerous tiny clear spine-like setae: SA 1 25-27, an oval pigmented area in middle of group; SA 2 12-15; SA 3 21, and single long seta.

Pleural humps with numerous minute setae on dorsal surface. Protrochantin with hemispherical tip.

Pupa.

Case anterior margin sometimes flaring out slightly, membrane flat, set in from margin, a curved slit below centre about 1/2 width of membrane diameter. Posterior membrane flat, with narrow slit of height about 1/2 membrane diameter. A single small stalked adhesive disc anteriorly, several large stalked discs posteriorly.

Midleg tarsi with sparse setae. Anterior hookplates with about 4 hooks, posterior plates almost square, 3-4 anteriorly directed hooks. Terminal processes relatively small, apex pointed, projecting slightly beyond base of terminal setae.

Right mandible more strongly hooked than left.

Remarks.

Pupates attached to rocks or sometimes wood, usually in small groups in crevices with anterior of case projecting outwards; commonly attached amongst retreats of net-spinners.

Material examined: cleared: 2L 229, 12.xi.88; 1L 45, 29.xi.88; 2L 68, 18.xi.88; 1L 9, 20.xi.87; 1L 124, 1.xi.88; 2L 51, 1.xii.88; other: 10L 210, 17.xii.87; 12L 68, 18.xi.88; 4L 124, 1.xi.88; 1L 208, 17.xii.87; 4L 150, 27.x.87; 5L 131, 27.x.87; 2L 295, 4.ii.88; 4L 207, 17.xii.87; 6L 138, 27.x.87; 6L 228, 18.xi.87; 8L 214, 21.xii.87; 5L 239, 21.x.87; 4L 23, 21.xi.87; 8L 252, 4.xi.87; 6L 265, 3.xi.87; 10L 18, 21.xi.87; 2L 6.ii.86, IFC; 5L 45, 29.xi.88; 3L 13, 20.xi.87; 10L 51, 1.xii.88; 5L 25, 21.xi.87; 3L 92, 5.ii.88; 6L 9, 20.xi.87; 10L 64, 22.xi.87; 10L 223, 20.i.88; 2P 150, 1.xi.88; 3P 124, 1.xi.88 em. 15.xi.88; 1P 47, 29.xi.88; 5P 229, 25.i.88 em. 12.ii.89.

Drawings based on specimens: 1L 68, 18.xi.88; 1L 229, 12.xi.88; 1P 47, 29.xi.88 em. 20.xii.88.
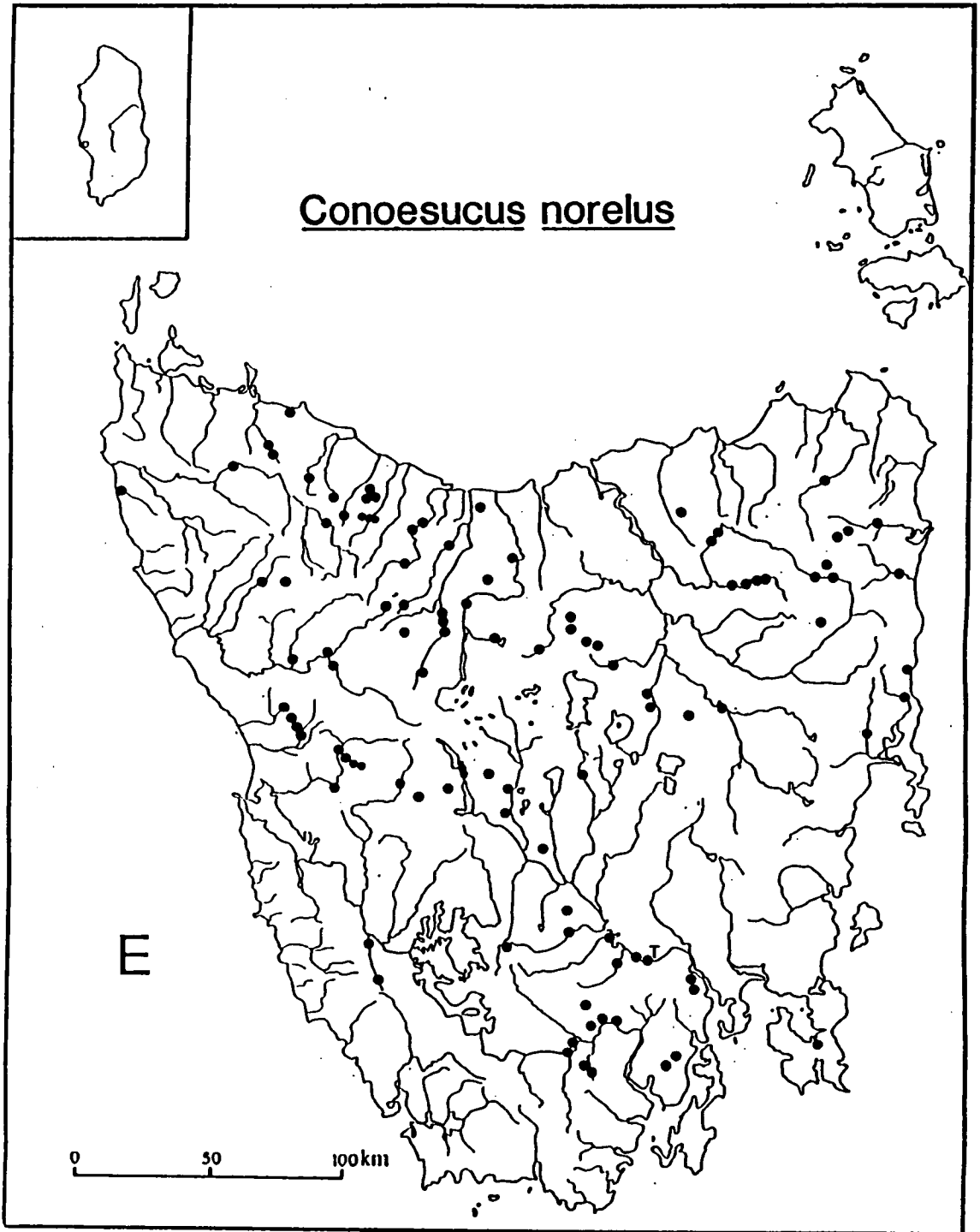
Figure 5.27. Distribution of *Conoesucus norelus*.

Distribution (Fig. 5.27). Endemic; widespread; often very common where collected.

Conoesucus notialis sp. n.
(Figs 5.28-5.31)

Etymology: the Latin *notialis*, southern; for the southern distribution of the species.

Adults. (Figs 5.30, 5.31)

Black coloured, abdominal sclerites charcoal black, flesh greenish. Wings: ♂ anterior length 5-5.5mm; ♀ 7mm; Cu_2 ending at margin, connected by cross vein to Cu_{1b} in both sexes; in posterior wing Sc may join R1; ♂ anterior wings without folds, small scale-like hairs below R from base, not extending to margin. Male posterior wing dc sometimes open.

Male maxillary palps 3-segmented, segment 1 short, segment 2 about 2x segment 1, segment 3 about as long as1+2, all segments covered with flattened black setae; maxillary palps 5-segmented and normal in female. Scutellum warts 1/2-2/3 length of scutellum.

Male genitalia: segment 9 dark brown, dorsally extended distally into pair of very broad curved processes, laterally slightly produced into rounded setose lobe. Superior appendages short round lobes, bearing pale setae; inferior appendages brown, tapering distally, only slightly curved, inner margin setal sockets produced into fingerlike processes. Segment 10 pale golden, consisting of two laterally flattened processes covered with short clear sharp setae, broadening slightly before tapering to apex, apex only slightly upturned. Phallus broad, apex truncate.

Female abdomen terminating bluntly, tergite 9 concave, median process with slight concavity in distal margin; distal lateral areas with short clear setae. Tergite 8 with single broad band of dark setae. Ventral plates about as wide as long, ventral incision with parallel sides or slightly narrower distally. Sternite 8 distal 1/2 densely setose with dark setae, other sternites with sparse dark setae; no distal process on sternite 7.

Larva. (Figs 5.28, 5.29)

Case entirely of golden silk, sometimes with a few sand grains; anterior margin slightly oblique, posterior opening a circular or slightly oval hole dorsad of centre, membrane filling in undercut ventral margin.

Abdominal gills small and indistinct: segment 1 dorsal, segment 2 anteroventral and small single anterodorsally. Lateral spicules on segment 8 about 10 single, on segments 3-7 narrow band of 20-30 single and row of 3-4 bifid, on segment 2 a single row of about 20 single. Anal prolegs with lateral sclerites lightly pigmented, margin indistinct.

Head tapering anteriorly in dorsal view, dark golden, scars paler and distinct. Frontoclypeus anterior margins fairly straight. Group of minute pale setae between lateral and ventral scars. Ventral apotome entirely pigmented, anterior half more darkly.

Pronotum dark brown, scars slightly darker and indistinct, elongate median scar pale and distinct; no large anterior setae. Anterolateral corner pointed, slightly

Figure 5.28. *Conoesucus notialis* sp. n. larva and pupa. **a, b, c:** case
lateral, posterior membrane, posterior ventral; **d, e, f:** pupal case lateral,
anterior membrane, posterior membrane; **g:** pupal abdomen dorsal; **h, i:**
terminalia lateral, process lateral; **j:** mandibles, ventral.

a

b c 0.5

d e

0.5

f

g

h

i

0.1

0.05

j

0.05

1

2

5

6

7

8

0.2
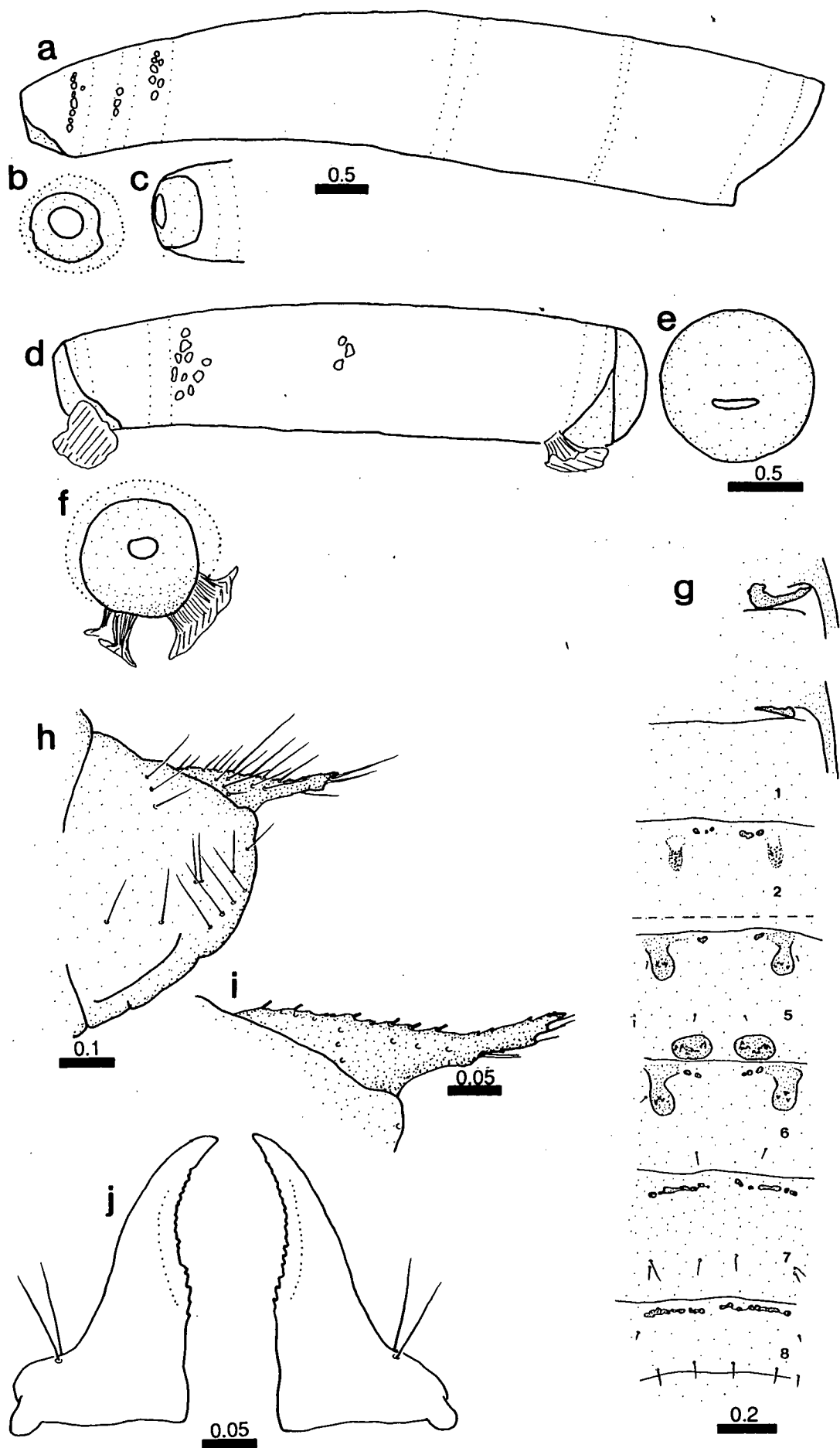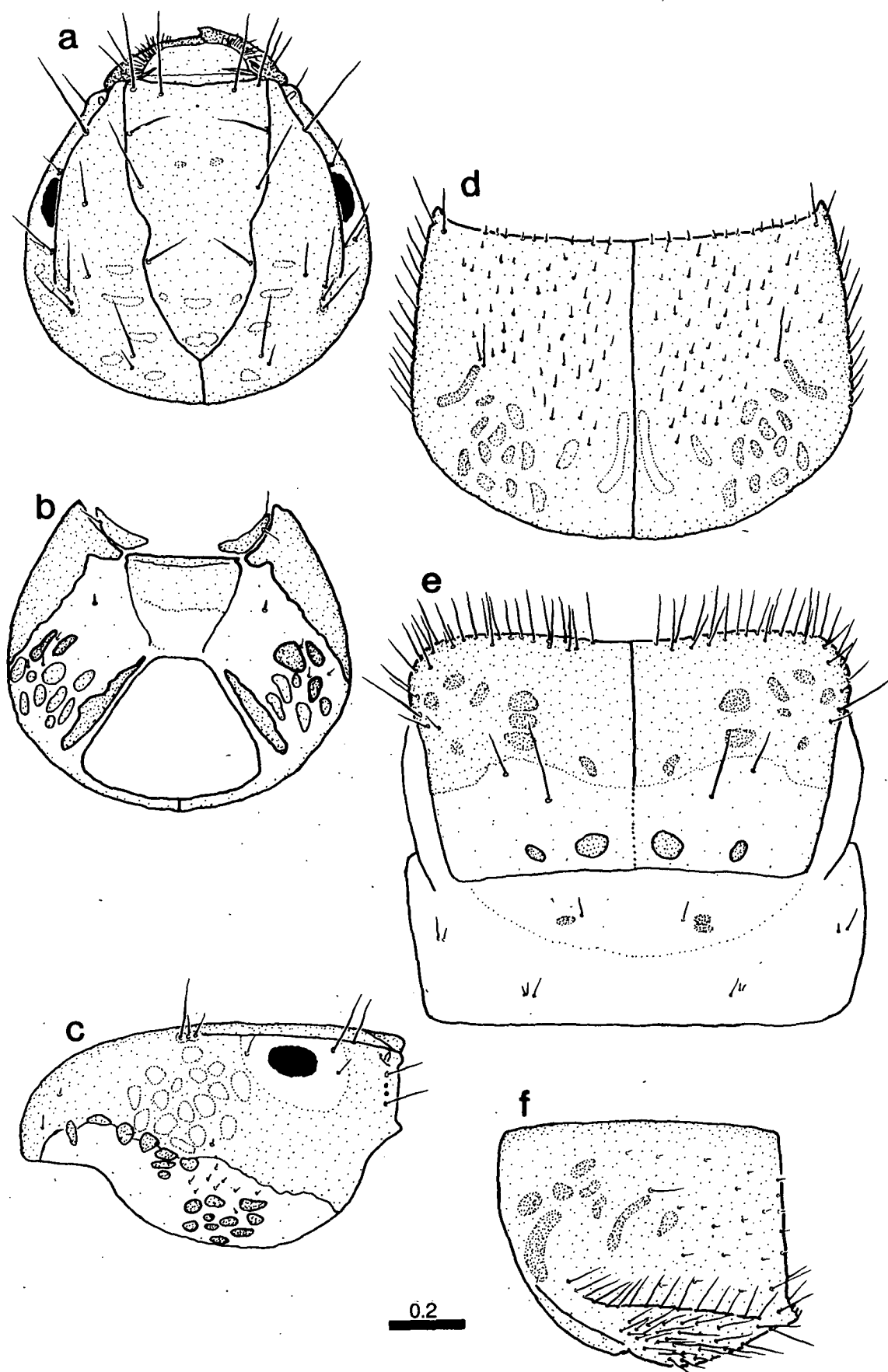
Figure 5.29. *Conoesucus notialis* sp. n. larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f:** pronotum lateral.
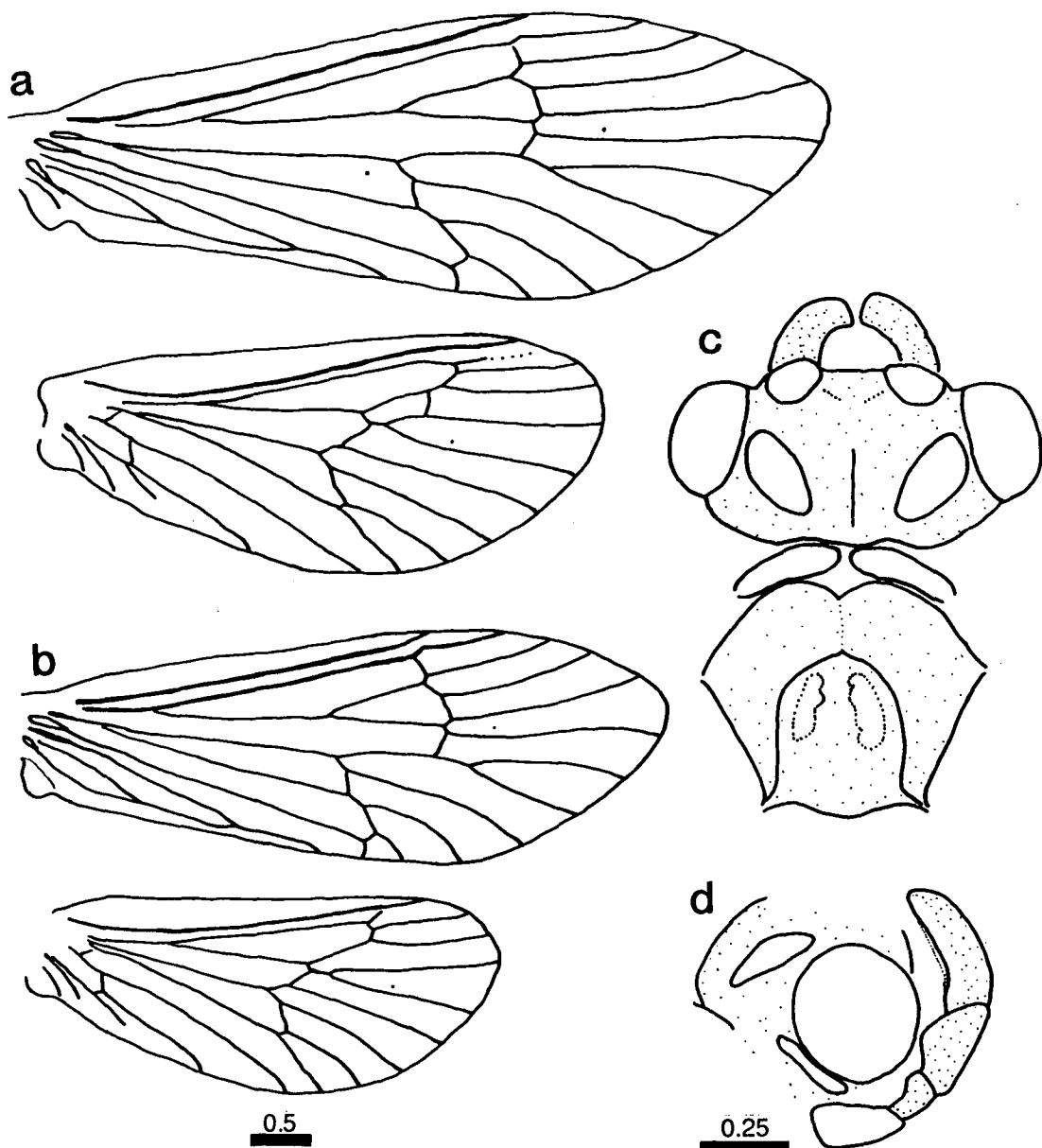
Figure 5.30. *Conoesucus notialis* sp. n. adults. **a, b:** ♀, ♂ wings; **c:** ♂ head and thorax, dorsal; **d:** ♂ head, lateral.
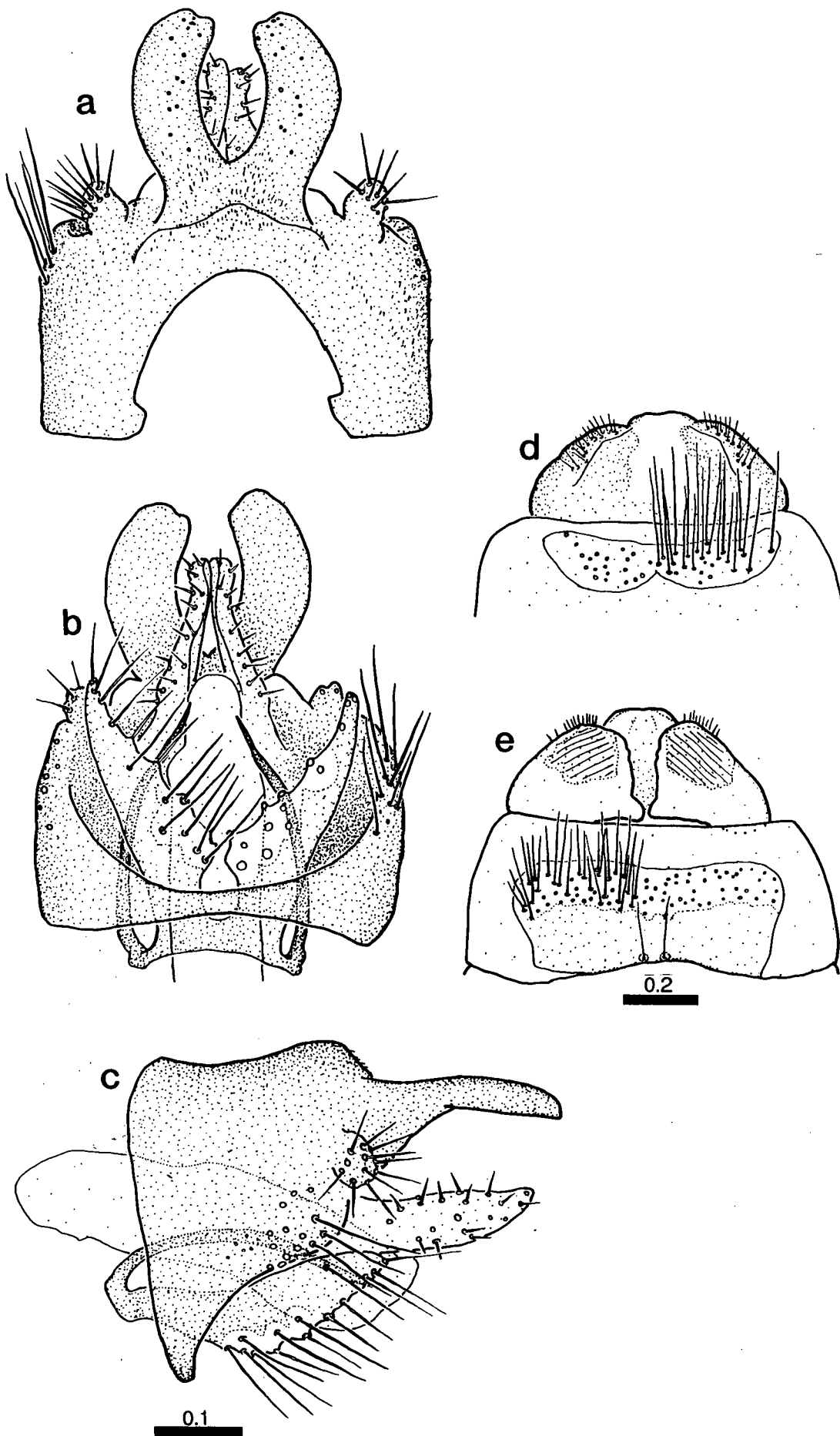
Figure 5.31. *Conoesucus notialis* sp. n. adults. **a, b, c:** ♂ genitalia dorsal, ventral, lateral; **d, e:** ♀ genitalia dorsal, lateral.

projected, 4 fine short hairs arising from bumps on anterior margin of projection; carina extending from behind corner, lateral face covered with medium length stout setae. Mesonotum anterior margin with irregular row, 1-2 wide, of medium length setae. Metanotum: each SA with 1-2 setae and 0-2 small setae; SA 1 sometimes with pigmented area.

Protrochantin triangular, tip upturned.

Pupa.

Undercut anterior margin of case filled in with silk. Anterior membrane domed, slit very slightly curved, just below centre; posterior membrane domed, opening a dorsoventrally flattened oval in distal end of membrane. Adhesive discs ventrally at both ends, arising from old (larval) case margin.

Midlegs lack hair fringe. Anterior hookplates with 3-4 hooks, posterior plates slightly wider than long, with about 6 larger hooks irregularly arranged and several smaller teeth. Additional small irregular sclerites sometimes present in row on anterior of segments 2-8. Sclerites on thorax just behind wing bases. Terminal processes with spiny apices, short projection beyond bases of terminal setae.

Remarks.

Found on rock surfaces in streams, rocks with film of algae. Pupates under rocks.

Type material: HOLOTYPE ♂: Twin Creeks, Scott's Peak Dam Rd. (site 183), 25.viii.88 em. 9.x.88; ALLOTYPE ♀: same locality and date; PARATYPES: 2♂ 1♀ same locality, 12.xi.88 em. 20.xi.88; 1♂ 1♀ same locality, 12.xi.88 em. 14.xi.88; 1♂ 1♀ Condominium Creek, Scott's Peak Dam Rd. (site 182), 25.viii.88 em. 12.x.88; 5L 183, 25.viii.88.

Material examined: adults: 6♂ reared 3♀ reared 183, 25.viii.88; 4♂ reared 5♀ reared same locality 12.xi.88; 12♂ reared 2♀ reared 182, 6.x.87. Drawings based on specimens: holotype ♂ and allotype ♀.

Larvae and pupae: cleared: 3L 182 25.viii.88; 2L 183, 25.viii.88; other: 40L 183, 3.vii.87, 9.ii.88, 25.viii.88; 12.xi.88; 12L 182, 26.iii.87, 25.viii.88; adults: 2M 182, 6.x.87 em. 9.xi.87, 1.xii.87; 7M1F 182, 25.viii.88 em. 12.x.88; 6M5F 183, 12.xi.88 em. 14-26.xi.88; 1M1F 183, 25.viii.88 em. 9.x.88. Drawings based on: 2L 183, 25.viii.88; 1P 183, 25.viii.88 em.12.x.88.

Distribution (Fig. 5.32). Endemic; collected from only a few sites in south-west; common where collected.
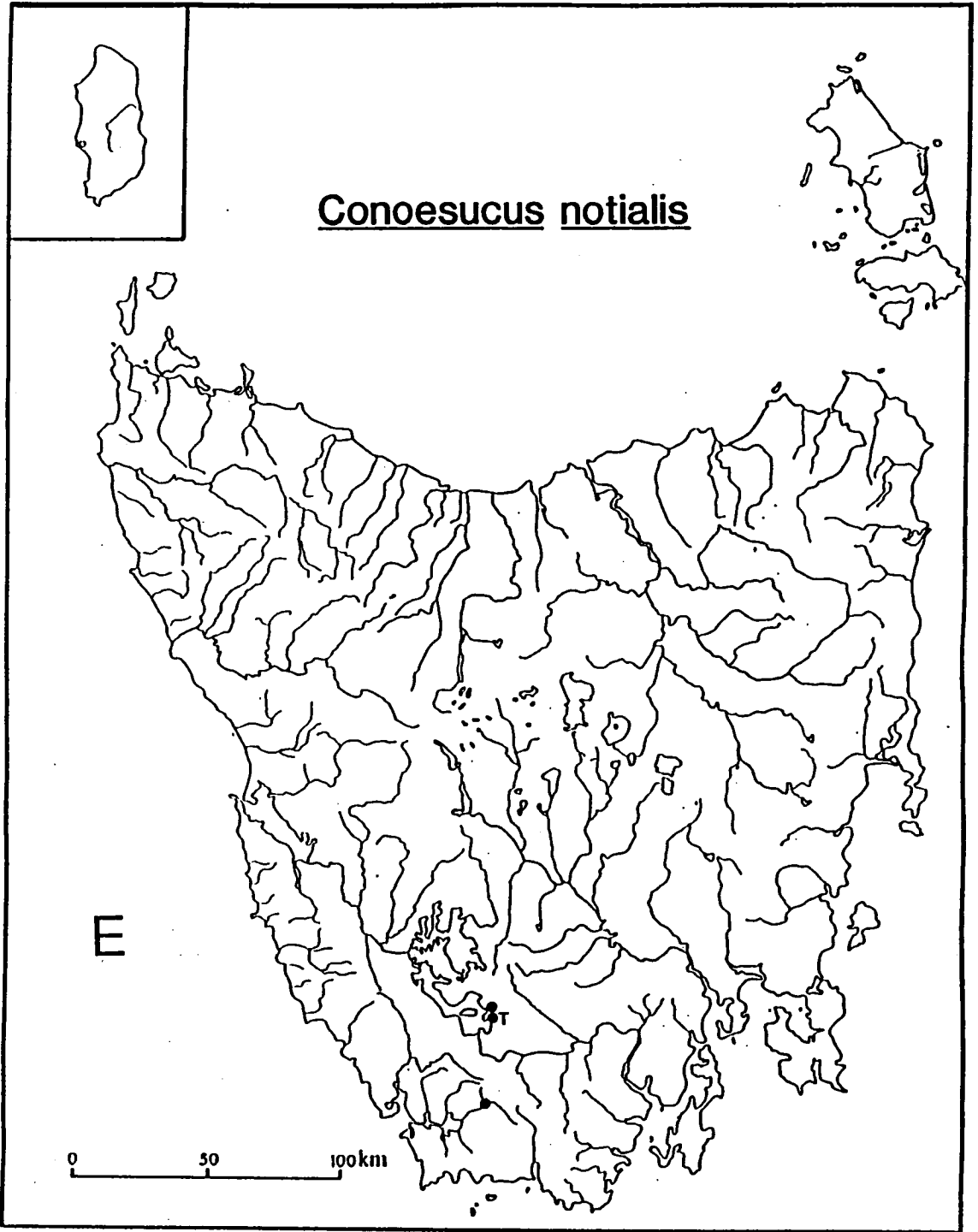
Figure 5.32. Distribution of *Conoesucus notialis*.

Genus **Costora** Mosely

Mosely, 1936, p. 403; Mosely & Kimmins, 1953, p. 45; Neboiss, 1977, p. 102.

Type species: *Costora iena.*

Larva

Case a long, tapering curved cylinder in all species except *ebenina*; of circularly arranged sandgrains or plant material, or entirely of silk. Anterior margin square, posterior membrane with circular hole.

Abdomen gills large, branched, on segments 1-3 or 4; segment 8 with lateral row of bifid spicules, segments 3-7 with band of single spicules 1-4 wide, decreasing in number on anterior segments; ventral bands of minute elongate sclerites on segments 4-8, no dorsal patches. Tergite 9 with single rectangular sclerite, pigmentation irregular, varying with species; on posterior margin 5-6 pairs of setae, 2 pairs long. Anal proleg lateral sclerite pigmentation varying with species; many large dark setae in posterior area; 4-5 dark scars anteriorly; ventral sclerite oval, brown.

Head dark golden to brown, texture polygonal reticulation or spiny. Carina generally weak, only extending behind eye in *delora*. Laterally, between lateral and ventral scars, a few short setae. Anterior margin of ventral apotome straight or produced forward into triangular shape. Ventral mandibular articulation prominent in some species.

Mandibles generally less stout than in *Conoesucus*, slightly longer than wide; apical teeth slight or lacking, left mandible with dorsal margin straight, about 5 finger shaped processes in mesal concavity distal to short brush; right with broad dorsal tooth, sometimes with thick bristles distal to brush.

Pronotum with weak polygonal reticulate texture; anterolateral corner shape varying with species, lateral carina absent in all species except *delora*. Lateral area densely setose.

Mesonotal anterior margin with regular row of fine small setae, and single row of large dark setae, band of large setae near posterior of pigmented area, fine pale setae scattered over pigmented area. Metanotal SAs all with 1-5 small-medium setae, pigmented areas usually present.

Protrochantin fused to propleuron; shape variable, apex upturned slightly or strongly; small setae on anterior margin.

Gonads: testis with 4 long lobes.

Pupa

Case an almost straight cylinder; anterior slit straight or curved, below centre of flat or projected membrane; posterior membrane flat or domed.

Midlegs with dense hair fringe on both edges. Anterior hookplates roughly oval, 2-4 large hooks; posterior plates almost square, 3-6 hooks. Dorsal setae: one lateral to each anterior hookplate and pair posteriorly about half way to back, plus setae on additional sclerites. Terminalia: dorsum of segment 9 with transverse row of setae; processes narrow basally, tapering to apex, apices minutely toothed or papillate.

Labrum with mid transverse row of 2 pairs of large setae and small on margin, posterolateral area with 2 large and 1 smaller setae.

Key to adult males of Tasmanian *Costora* species (modified from Neboiss 1977 p. 102; couplets 1-4 as in Neboiss).

5.-Segment 10 dorsal projections about as long as superior appendages, basal on segment 10, truncate and serrate at apex........ *C. seposita*
-Segment 10 dorsal projections very small, some distance distal along segment
.... *C. luxata*

Key to larvae of Tasmanian *Costora* species.

1.-Mesonotum with pair of large posterior setae.... 2
-Mesonotum with row or band of large posterior setae
.... 3

2.-Pronotum with lateral carina; anterolateral corner sharply pointed; head texture polygonal reticulate, not spiny..............*C. delora* [silk case]
-Pronotum without lateral carina; corner very rounded; head spiny
.... *C. ebenina* [plant case]

3.-Mesonotum anterior setae with tips spatulate/clubbed
.... 4
-Mesonotum anterior setae with tips tapering evenly
.... 5

4.-Pronotum anterolateral corner rounded square, projecting slightly but distinctly forward; head colour golden, scars indistinct or slightly paler; ventral mandibular articulation prominent......... *C. seposita* [sand case]
-Pronotum anterolateral corner rounded square, very slight or no projection; head dark brown, scars paler and distinct; ventral mandibular articulation not prominent.. *C. luxata* [sand case]

5.-Head golden, scars not very distinct; mesonotum setae long, dark; anterior row of 6-8 pairs......................................*C. ramosa*
C. krene *
*[no characters enable diagnosis of these species]
-Head dark brown, scars paler and distinct; mesonotum setae short, relatively fine; anterior row of 5-6 pairs...................... *C. rotosca* [sand case]

Key to pupae of *Costora, Lingora, Hampa* and *Matasia* species.

1.-Labrum with >5 large pairs of posterior-lateral setae
.... 2
  -Labrum with 2 large pairs of posterior-lateral setae
.... 3

2.-Terminal processes smooth; tergite 9 with 4-6 pairs of setae;
  labrum with many posterior-lateral setae.......... *Matasia satana*
  -Terminal processes minutely toothed; tergite 9 with many setae;
  labrum with about 6 pairs of posterior-lateral setae
.... *Lingora aurata*

3.-Mandibles equally hooked......................... 4
  -Right mandible more strongly hooked than left   5

4.-Terminal processes turned up, pointed, dorsally papillate, apices smooth;
  posterior hookplates with 3-7 hooks; mandibles curve
  strongly.. *Costora delora*
  -Terminal processes straight, rounded, tips dorsally smooth, apices
  papillate; posterior hookplates with 2-4 hooks; mandibles curve
  weakly.. *Costora seposita*

5.-Mandibles with many outer basal setae........... *Costora ebenina*
  -Mandibles with 2 outer basal setae................6

6.-Terminal processes with dorsal hump............. *Costora ramosa*
  -Terminal processes straight........................7

7.-Tergite 9 with many setae; terminal processes with apices turned up; terminal
  processes minutely toothed dorsally and apically
.... *Hampa patona*
  - Tergite 9 with 4-6 pairs of setae; terminal processes with straight apices;
  terminal processes smooth dorsally, apices papillate
.... 8

8.-Mandibles curved slightly.......................... *Costora luxata*
  -Mandibles curved strongly.........................*Costora krene*
                                        C. rotosca..........9

9.These two species cannot be separated on the basis of caseless pupae alone;
  however, *C. krene* has a plant material case, *C. rotosca* a sand case.

Costora delora Mosely
(Figs 5.33, 5.34)

Costora delora Mosely in Mosely & Kimmins, 1953, p. 49; Neboiss, 1977, p. 103.

Larva

Case entirely of smooth silk, posterior membrane domed.

Abdomen orange; gills on segment 1 posterodorsal and ventral, segments 2 and 3 anterodorsal, lateral and ventral, segment 4 with small anteroventral gill. Lateral spicules: segment 8 with about 19 , segments 3-7 with 60-80. Tergite 9 sclerite not pigmented, 5 pairs of fine setae posteriorly. Anal prolegs lateral sclerites with light brown posterior margin, about 4 stout setae, others finer.

Head golden, tapering anteriorly; scars slightly darker, not greatly wider than long. Strong carina extending from anterior margin to behind eye. A group of about 10-15 fine short setae on posterolateral area of dorsum. Frontoclypeus broad anteriorly, anterior margins straight, constriction pronounced. Anterior margin of ventral apotome a triangular projection. Ventral mandibular articulation a fingerlike projection.

Mandibles without apical teeth.

Pronotum golden, scars slightly darker; anterior margin slightly concave in middle and convex laterally; anterolateral corner pointed acutely, projected forward of margin, strong carina extending from apex, curving to dorsum midway along, curving slightly dorsad posteriorly; row of medium length setae along carina. Lateral face narrow and sparsely setose.

Mesonotum with medium-long anterior setae, pair on posterior of pigmentation, 1 long 1 shorter. Posterior margin strongly concave. Metanotum anterior hemispherical area weakly sclerotised, SA 1: 1 medium length seta, 2 lateral pigmented areas; SA 2: 3 very small setae; SA 3 : 1-2 minute setae.

Protrochantin tip rounded, not upturned. Pleural humps with many minute setae and one long.

Pupa

Case anterior membrane projecting in convex cone, slit slightly curved, width about 1/3-1/4 membrane diameter. Posterior membrane conical, with central circular small hole. One large ventral stalked adhesive disc at each end.

Anterior hookplates with 2-3 small hooks; posterior with about 6 small hooks; brown sclerotized areas around dorsal setae. Terminal processes setose dorsally for entire length, dorsal surface toothed, apices rounded and very slightly upturned.

Mandibles equally hooked.

Remarks

Found on water plants or rocks, occurs in fast and slow-flowing streams. Pupates singly on water plant leaves or more rarely in groups of 1-3 in rock crevices.

Material examined: cleared: 1L 299, 5.ii.88; 1L 15, 21.xi.87; 1L 18, 21.xi.87; 1L 257, 4.xi.87; Victoria: 1L Tanjil River, Walhalla Rd Bridge, 4km N of Moe, 8.xi.77, AN; other: 2L 72, 18.xi.88; 8L 257, 18.viii.88; 1L 90, 9.i.90; 10L 91, 9.i.90; 7L 17, 20.ix.88; 1L 229, 12.xi.88; 5L 29, 21.ix.88; 30L 15, 21.ix.88, 21.xi.87; 3L 79, 18.xi.88; 4L 78, 18.xi.88; 5L 107, 20.ix.88; 6L

Figure 5.33. *Costora delora* larva and pupa. **a, b, c:** larval case lateral, posterior enlarged, posterior membrane; **d:** larva, lateral; **e, f:** tergite 9 and anal legs dorsal, ventral; **g:** protrochantin; **h, I, J:** pupal case lateral, anterior membrane, posterior membrane; **k:** midleg fringe; **l, m, n:** terminalia dorsal, lateral, process lateral; **o:** hookplates; **p:** mandibles ventral.
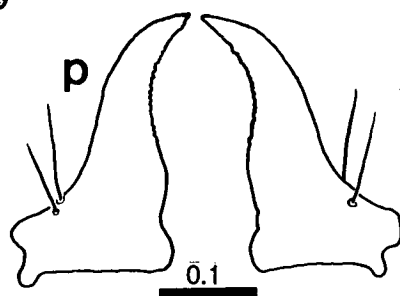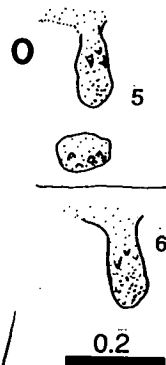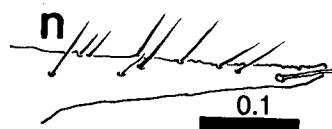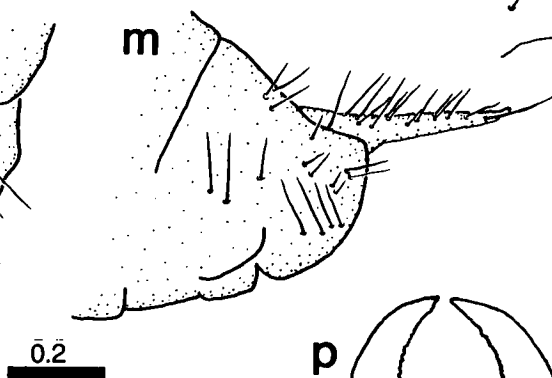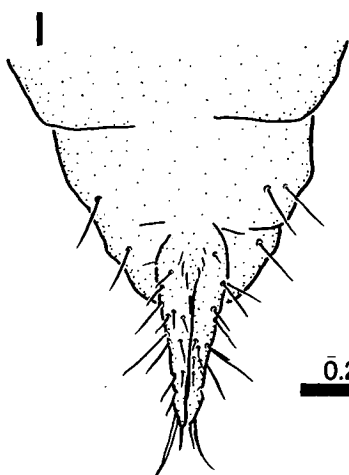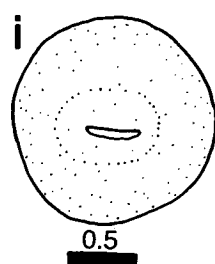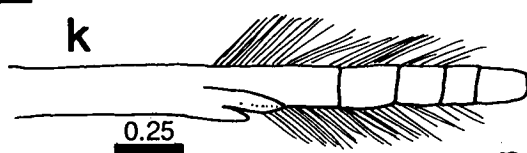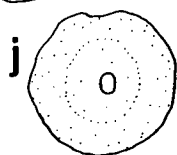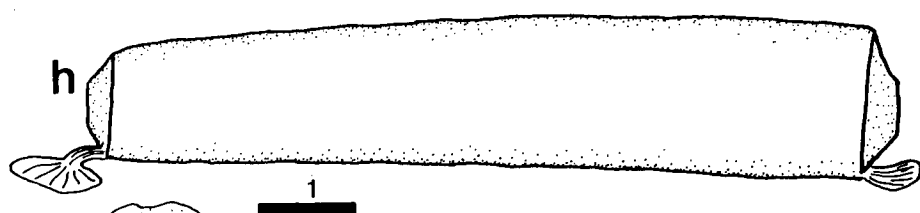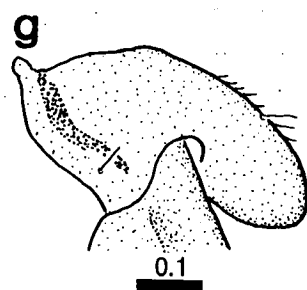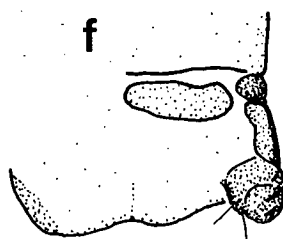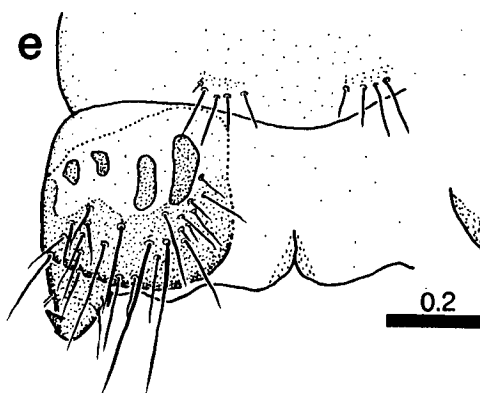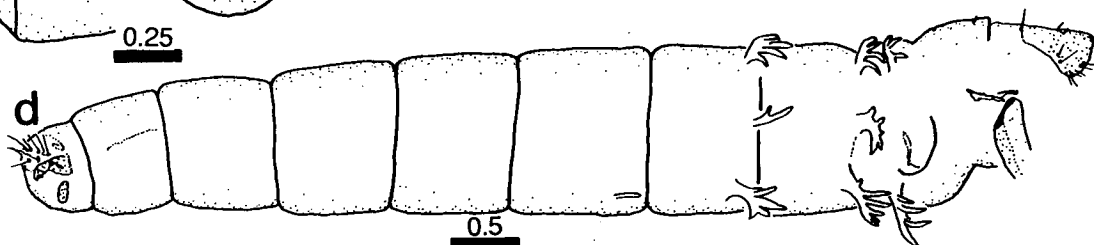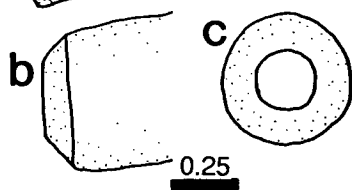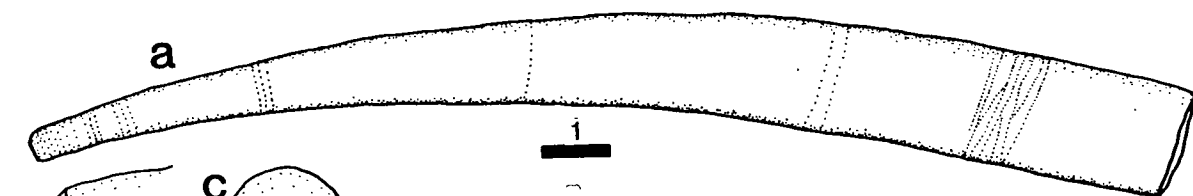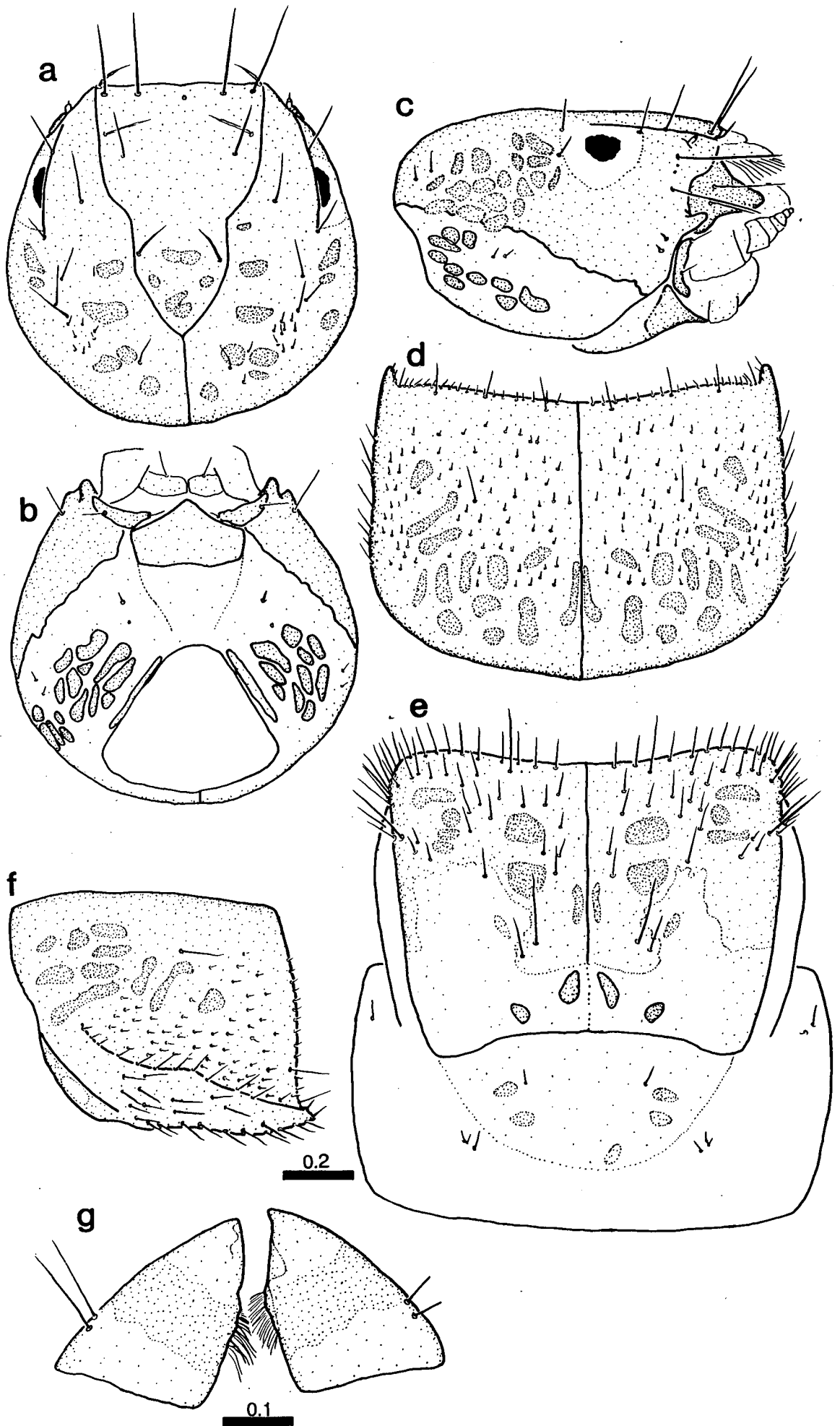
Figure 5.34. *Costora delora* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f:** pronotum, lateral; **g:** mandibles, dorsal.
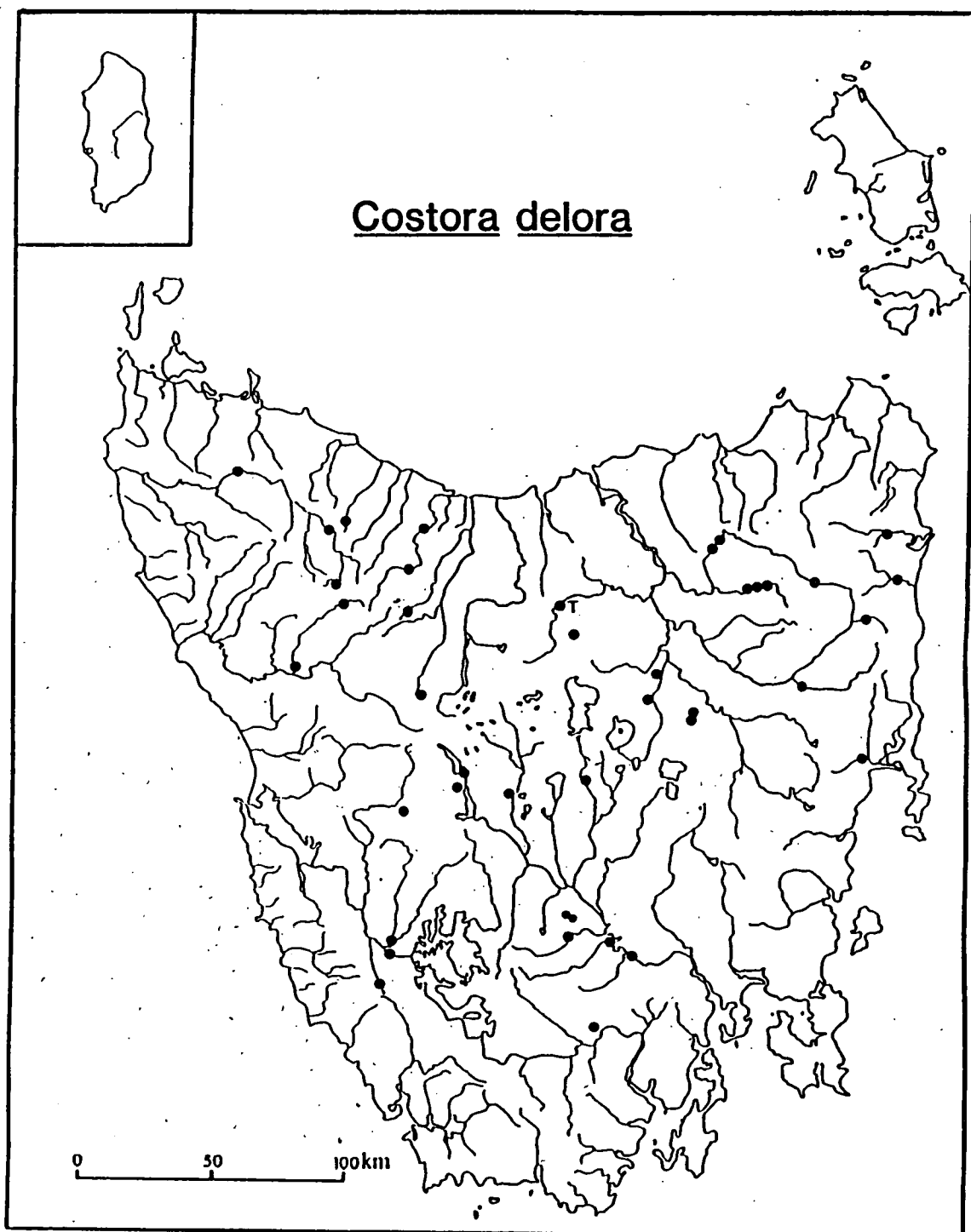
Figure 5.35. Distribution of *Costora delora*.

39, 22.ix.88; 3L 64, 22.xi.87; 1L 265, 3.xi.87; 6L 18, 2.xi.87; 8L 229, 5.ii.88; 2L 89, 9.i.90; 1L 289, 19.xii.89; 1P 90, 9.i.90; 5P 91, 9.i.90; 3P 89, 9.i.90; 5P 15, 21.xi.87 em. 14.xii.87; 2P 229, 5.ii.88 em. 7.iii.88; 2P 73, 18.xi.88 em. 14.xii.88; **Victoria**: 6L, 4P Tanjil R, Walhalla Rd 5km N of Moe, 17.xi.74, AN; 10P Tanjil R, Walhalla Rd Bridge 4km N of Moe, 8.xi.77. Drawings based on specimens: 1L 257, 4.xi.87; 1L 299, 5.ii.88; 1P 299, 5.ii.88; 1P 15, 21.xi.87.

Distribution (Fig. 5.35). Tasmania and SE Australia; widespread within Tasmania; may be numerous where collected.

Costora ebenina Neboiss
(Figs 5.36, 5.37)

Costora ebenina Neboiss, 1977, p.104.

Larva

Case of plant material; truncate, not strongly curved and tapered; posterior membrane projected into cone with concave sides, opening about 1/2 membrane diameter. Anterior margin straight, sometimes with slight dorsal extension; posterior margin with small dorsal extension.

Abdominal gills on segment 1 posterodorsal and ventral, segments 2 and 3 with anterodorsal, lateral and ventral. Lateral spicules: segment 8 with about 10 bifid, segments 3-7 with about 18-30, segment 2 with group of 6 single. Tergite 9 sclerite elongate oval, with dark scars, small setae anterior to posterior row.

Head brown; dorsum and upper lateral areas spinulose. Scars pale and distinct, very thin and wide. Minute setae scattered on dorsum, visible as clear spots amongst spines. Carina extending to posterior margin of eye. Frontoclypeus relatively narrow in relation to head size; group of fine hairs in anterior 1/3.

Mandibles with many outer basal setae (about 18), of which 1 or 2 are stout.

Protrochantin with strongly upturned apex; pleural humps with many long setae.

Pronotum distinctly wide and short, anterolateral corner rounded; lateral setae medium length; dorsal scars pale and distinct. Mesonotum entirely pigmented; anterior large setae with evenly tapering tips; several large setae scattered across at about 2/3 length of sclerite. Metanotum SAs each with 1-3 setae, SA 1 and 2 with distinct sclerites.

Pupa

Case anterior membrane flat, wide crescent about 1/2 width of membrane diameter; posterior opening slit on prominent hump.

Anterior hookplates with row of about 4 hooks, posterior with small hooks. Dorsum of segment 9 with about 14 medium-short setae in 2 rows; terminal processes relatively short, apex projecting only slightly beyond base of terminal setae.

Right mandible more strongly hooked than left; each with outer row of at least 6 large setae.

Remarks

Pupates amongst moss on rocks, or at base of grass-like plants.

Material examined: 2L 175, 7.xii.87; 10L 169, 1.ix.88; 1L 150, 27.x.87; 1L 151, 27.x.87; 7L

Figure 5.36. *Costora ebenina* larva and pupa. **a, b, c:** larval case lateral, posterior membrane, posterior; **d:** pleural humps; **e:** tergite 9 and anal legs, dorsal; **f, g, h, l:** pupal case lateral, posterior dorsal, posterior membrane, anterior membrane; **J:** hookplates; **k, l:** terminalia dorsal, process enlarged; **m:** pupal mandibles, ventral.

a

b

c

d   mesonotum

hindleg   midleg

e

1

0.2

f

g

h

i

j

5

6

k

l

m

1

0.2

0.2

0.1

0.1
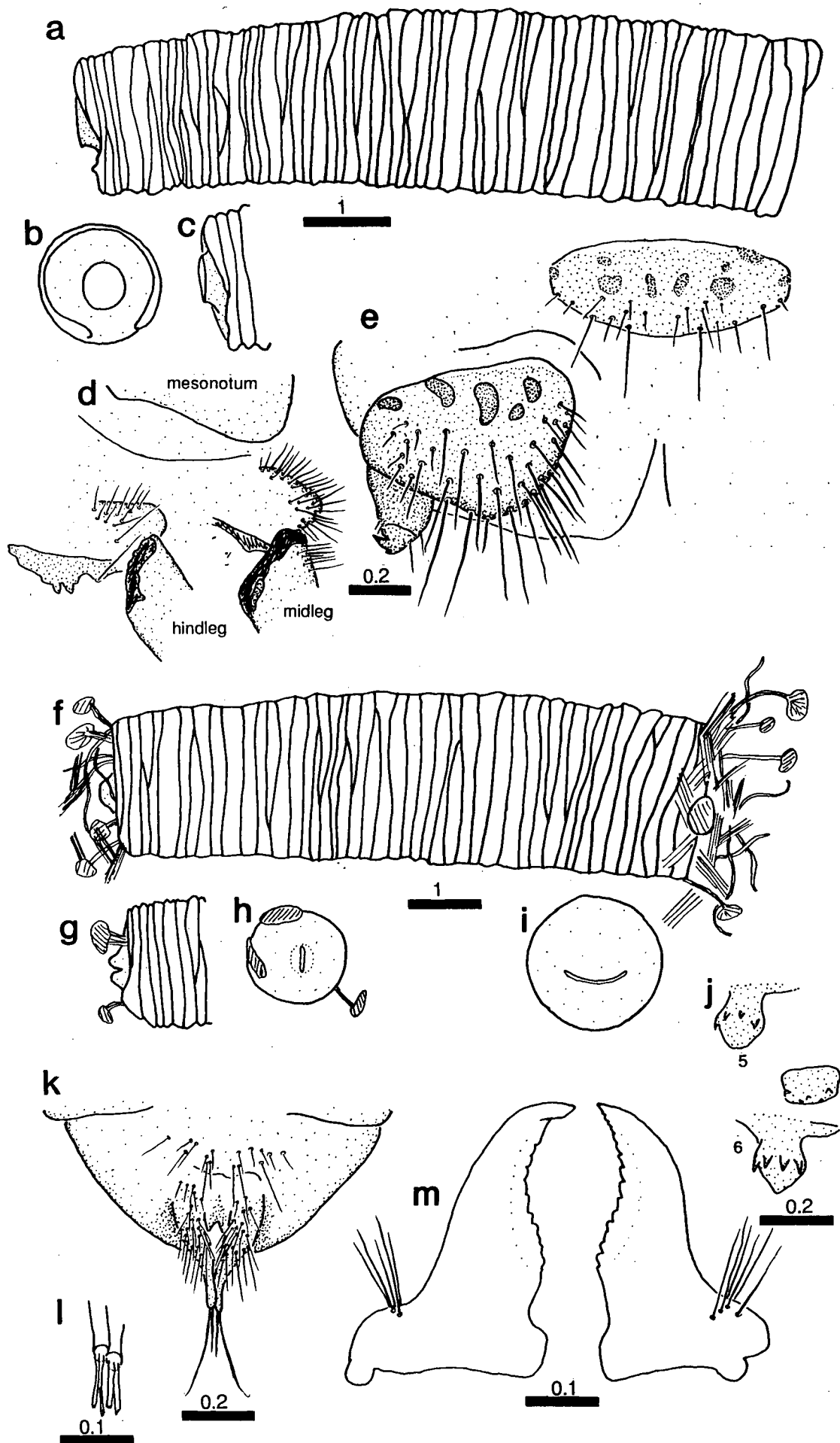
Figure 5.37. *Costora ebenina* larva. **a, b, c, d, e:** head dorsal, spines enlarged, ventral, lateral, spines enlarged; **f, g:** pronotum, meso- and metanotum; **h:** pronotum, lateral; **I:** protrochantin; **j, k:** mandibles dorsal, outer face (setae not shown).
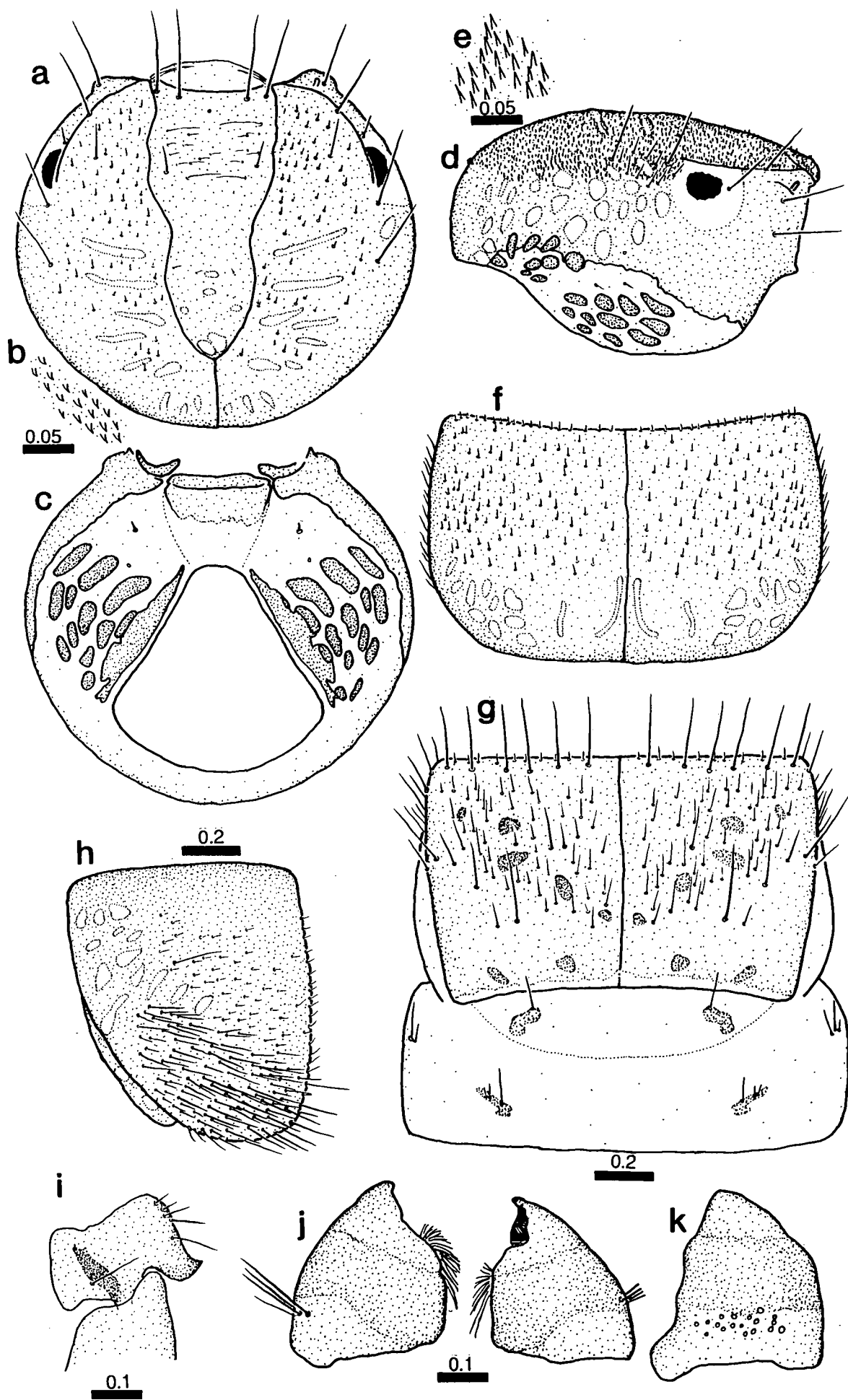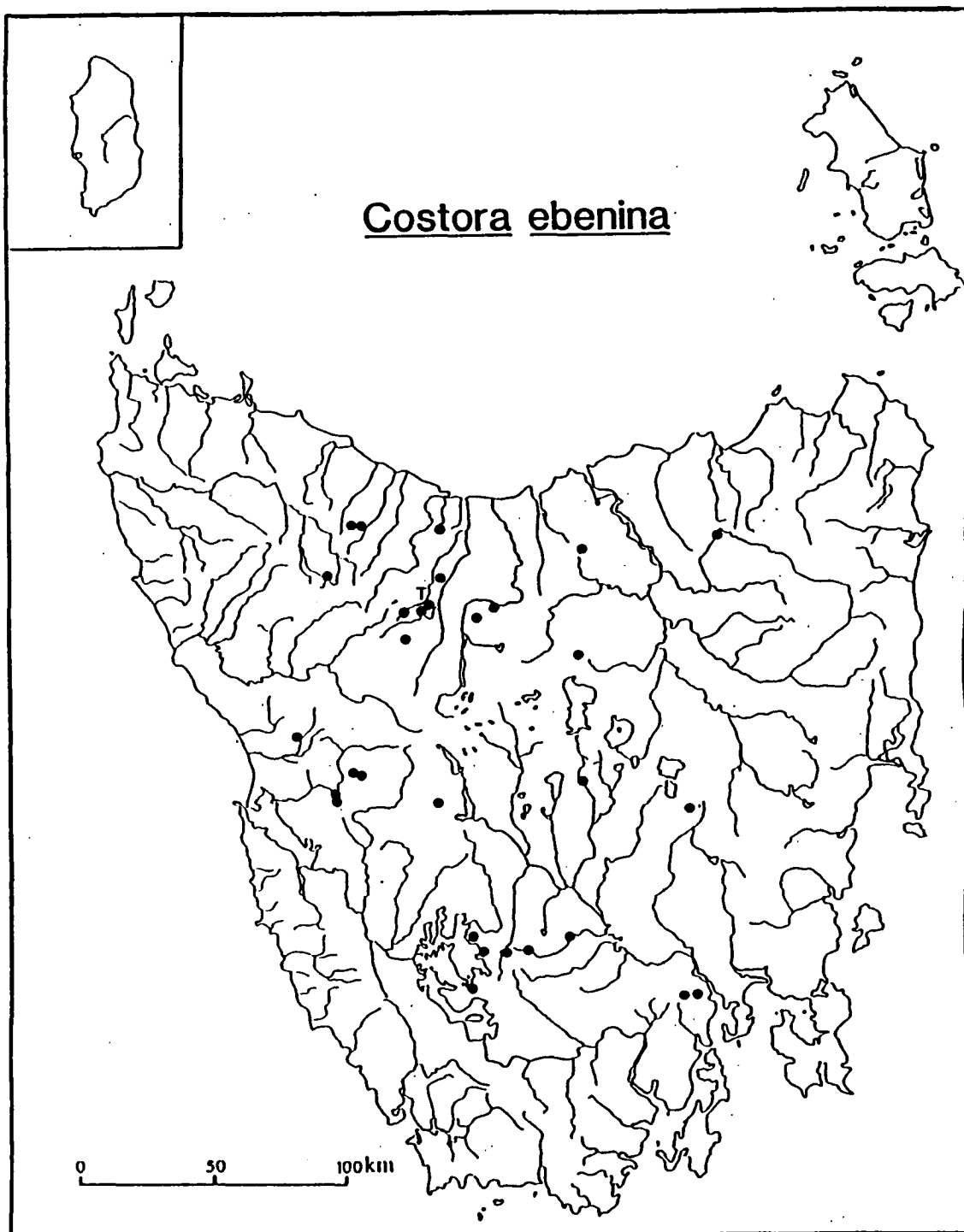
Figure 5.38. Distribution of *Costora ebenina*.

233, 5.x.87, 25.viii.88; 2L 173, 7.xii.87; 9L 169, 11.xi.88, 1.ix.88; 7L 31, 21.ix.88; 2L 142, 19.ix.88; 8L 233, 20.x.88; 1L 19, 21.ix.88; 2L 20, 21.ix.88; 3L 134, 19.ix.88; 3L 124, 1.xi.88; 3L 37, 21.ix.88; 2P 133, 31.x.88 em. 28.xi.88; 1P 169, 11.xi.88 em. 2.i.89; 1P 175, 7.xii.87. Drawings based on: 2L 233, 22.x.87; 1P 175, 7.xii.87; 1P 233 22.x.87 em. 18.xi.87.

Distribution (Fig. 5.38). Tasmania and SE Australia; fairly widespread within Tasmania, not recorded from far south, NW or east; not numerous where collected.

Costora iena Mosely

Costora iena Mosely, 1936, p.403; Mosely & Kimmins, 1953, p. 47.

No material has been available for this study. The apparent lack of good diagnostic adult characters means that further investigation is needed to determine the validity of this species.

Costora krene Neboiss
(Fig. 5.39)

Costora krene Neboiss, 1977, p. 105.

No characters were found to diagnose larvae of *C. krene* from *C. ramosa*. Descriptions of these two species are therefore based on larval sclerites from reared adults.

Larva

Case of plant material.

Head golden; scars not thin, width about 2.5x length, slightly darker but indistinct. Carina extending to anterior of pale area surrounding eye. Frontoclypeus margins with minute weak crenulations.

Mandibles slightly longer than wide; 1 indistinct apical tooth.

Pronotum golden, weakly textured, scars slightly paler, indistinct; anterolateral corner rounded, angle about square; anterior margin with minute setae fairly widely spaced, few pale stouter setae. No lateral carina, lateral face setae short-medium. Mesonotal anterior long setae with tapering tips; posterior group of large setae in middle 1/3.

Protrochantin broad, tapered and upturned.

Pupa

Case anterior membrane flat, opening slit curved, width about 1/2 membrane diameter; posterior membrane flat; case more cut away ventrally. Several thinly stalked small adhesive discs at both ends.

Hookplates with 4-5 hooks, anterior hooks sometimes multibranched and irregular. Segment 9 with dorsal transverse row of three pairs of setae. Apices of processes minutely serrate.

Mandibles with relatively large inner serrations; right tip more hooked and strengthened than left.

Remarks

Occurs in rocky streams with algae (*Batrachospermum?*) and sometimes moss

65

Figure 5.39. *Costora krene* larva and pupa. **a, b, c:** pupal case lateral, posterior membrane, anterior membrane; **d:** pupal mandibles, ventral; **e, f, g:** terminalia lateral, process lateral, dorsal; **h:** hookplates; **i, j:** head dorsal, lateral; **k, l:** pronotum dorsal, lateral; **m:** mesonotum.

a

0.5

b

c

d

0.1

h

4

5a

5p

6

0.05

0.1

e

0.2

f

g

0.05

i

j

k

l

m

0.2

Costora krene

E

0   50   100km
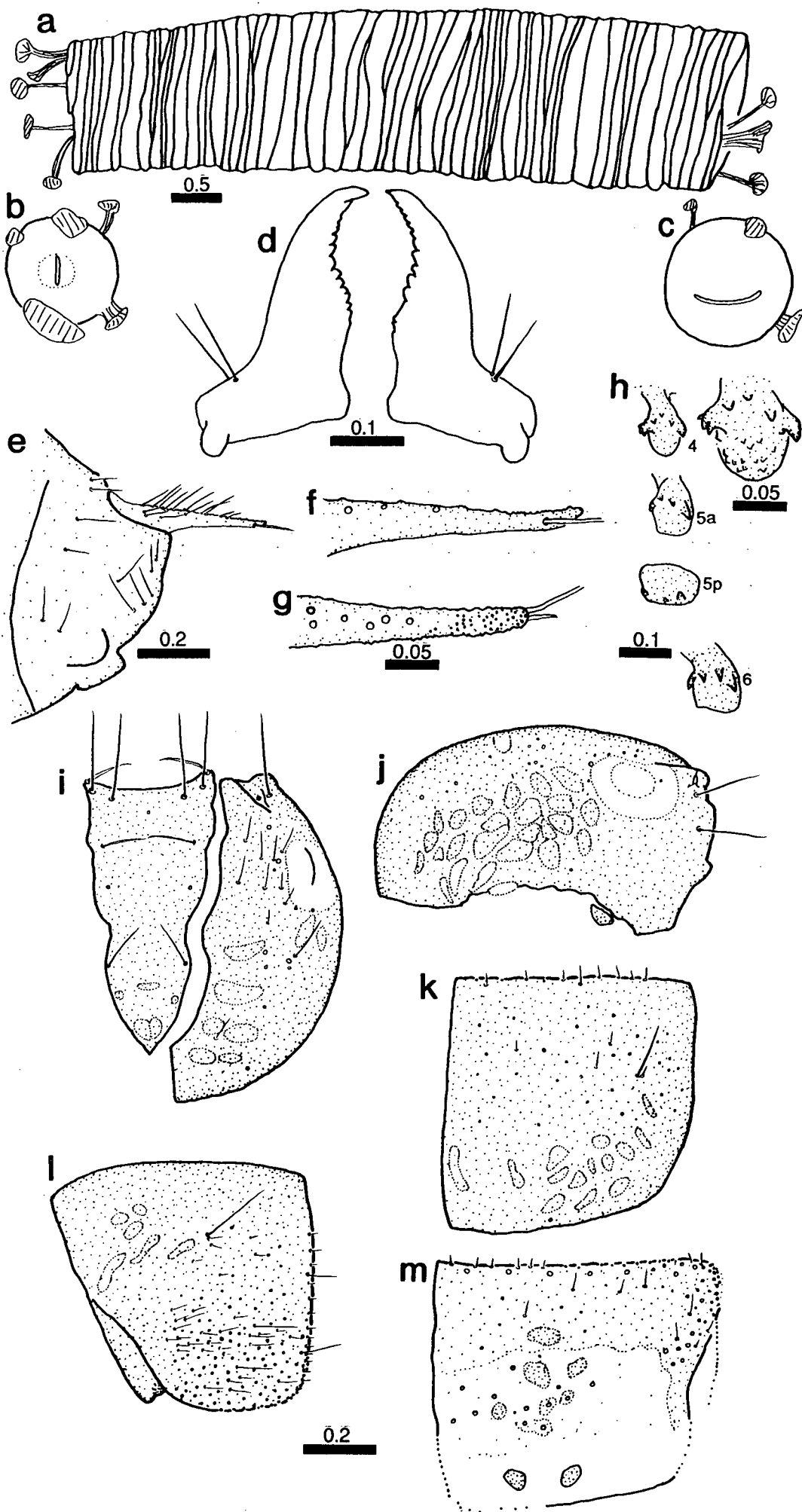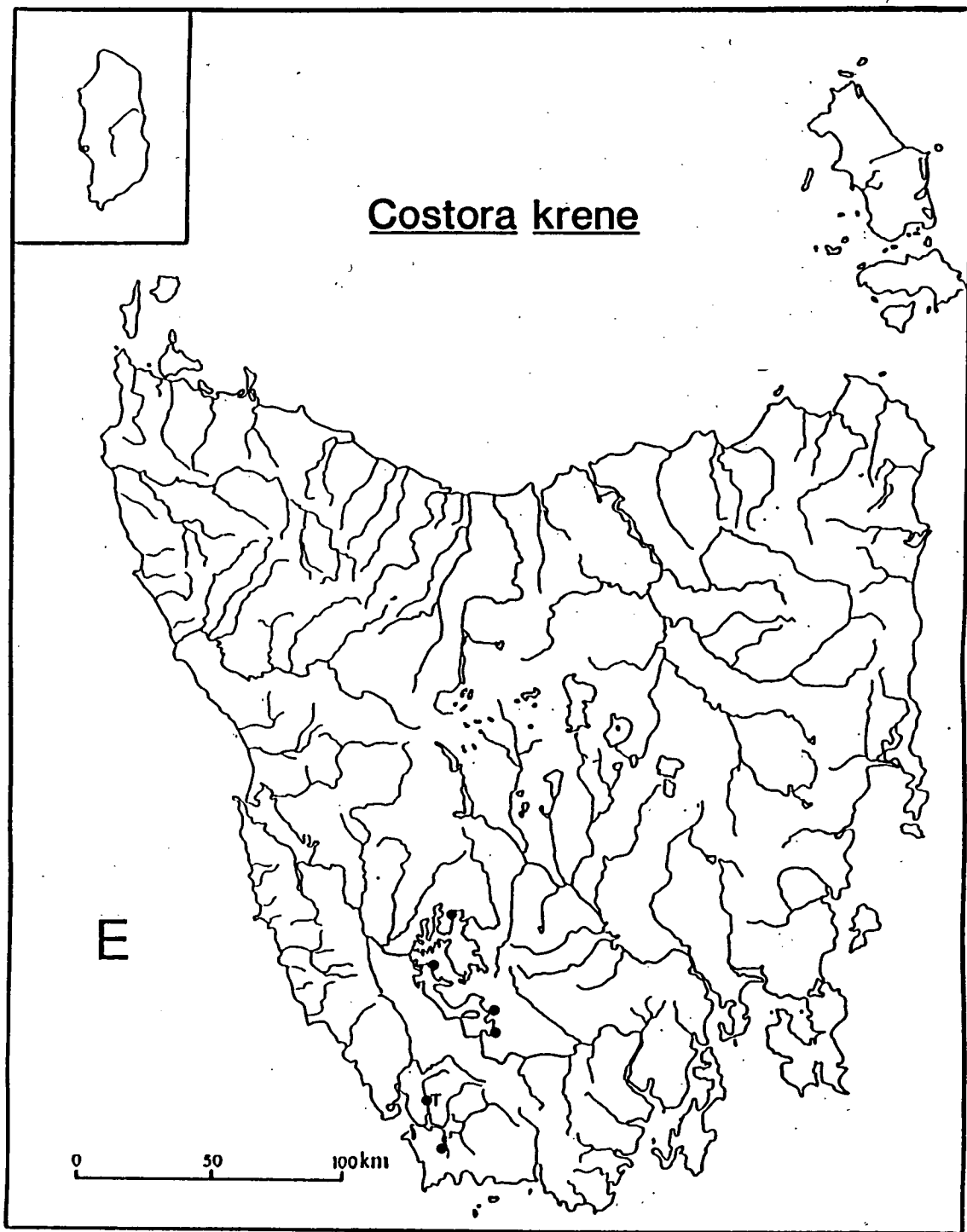
Figure 5.40. Distribution of *Costora krene*.

and liverwort. Pupates under rocks or amongst liverwort.

Material examined: 3L sclerites and P 166, 29.xii.88 em. 15.i.89. Whole larvae listed under *C. ramosa*. Drawings based on specimens: 1L sclerites, P 166, 29.xii.88.

Distribution (Fig. 5.40). Endemic; recorded from few localities in the SW; may be fairly numerous where collected.

Costora ramosa Jacquemart
(Fig. 5.41)

Costora ramosa Jacquemart, 1965, p.12; Neboiss, 1977, p. 104.

Refer to comments about *C. krene* description.

Larva

Case of plant material.

Head dark gold, scars slightly paler, scar width 2-3x length. 1 or 2 large setae between each scar. Carina short. Frontoclypeus with irregular bulges about half way between constriction and anterior margin.

Pronotum scars paler or same colour, indistinct; anterolateral corner rounded, angle 90°-slightly obtuse; carina lacking. Mesonotal anterior large setae with evenly tapering tips, two transverse rows of about 9 large setae near posterior margin of pigmentation.

Mandibles lacking apical teeth.

Pupa

Case anterior membrane flat, wide crescent slit; posterior opening slit in raised hump. Several thinly stalked, small adhesive discs around anterior and posterior ends.

Terminal processes with apices minutely papillate/toothed; in lateral view a dorsal hump on process just distal to segment 9.

Right mandible with more strongly hooked tip.

Remarks

Occurs in fast flowing streams usually in association with algae. Pupates amongst liverwort and on algae-covered rocks.

Material examined: 2L sclerites and P 166, 11.xi.88 em. 29.xii.88. Whole larvae of krene/ramosa: 8L 176, 7.xii.87; 14L 166, 13.i.89, 11.xi.88, 14.x.87; 7L 164, 14.x.87, 29.xii.88; 4L 182, 12.xi.88; 1L 168, 11.xi.88; 7L 169, 11.xi.88, 29.xii.88; 2L 233, 22.x.87; 1L 173, 7.xii.87; 3L 133, 27.x.87; 2L 180, 5.x.87; 3L 153, 27.x.87. Drawings based on: 1L sclerites and P 169, 11.xi.88.

Distribution (Fig. 5.42). Endemic; fairly widespread in the west; may be faily numerous where collected.

Costora krene/ramosa female
(Fig. 5.43).

Anterior wing length about 6mm; Cu joins Cu_{1b} (as in the M); in posterior wing R1 joins Sc before margin (except in one specimen).

Thoracic scars uniting or abutting to form one large wart, about 2/3 length of scutellum or almost reaching posterior.

Figure 5.41. *Costora ramosa* larva and pupa. **a, b, c, d:** pupal case lateral, posterior dorsal, posterior membrane, anterior membrane; **e:** pupal mandibles, ventral; **f, g, h:** ♂ terminalia lateral, dorsal, process lateral; **i:** head dorsal; **j, k:** pronotum dorsal, lateral; **l:** mesonotum.

a b c d e f g h i j k
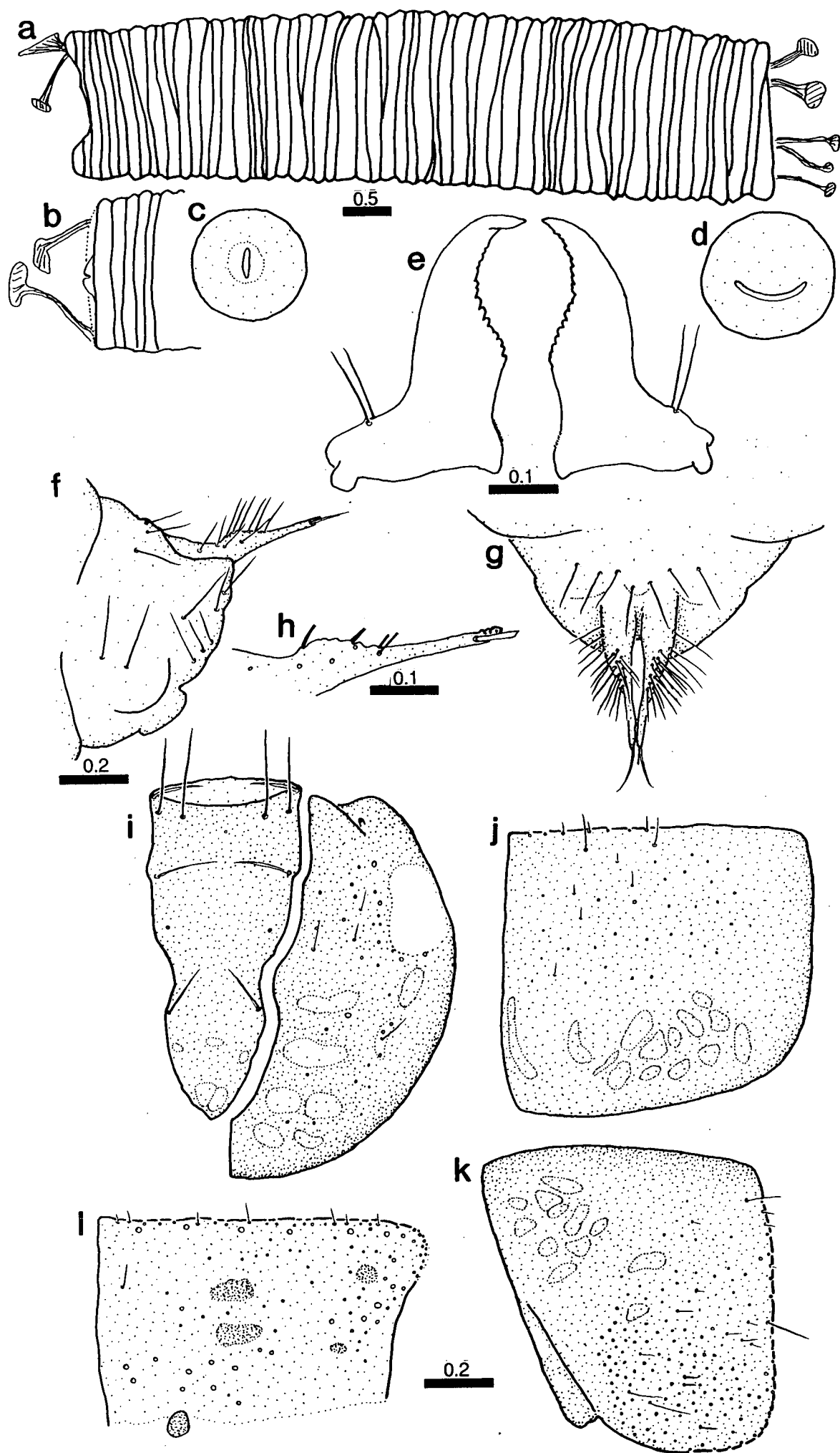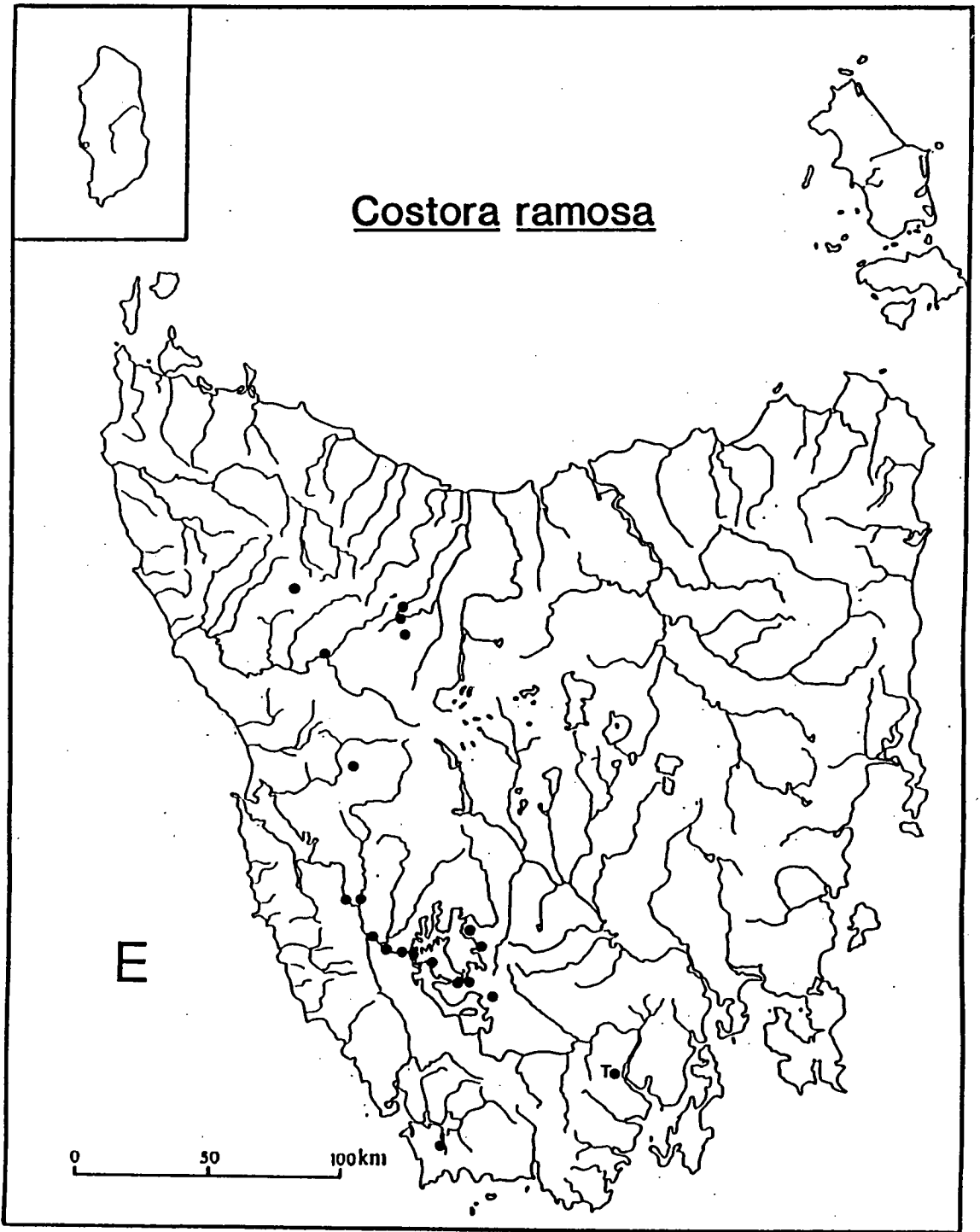
Figure 5.42. Distribution of *Costora ramosa.*
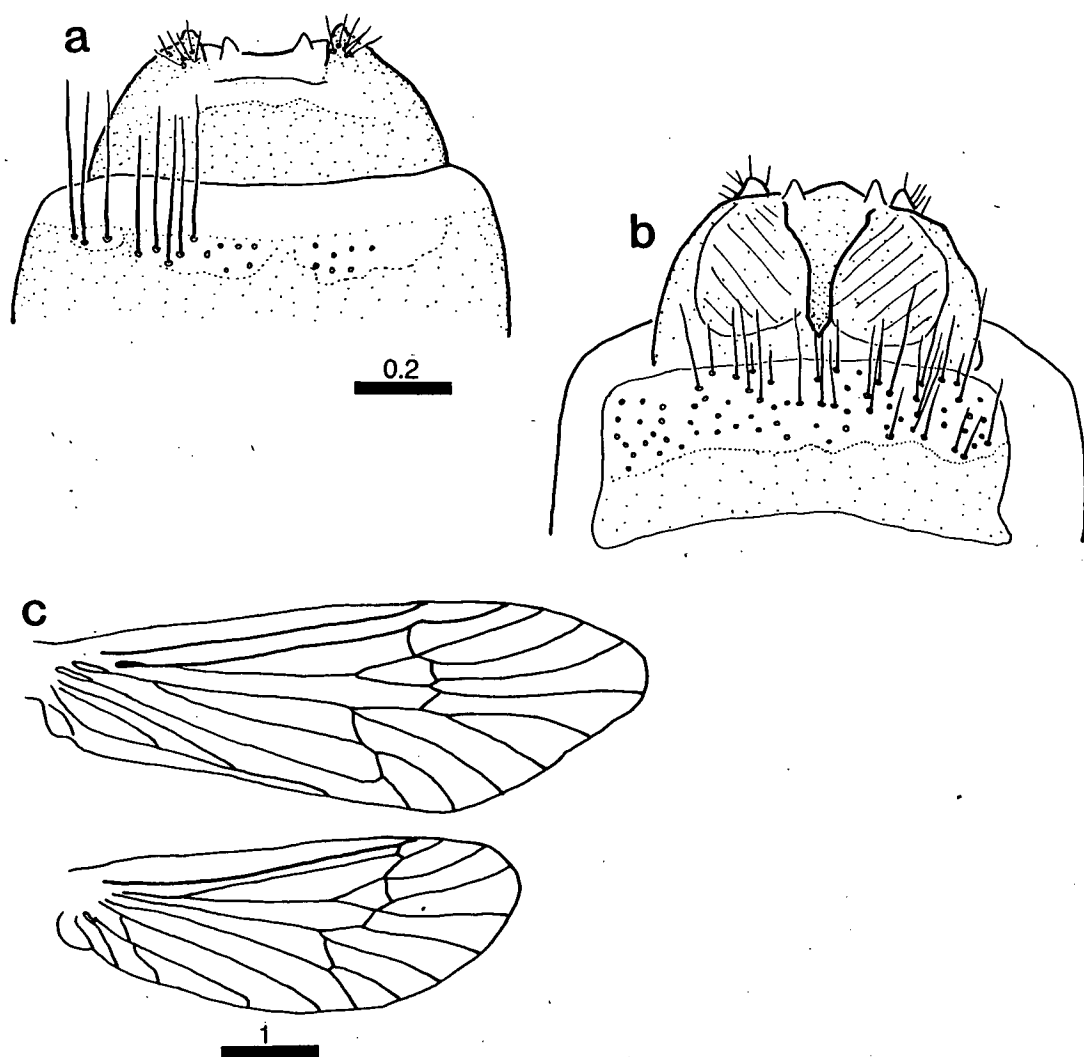
Figure 5.43. *Costora krene/ramosa* ♀. **a, b:** genitalia dorsal, ventral; **c:** wings.

Terminalia: tergite 9 without median domed process, prominent distal setose processes dorsolaterally, visible from ventral; on each side of ventral incision a transparent process. Ventral plates longer than wide; incision straight sided, narrow proximally widening distally. Sternite 8 with distal half densely covered with dark setae, other sternites with only fine short pale setae; no process on sternite 7.

Material examined: 2 reared 1♂♂ 29.xi.88; 1 reared same locality 11.xi.88; 1 same locality netted 29.xi.88. Drawings based on specimen from 1♂♂, 29.xi.88 em. 8.ii.89.

Costora luxata Neboiss
(Figs 5.44, 5.45, 5.53)

Costora luxata Neboiss, 1977, p.106.

Female (Fig. 5.53)

Dark coloured. Anterior wing length 5.5-6.5mm, width about 2mm; Cu joins Cu_{1b} in most specimens, not produced downwards as in *seposita*; reaching margin in about 1/4 of specimens in one or both wings. Posterior wing Sc joins R at margin.

Thoracic scars widely separated.

Abdomen terminating bluntly, tergite 9 with low median process, deep cleft; ventral incision margins rounded to form U-shape, plates longer than wide; distinct distal dorsolateral setose projections visible from ventral side. Tergite 8 with band of dark setae about 3 wide, divided into 2 groups, other tergites less densely setose; sternite 8 distal 1/2 densely setose, other sternites with no dark setae, only fine setae visible in cleared specimens; no process on sternite 7.

Larva

Case of sandgrains, more curved than *rotosca*. Posterior lacking membrane.

Abdominal gills on segments 2 and 3 anterodorsal, lateral and ventral. Lateral spicules: segment 8 with about 20 bifid, segments 3-7 with 35-50 single spicules. Tergite 9 sclerite roughly quadrate, about 12 medium posterior setae. Anal prolegs lateral sclerite dark brown.

Head brown, scars gold and distinct, width about 2-2.5x length. Weak carina extending almost to eye.

Pronotum brown, scars paler and distinct; median medium length seta on each side behind anterior margin. Anterolateral corner square but not pointed; carina lacking. Mesonotal anterior long setae with spatulate tips; band of large setae near posterior margin of pigmentation. Metanotum SA 1: irregular oval brown sclerite, with 5 medium setae along anterior margin; SA 2 with 1 long and 2 minute setae, pigmented area; SA 3 with small sclerite and 2 setae.

Apex of protrochantin short and square, slightly produced into tip.

Pupa

Case anterior membrane flat, inset from margin, with straight slit; posterior membrane flat with small vertical slit. Several thinly stalked adhesive discs around margins, larger posteriorly.

Apices of terminal processes papillate, projecting beyond base of terminal setae. Mandibles equally hooked.
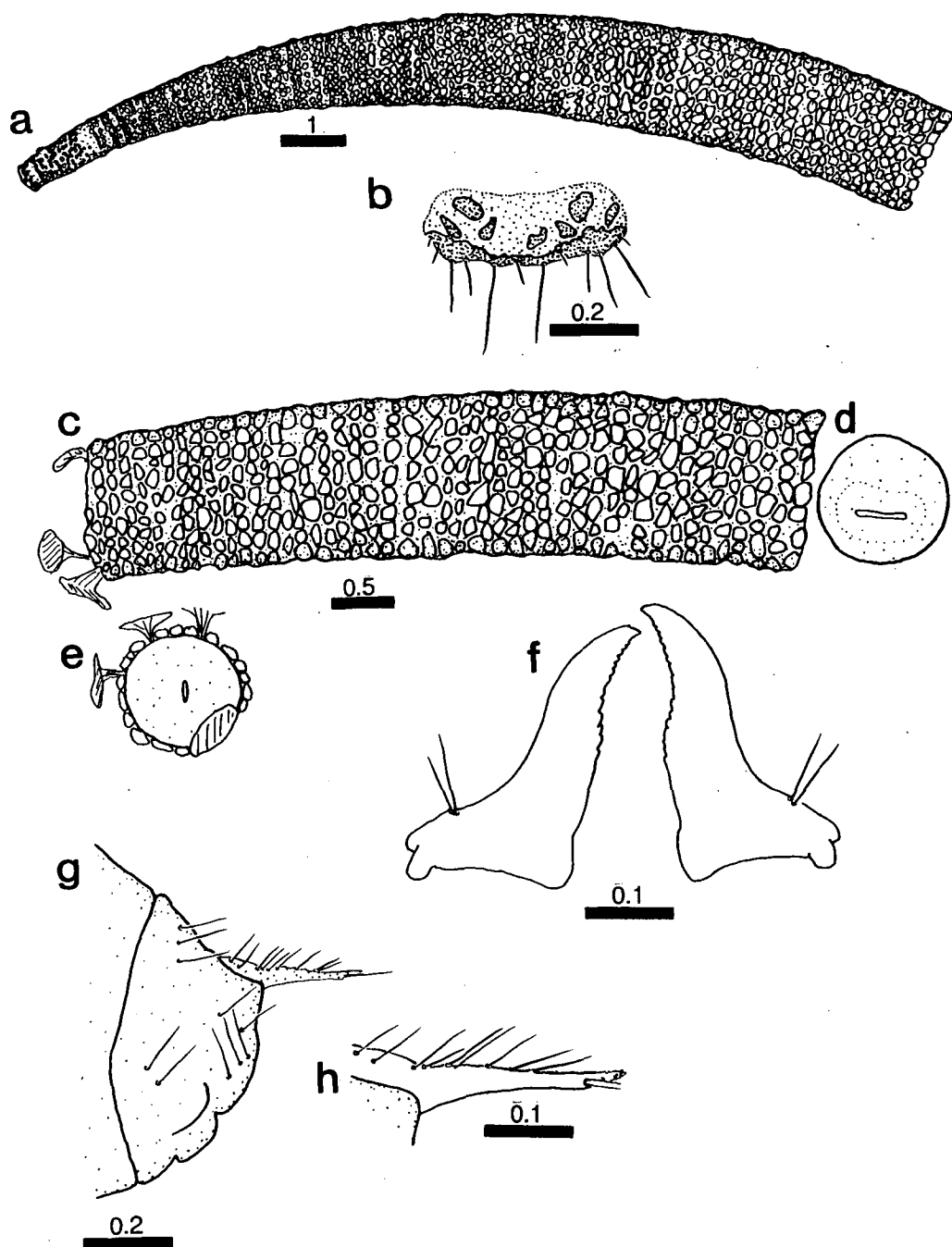
Figure 5.44. *Costora luxata* larva and pupa. **a:** larval case lateral; **b:** tergite 9; **c, d, e:** pupal case lateral, anterior membrane, posterior membrane; **f:** pupal mandibles ventral; **g, h:** terminalia lateral, process enlarged.

Figure 5.45. *Costora luxata* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e, f:** pronotum, meso- and metanotum, mesonotal anterior seta; **g:** pronotum, lateral.

a

b

d

f

0.05

c

e

g
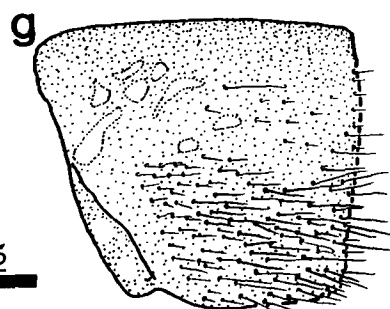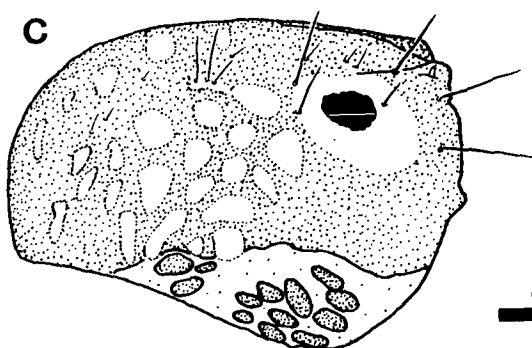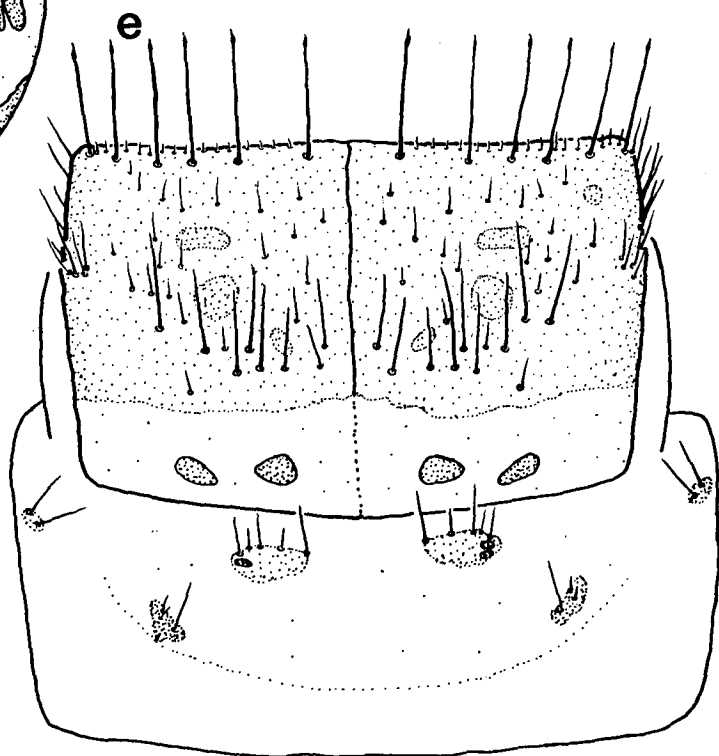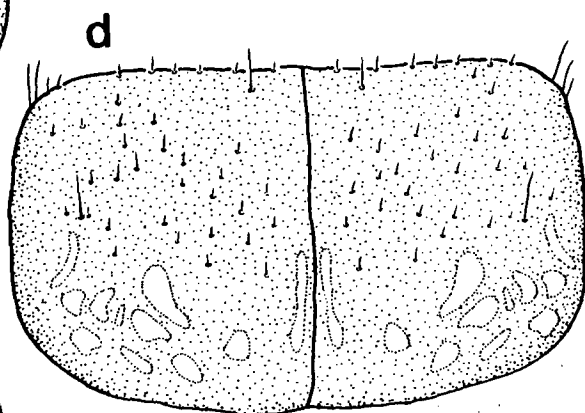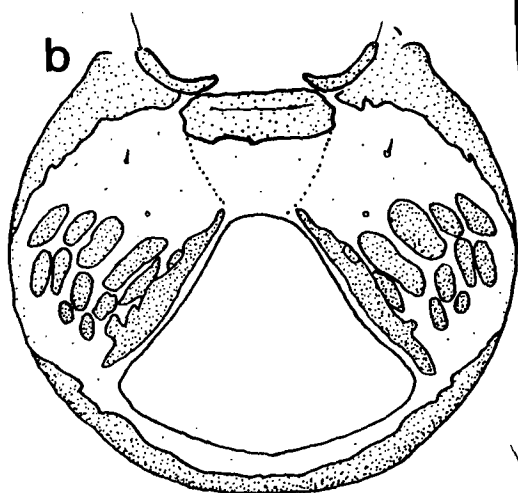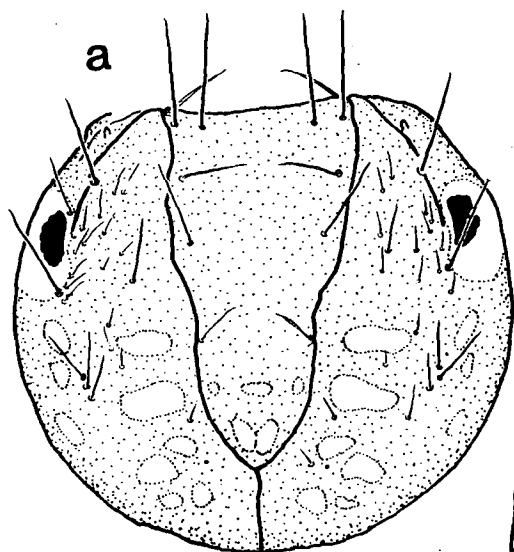
0.2
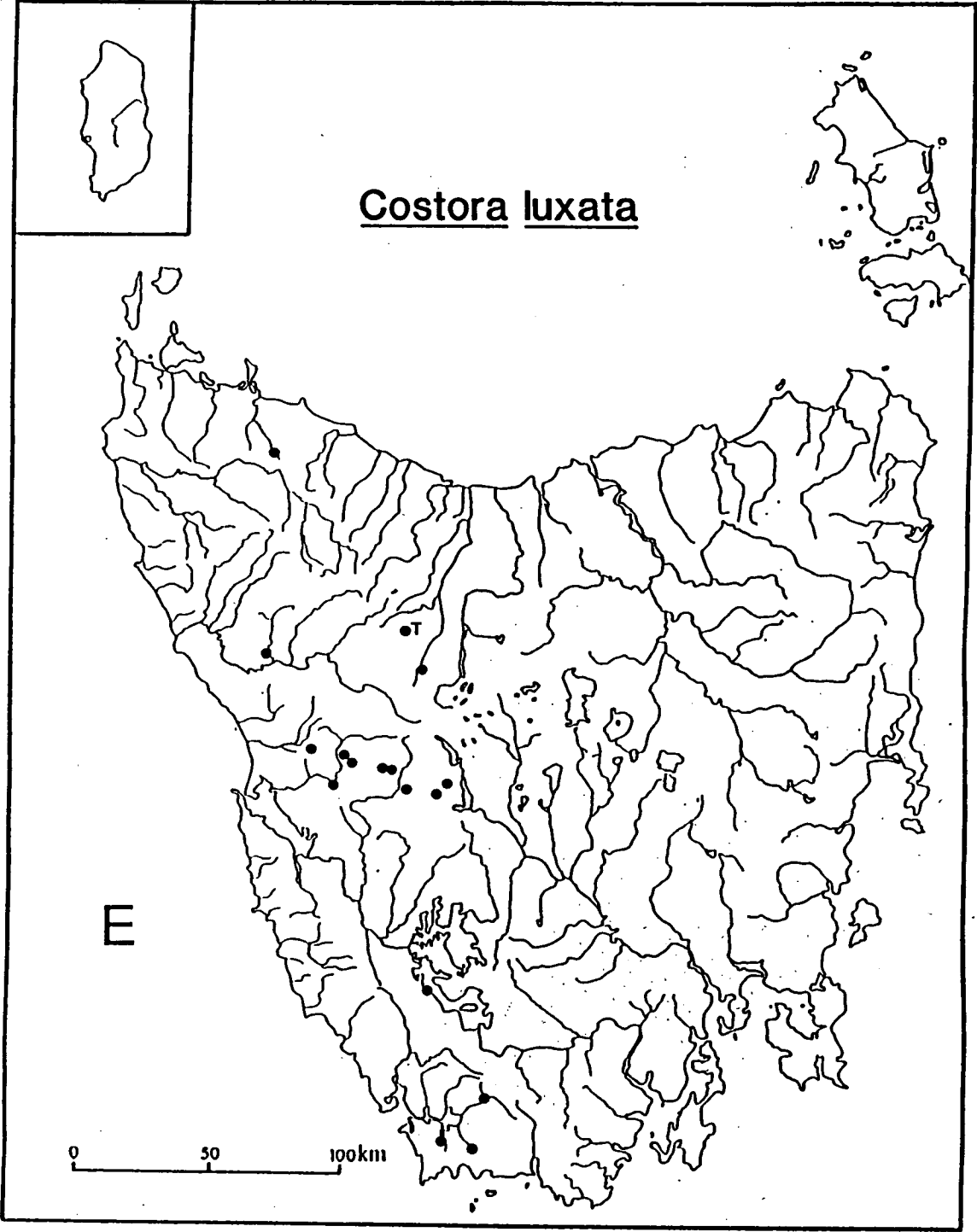
Figure 5.46. Distribution of *Costora luxata*.

Remarks

Occurs in fast flowing streams on plants or in moss; pupates attached vertically, anterior up, at base of grass-like plants or long moss growing on stones.

Material examined: females: 15 reared 41, 7.xii.88; 4 reared same locality 7.xii.89; 7 reared 137, 31.x.88. Drawings based on specimen from 137, 31.x.88 em. 14.xii.88.

Larvae and pupae: cleared: 3L 41, 7.xii.88, 22.ix.88; 1L 137, 31.x.88; 19P 41, 7.xii.88 em. 27.xii.88, 11.i.89; 10P 137, 12.i.89; other: 30L 41, 7.xii.88, 10.xii.89; 1L 1, 8.xii.89; 10L 137, 12.i.89; 1L 127, 1.xi.88; 1L 132, 27.x.87; 1L 150, 27.x.87. Drawings based on: 1L 137, 31.x.88; 1L 41, 7.xii.88; 1P 137, 31.x.88 em. 2.i.89.

Distribution (Fig. 5.46). Endemic; widespread in the west; may be very numerous where collected.

Costora rotosca Mosely
(Figs 5.47, 5.48)

Costora rotosca Mosely in Mosely & Kimmins, 1953, p.49; Neboiss, 1977, p. 106.

Larva

Case of sandgrains and some plant fragments; curvature not as strong as in *C. luxata*. Posterior end of case soft and ragged, membrane lacking, opening irregular.

Abdominal gills on segments 2 and 3 anterodorsal, lateral and ventral. Tergite 9 rounded rectangular sclerite with dark diagonal scars; lateral sclerites of anal prolegs with fewer setae than in other species. Lateral spicules: segment 8 with 20 bifid, segments 3-7 with 40-60 single.

Head dark brown, scars pale and very distinct, about 3x wider than long. A few small setae between scars at posterior and in posterolateral area; fine pale setae scattered in anterodorsal area. Carina extending almost to eye. Frontoclypeus anterior lateral margins straight and parallel, constriction distinct.

Pronotum scars pale. Anterolateral corner rounded, anterior margin very slightly upturned; carina absent. Anterior mesonotum with row of large setae with tapering tips, band 2-3 wide of large setae at posterior margin of pigmented area. Metanotum SA 1 with irregular sclerite, 3-5 anterior setae; SA 2 with one long and two minute setae on elongate sclerite; SA 3 with 2-3 setae and sclerite.

Protrochantin narrow, tapered and upturned.

Pupa

Case anterior membrane flat, wide crescent slit; posterior slit on hump in membrane. A few stalked adhesive discs.

Abdominal segments 3-6 with lateral longitudinal sclerites on dorsum. Apices of terminal processes extending beyond base of terminal setae.

Right mandible with tip more strongly hooked than left.

Remarks

Occurs on rocks and plants in fast streams; pupates at base of plants or under rocks.

Material examined: cleared: 1L 257, 4.xi.87; 2L 276, 26.i.88; 3P 276, 26.i.88 em.25.ii.88;
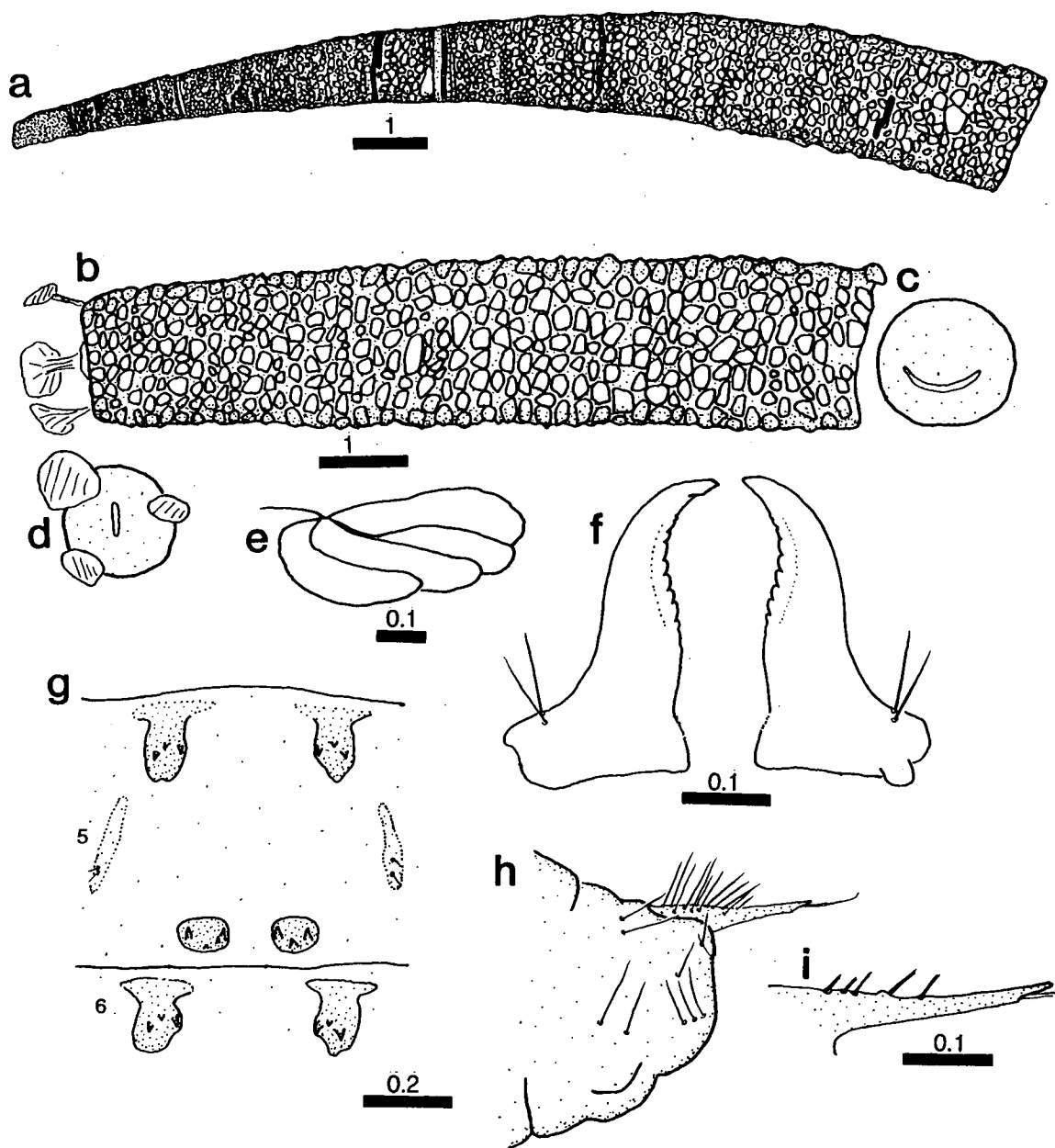
Figure 5.47. *Costora rotosca* larva and pupa. **a:** larval case, lateral; **b, c, d:** pupal case lateral, anterior membrane, posterior membrane; **e:** testis; **f:** pupal mandibles ventral; **g:** pupal abdomen segments 5 and 6; **h, i:** terminalia lateral, process enlarged.
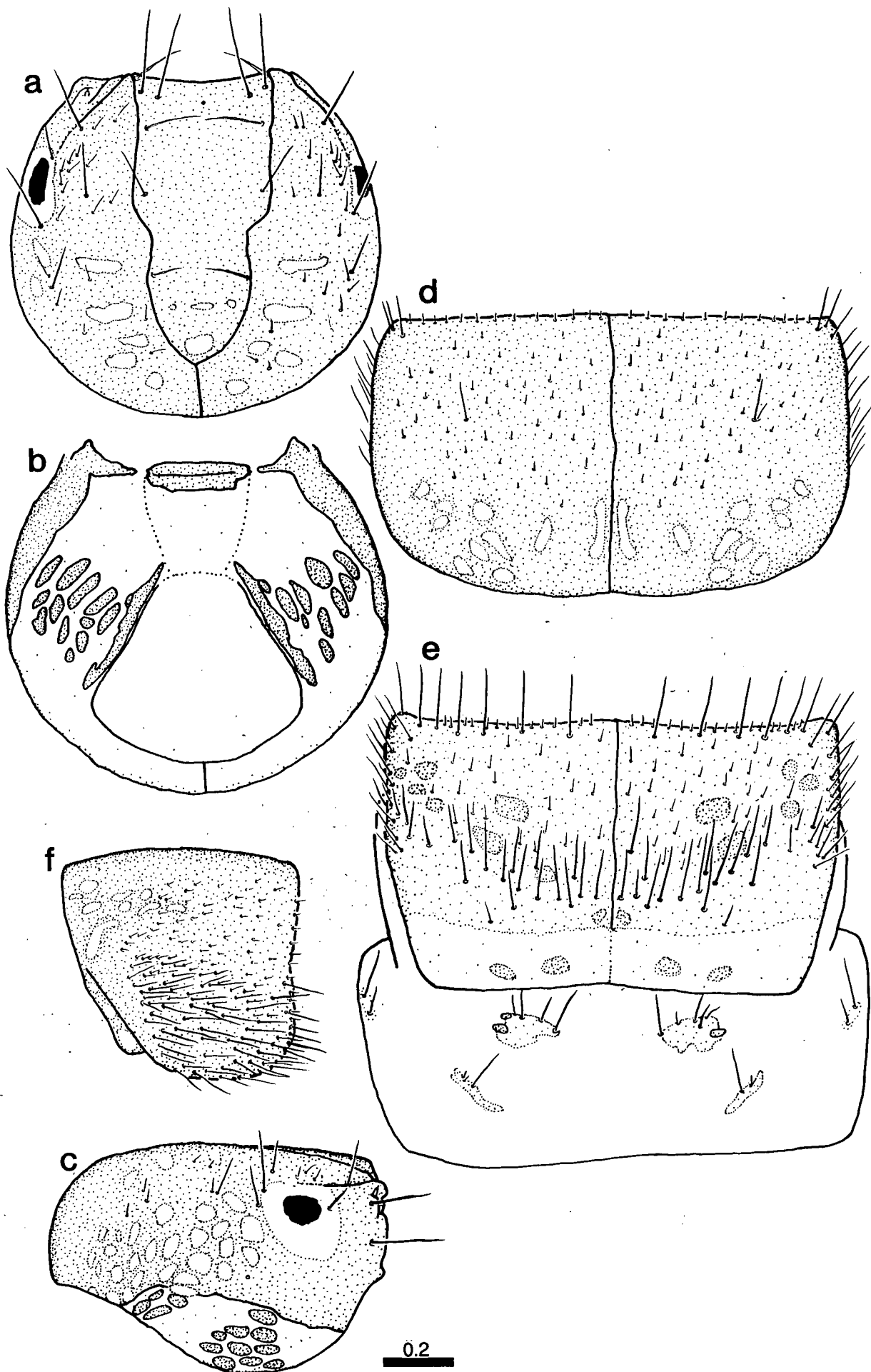
Figure 5.48. *Costora rotosca* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f:** pronotum, lateral.

Costora rotosca

E

0   50   100 km
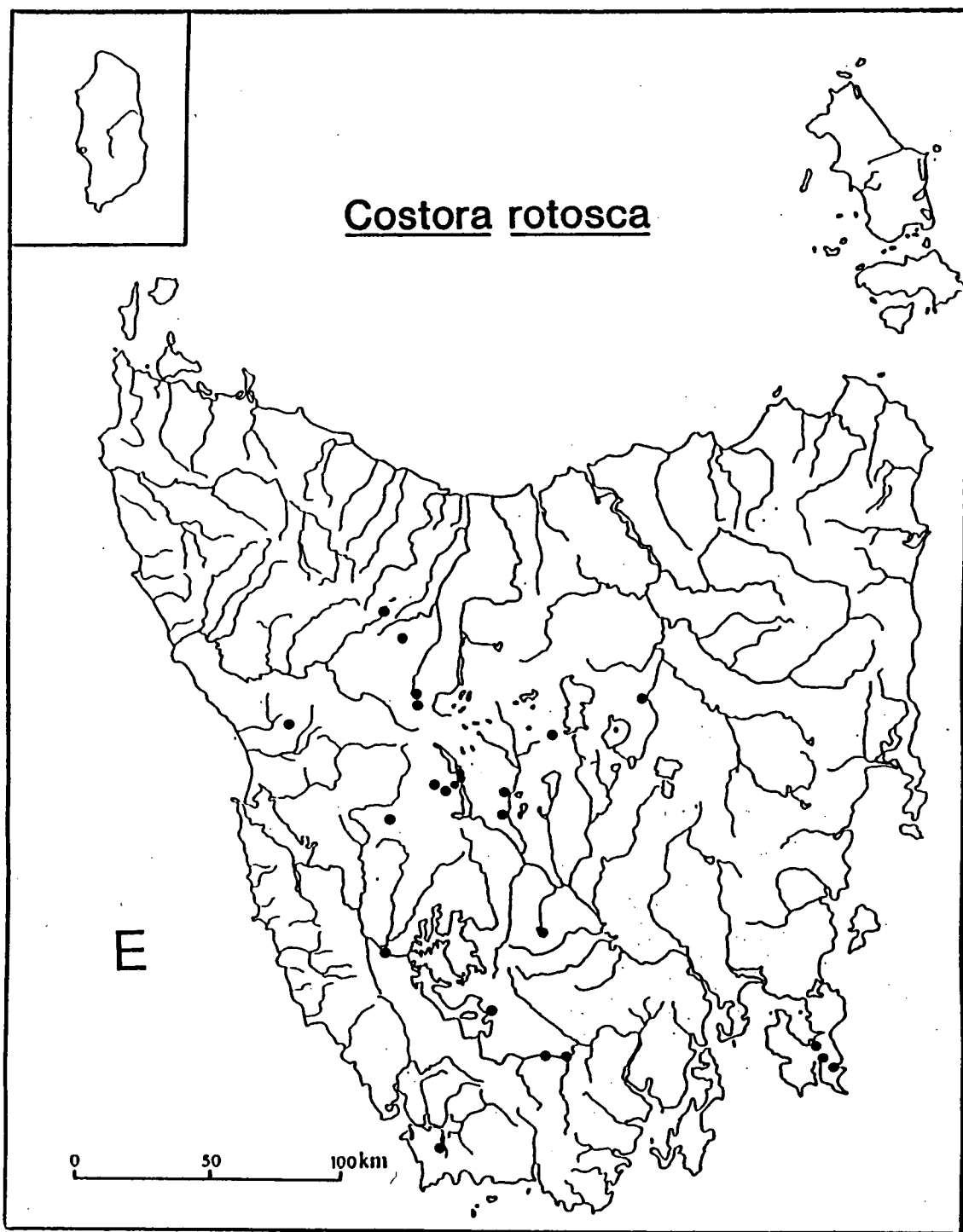
Figure 5.49. Distribution of *Costora rotosca*.

other; 1L 246, 4.xi.87; 10L 276, 26.i.88; 5L 237, 29.v.87; 12L 277, 2.xi.87; 1L sclerites 155, 29.i.88; 15L 278, 2.xi.87; 2L 275, 2.xi.87; 15L 257, 4.xi.87; 1L 259, 1.xi.88; 1L 155, 10.xii.89; 1P 257, 4.xi.87 em. 21.xii.87; 4P 276, 26.i.88 em. 8.ii.88, 24.ii.88; 1P 259, 1.xi.88 em. 15.i.89. Drawings based on: 2L 276, 26.i.88; 1P 276, 26.i.88 em. 25.ii.88.

Distribution (Fig. 5.49). Endemic; not recorded from NW, NE or mid-E areas, widespread elsewhere; may be very numerous where collected.

<div align="center">

Costora seposita Neboiss
(Figs 5.50, 5.51, 5.53)

</div>

Costora seposita Neboiss, 1977, p.106.

Female (Fig. 5.53)

Brown coloured. Wings relatively narrow in relation to length, anterior length 7-7.5mm. Anterior wing Cu_2 joining Cu_{1b}, produced downwards before turning up to meet Cu_{1b}. In posterior wing Sc and R1 running separately to margin, 2A not reaching margin. Thoracic scars joined, very long, sometimes reaching posterior of scutellum.

Terminalia: tergite 9 median process usually low, not projecting distad of lateral processes; distal dorsolateral areas setose, square but without process. Tergite 8 with narrow band (2-3 wide) of long setae, divided into two groups; other tergites also setose. Ventral plates about as wide as long, incision V-shaped; sternite 8 distal 1/2 densely setose with dark setae, other sternites with sparse minute pale hairs only, visible on cleared specimens under compound microscope. No process on sternite 7.

Larva

Case of neat rows of sandgrains; posterior membrane narrow.

Gills on segments 2 and 3 anterodorsal, lateral and ventral. Tergite 9 with anterior area unpigmented, posterior patchy pigmentation and scars. Anal prolegs squareish, lateral sclerites entirely pigmented.

Head golden, scars same colour; carina extending 1/2 way to eye. Fine scattered setae in anterolateral area of dorsum. Ventral mandibular articulation projecting prominently.

Mandibles slightly longer than wide, each with several thick bristles in mesal hollow distal to brush, several apical teeth.

Pronotum golden, scars just darker, indistinct; anterolateral corner angle square but not pointed, anterior margin turning slightly forward. Carina absent but lateral face at angle to dorsum, lateral face relatively narrow. Mesonotal anterior large setae with tips spatulate; band of about 10 large setae near posterior margin of pigmentation. Metanotum SA 1 with transverse row of 4-5 setae; SA 2 with 1 long seta and 2 minute; SA 3 with 2 setae.

Protrochantin anterior margin straight, apex very slightly upturned. Pleural hump setae minute.

Pupa

Case anterior membrane flat, flush with margin, slit slightly curved, width about 1/3 of membrane diameter; posterior membrane with central vertical oval opening. Ventral adhesive discs at both ends.
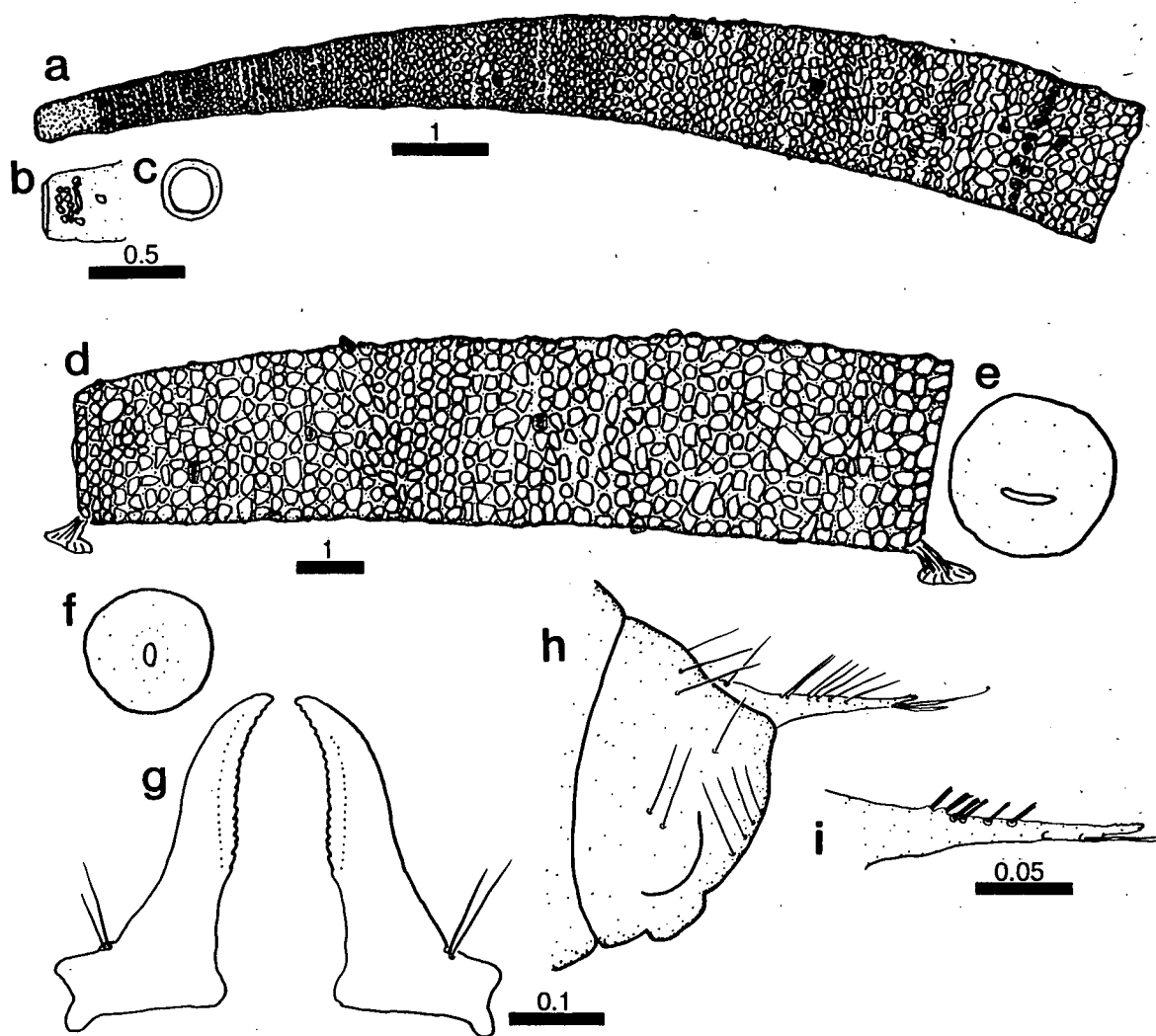
Figure 5.50. *Costora seposita* larva and pupa. **a, b, c:** larval case lateral, posterior enlarged, posterior membrane; **d, e, f:** pupal case lateral, anterior membrane, posterior membrane; **g:** mandibles, ventral; **h, I:** terminalia lateral, process enlarged.
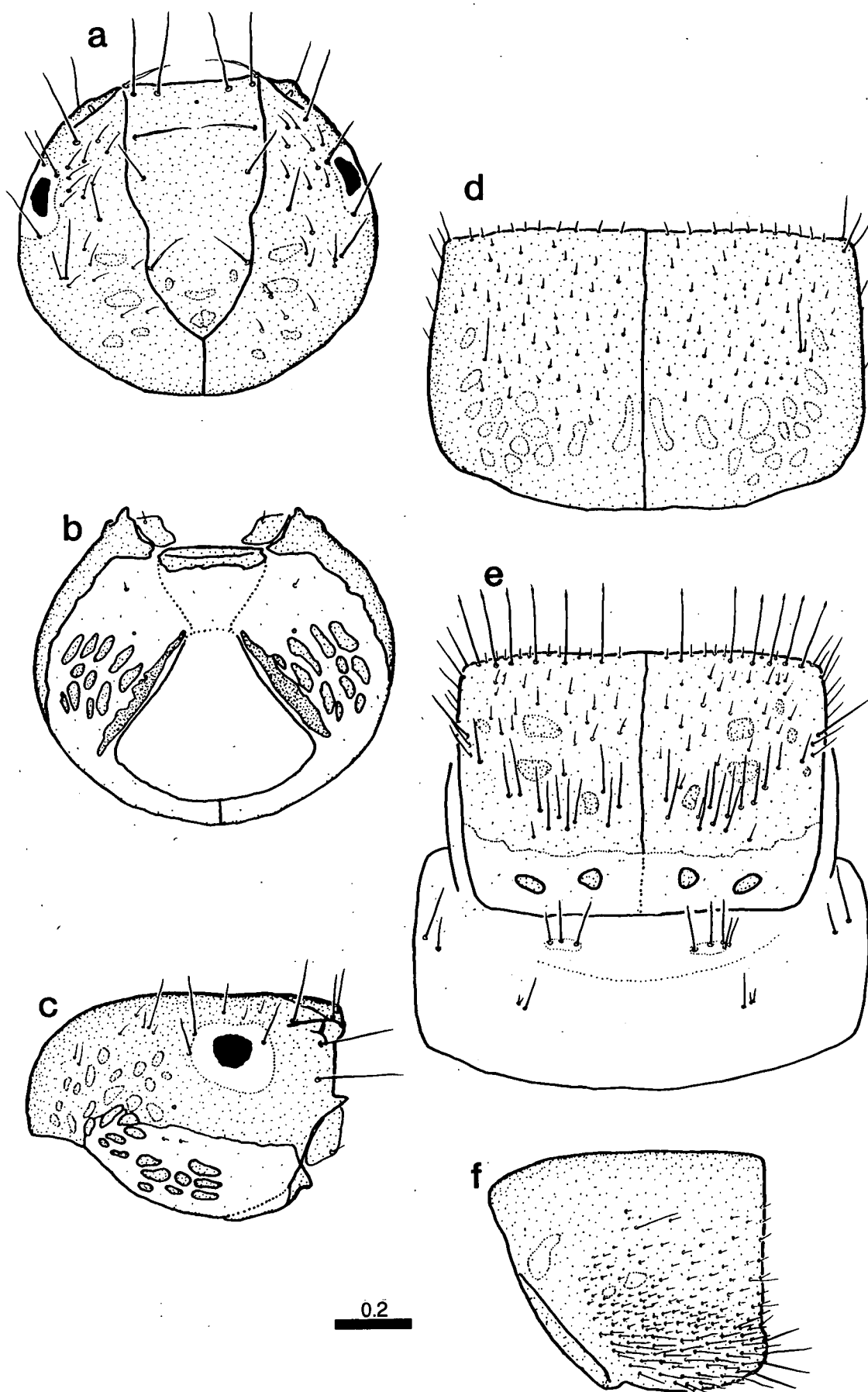
Figure 5.51. *Costora seposita* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** pronotum, meso- and metanotum; **f:** pronotum, lateral.
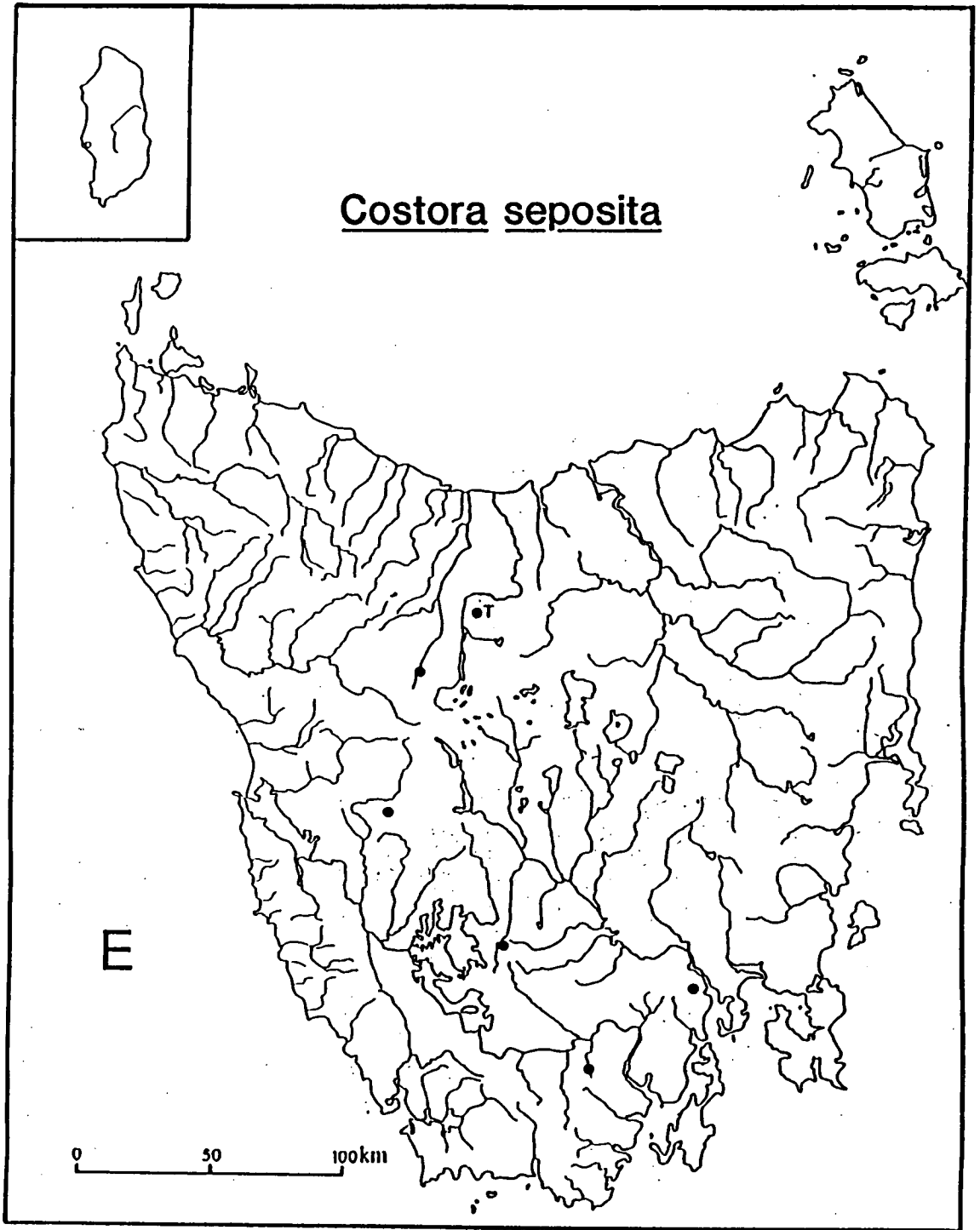
Costora seposita

Figure 5.52. Distribution of *Costora seposita*.
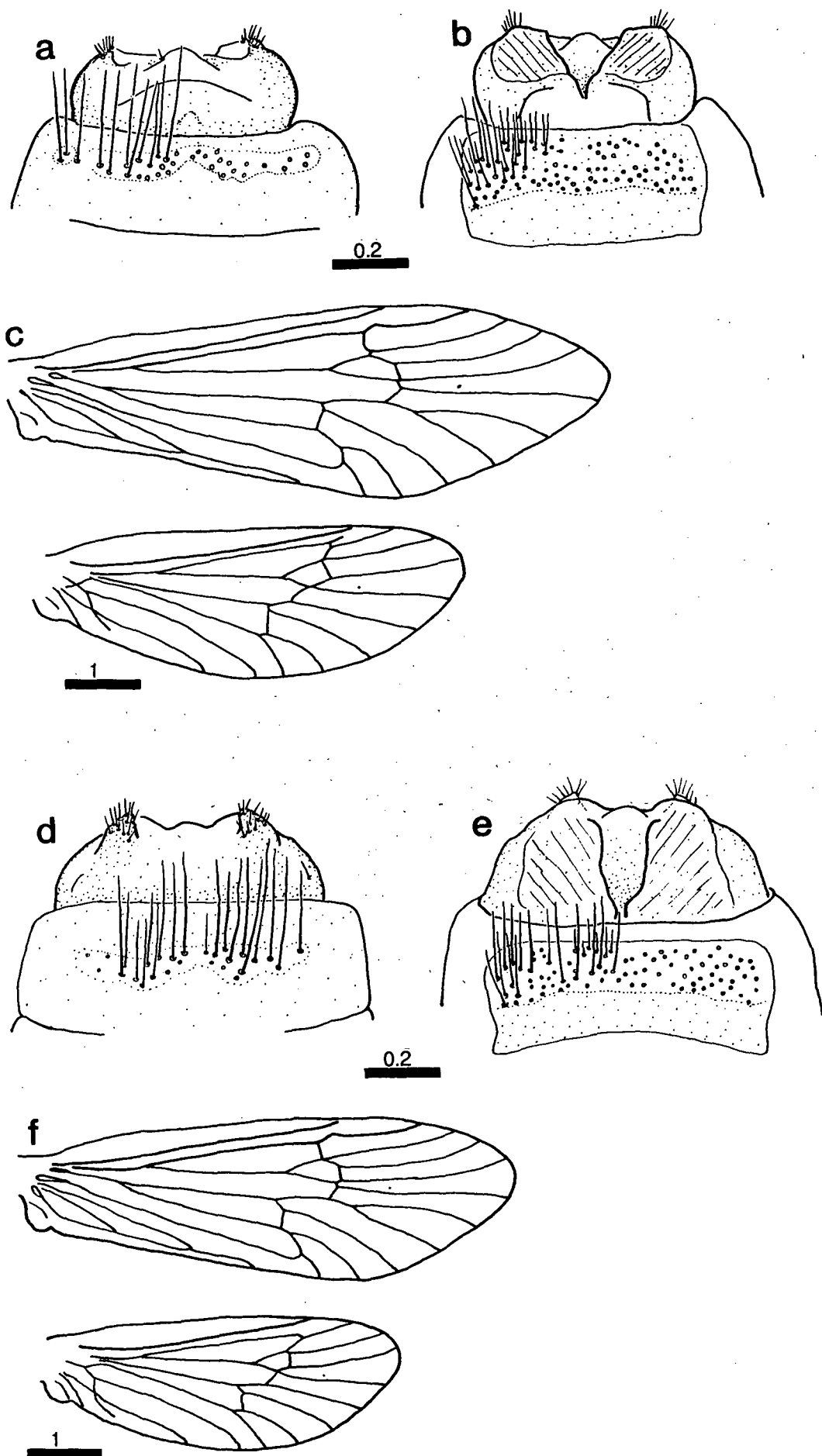
Figure 5.53. *Costora seposita* and *C. luxata* females. **a, b:** *C. seposita* genitalia dorsal, ventral; **c:** *C. seposita* wings; **d, e:** *C. luxata* genitalia dorsal, ventral; **f:** *C. luxata* wings.

Terminal processes extending beyond bases of terminal setae. Dorsally, sclerotized areas lateral to hookplates. Mandibles equally hooked.

Remarks

Occurs in rocky streams; pupates in rock crevices with anterior end of case outwards, or in moss on rocks.

Material examined: females: 4 reared 4 pharate 233, 22.x.87; 3 reared same locality 5.x.87; 1 reared same locality 25.viii.88; 2 reared same locality 12.xi.88; 2 reared same locality 12.ix.89; 1 reared 223, 4.ix.87; 2 reared same locality 12.x.87. Drawings based on specimen from 223, 12.x.87.

Larvae and pupae: 12L 223, 5.viii.87, 11.x.88; 30L 233, 5.x.87, 25.viii.88, 12.iv.89, 12.ix.89; 10L 52T, 22.ix.88; 11P 233, 25.viii.88 em. 29.ix.88, 12.ix.89 em. 26.ix.89, 22.x.88 em. 8.xi.88,12.xi.88 em. 19.xi.88, 25.viii.88 em.25.ix.88; 3P 223, 4.ix.87 em. 14.x.87, 12.x.87 em. 9.xi.87. Drawings based on specimens: 2L 223, 11.x.88; 1P 223, 12.x.87 em. 12.xi.87; 1P 233, 5.x.87 em. 18.x.87.

Distribution (Fig. 5.52). Endemic; from few widespread localities in the west; may be numerous where collected.

5.3.1.3

"Genus" Lingora-Hampa-Matasia

Genus Lingora Mosely, 1936, p. 406; Mosely & Kimmins, 1953, p. 93

Genus Hampa Mosely in Mosely & Kimmins, 1953:44

Genus Matasia Mosely, 1936, p.411; Mosely & Kimmins, 1953, p. 42

No intact larvae of *Hampa patona* were available, only sclerites from pupal cases, therefore no abdominal characters of *H. patona* are included in this "generic" description.

Larva

Case cylindrical, very slightly tapered, straight or slightly curved; constructed of silk and/or sandgrains; anterior margin square or slightly oblique; posterior membrane flat or projected, with circular or oval hole central or slightly dorsal.

Abdominal gills present; lateral spicules on segment 8 bifid, in a band 2 wide, segments 3-7 with band of single spicules, segment 2 lacking lateral spicules. Ventral bands of minute elongate spicules on each segment. Dorsal hump of segment 1 small; ventral bulge. Tergite 9 single oval sclerite, setose, anterior margin indistinct, may be largely unpigmented.

Anal proleg lateral sclerites facing posteriorly, median area very dark brown, a few indistinct scars in dorsal area; very stout black setae directed posteriorly, many short very fine pale hairs scattered; texture of small low papillae. Ventral sclerite narrow bar, unpigmented in some species.

Head round in dorsal view, gold to dark gold colour; scars same colour or paler, very wide and thin or oval. Dorsum covered with short upright spines, extensions of sclerite (not articulated), spines not extending down lateral face below scars. Anterior half of dorsum with many minute fine setae. Carina extending from anterior margin to

just behind eye. Frontoclypeus margins sometimes irregular, constriction slight, maximum width just behind anterior margin; 6-8 medium clear setae in anterolateral corners, in addition to long dark pair. Ventral mandibular articulation projecting prominently.

Mandibles each with about 10-12 outer setae in rows, in addition to large pair. Left mandible with flat transparent or fingerlike structures distal to brush.

Pronotum dark golden; part or all of dorsum densely spinulose, scattered with minute setae; lateral carina present, with row of closely spaced setae. Lateral face paler than dorsum, setose. Mesonotum width 2-3x length; anterior margin with regular row of medium length setae; irregular band of medium setae along posterior margin of pigmentation, fine setae scattered over pigmented area. Metanotum setation differing between species: SA 1 with 1-2 setae, sometimes pigmented area; SA 2 with 2-3 setae; SA 3 with 1-2 large and 0-3 fine setae.

Protrochantin fused to propleuron, tapered and upturned, 3-4 setae on anterior edge. Pleural humps with single long seta.

Gonads: each testis with two long lobes.

Pupa

Case anterior membrane domed, opening below centre; posterior membrane flat with small central oval opening, or with projected central vertical slit. Adhesive discs at both ends. Midlegs with dense hair fringes on both edges.

Anterior hookplates roughly oval, broad anteriorly, 2-5 hooks; posterior plates rounded quadrate, 3-4 hooks.

Mandibles each with pair of large basal setae. Labrum tapering to straight anterior margin, 2-many long brown setae in posterolateral area.

Terminalia: segment 9 with fine setae dorsally; processes tapering evenly to tip, setose dorsally.

Remarks

Found on rocks and amongst plant roots in fast and slow flowing streams. Pupate singly or in large aggregations attached at both ends to surface of substrate such as rock, wood, roots.

Key to larvae of Tasmanian *Lingora-Hampa-Matasia* species.

1.-Head scars oval, width 2-4x length; pronotum anterior margin with band of spines.......................................*Hampa patona*
[sand case]

-Head scars elongate, thin, width much > length; anterior 2/3 of pronotum spiny... 2

2.-Pronotum lateral carina very strong, posterior end extending onto dorsum almost to median suture; anterolateral corner sharply pointed, projecting forward ....*Matasia satana*
[silk and sand case]

-Pronotum lateral carina weak, posterior end turning only slightly dorsad; anterolateral corner not sharply pointed............ *Lingora aurata*
[sand and silk case]

Pupae of *Lingora*, *Hampa* and *Matasia* are keyed to species in section 5.3.1.2 (*Costora*).

<div align="center">

Lingora aurata Mosely
(Figs 5.54, 5.55)

</div>

Lingora aurata Mosely, 1936, p. 407; Mosely & Kimmins, 1953, p. 93; Neboiss, 1977, p.107.
Lingora caparti Jacquemart, 1965, p. 8. synonymized by Neboiss 1977).

Larva

Case entirely of sand grains or with varying proportions of silk. Anterior margin straight or very slightly oblique, posterior membrane flat, with central circular opening about 1/2 width of membrane.

Abdominal gills on segment 1 dorsal and ventral, segment 2 anterodorsal, ventral and lateral, segment 3 anterodorsal and ventral. Lateral abdominal spicules: segment 8 with about 16 bifid in band 2 wide, segments 3-7 with long band 1-4 wide of 60-70 single spicules. Anal proleg lateral sclerites with many medium length and fine setae in addition to stout setae; ventral sclerite pigmented; fleshy process ventromesad to anal claw. Tergite 9 posterior margin convex; textured with round spots posteriorly; entire sclerite with fine-medium setae, about 6 longer setae near posterior margin.

Head scars slightly paler than head colour, very wide and thin (about 8x wider than long); weak carina. Laterally, about 6 medium length setae between eye and anterior margin.

Left mandible with two mesal blade-like processes.

Pronotum with anterior 2/3 spinulose; scars paler and fairly distinct; anterolateral corner an obtuse angle, not produced forward to a point. Large setal sockets on anterior margin at corner; lateral face with medium length setae. Carina extending from corner in sigmoid line to dorsum, not extending across dorsum. Mesonotum width about 2.5x length, pair of muscle scars in posterior area on each side. Metanotum SA 1 with 1-2 setae, small pigmented area; SA 2 with about three setae; SA 3 with 2 longer and 2-3 fine setae.

Pupa

Case with anterior opening slit slightly curved; posterior membrane flat with central oval opening.

Figure 5.54. *Lingora aurata* larva and pupa. **a, b:** larval case lateral, posterior membrane; **c:** larva lateral; **d, e, f, g:** tergite 9 and anal legs posterodorsal, lateral sclerite texture, claw, anal legs ventral; **h:** testis; **i, j, k:** pupal case posterior membrane, lateral view, anterior membrane; **l, m:** terminalia dorsal, process lateral; **n:** hookplates; **o:** midleg fringe; **p:** mandibles; **q:** labrum.

a

b

c

0.5

d

0.2

e

f

0.1

g

h

0.1

i

j

0.5

k

l

o

0.25

m

0.05

n

2

5a

5p

6

p

0.05

q

0.1

0.1
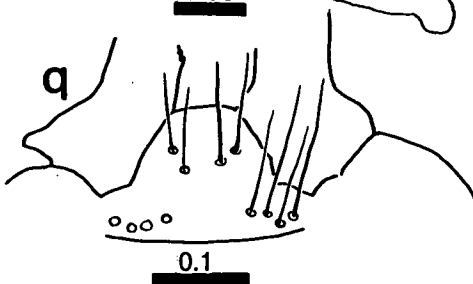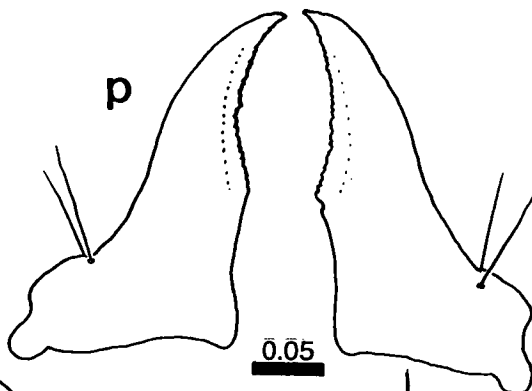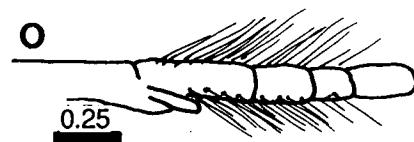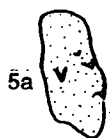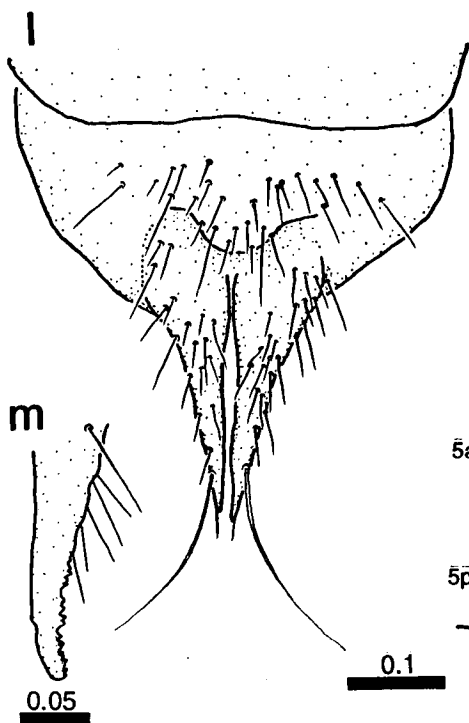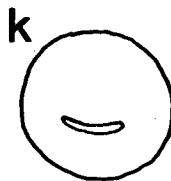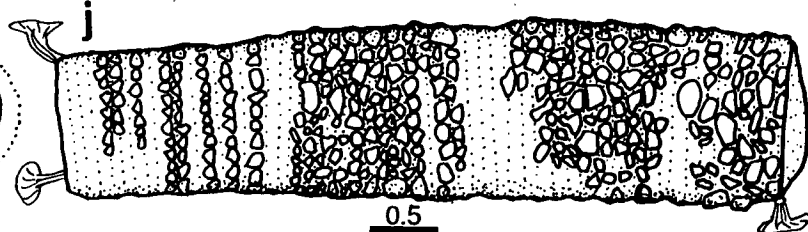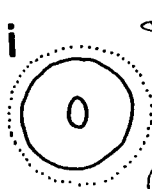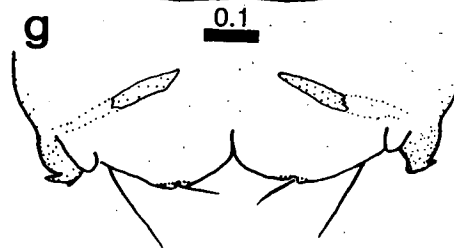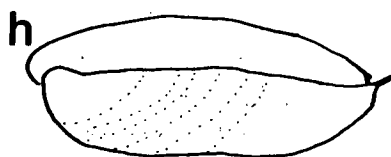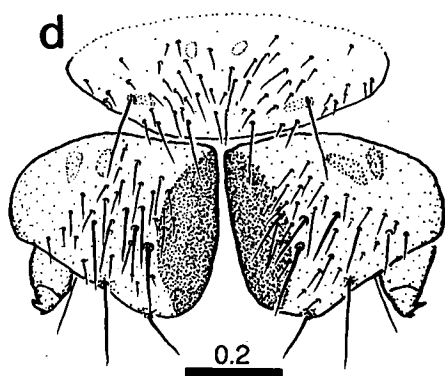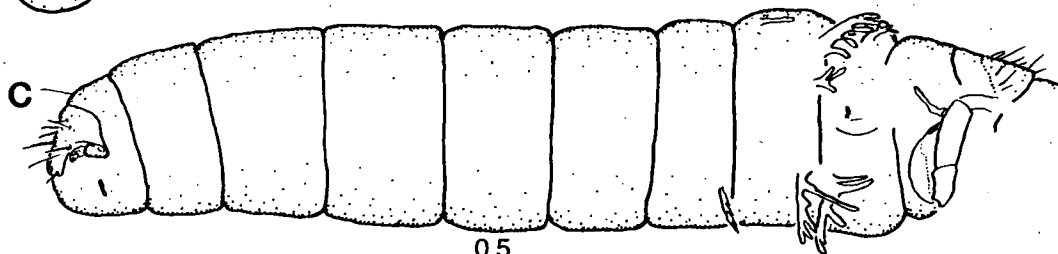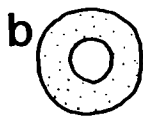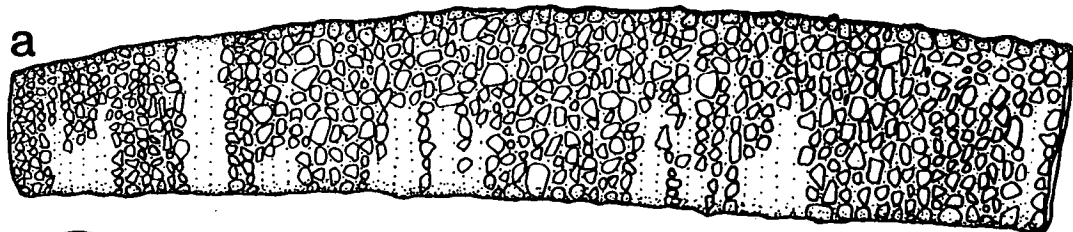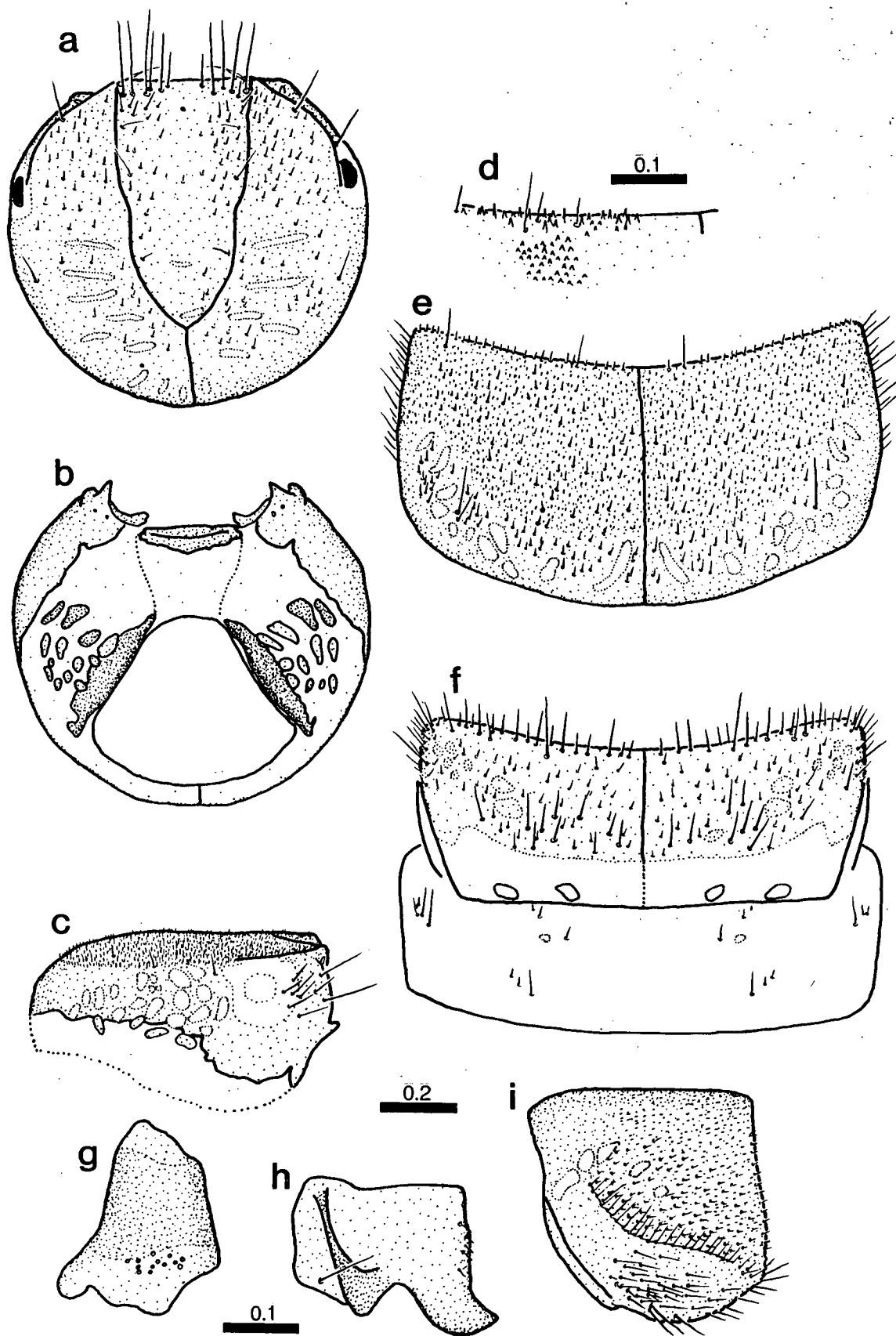
Figure 5.55. *Lingora aurata* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e, f:** pronotum spines enlarged, pronotum, meso- and metanotum; **g:** mandible, outer face; **h:** protrochantin; **i:** pronotum, lateral.
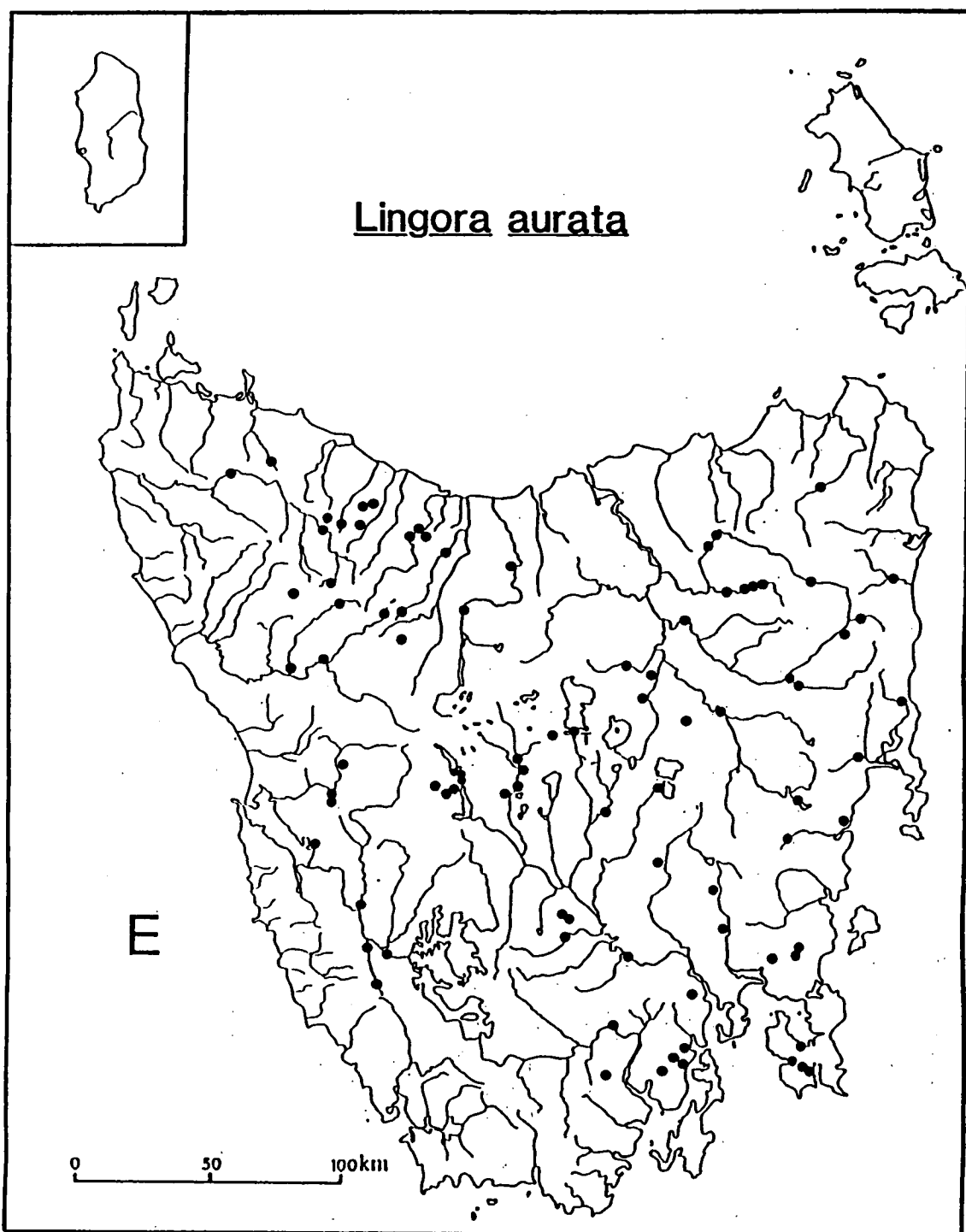
Figure 5.56. Distribution of *Lingora aurata*.

Labrum with 4 large setae on each posterolateral area.

Terminal processes with dorsal suface toothed apically, apex extended beyond base of terminal setae. Segment 9 dorsum with many short-medium setae.

Remarks

Pupates singly, attached at both ends, usually to roots or macrophyte leaves, less commonly rocks or wood.

Material examined: cleared: 2L 275, 2.xi.87; 1L 210, 17.xii.87; 1L 282, 11.xi.87; 1L 273, 2.xi.87; 1L 218, 26.xi.87; other: 2L 34, 21.ix.88; 115L 39, 22.ix.88; 8L 17, 20.ix.88; 13L 208, 17.xii.87; 8L 107, 20.ix.88; 12L 29, 21.ix.88; 2L 259, 18.ix.88; 2L 14, 21.xi.87; 4L 150, 27.x.87; 2L 293, 4.ii.88; 8L 83, 4.ii.88; 3L 280, 11.xi.87; 7L 18, 21.xi.87; 1L 217, 26.xi.87; 6L 279, 2.xi.87; 8P 268, 7.xi.88; 2P 273, 2.xi.87 em. 30.xi.87; 3P 284, 22.i.88 em. 7.ii.88; 1P 71, 19.ii.88 em. 4.xii.88; 1P 92, 5.ii.88 em. 1.iii.88; 1P 273, 2.xi.87; 1P 284, 22.i.88 em. 2.ii.88; 1P 275, 2.xi.87 em. 15.xii.87; 5P 282, 16.xi.87 em. 1.xii.87.

Drawings based on: 2L 275, 2.xi.87; 1P 275, 2.xi.87 em. 15.xii.87.

Distribution (Fig. 5.56). Endemic; widespread; often very numerous where collected.

Hampa patona Mosely
(Figs 5.57, 5.58)

Hampa patona Mosely in Mosely & Kimmins, 1953, p. 44; Neboiss, 1977, p.100.

Larva (sclerites only, no intact larval material was obtained).

Case: on the basis of pupal case, straight/slightly curved, slightly tapered cylindrical sand-grain case.

Head scar width about 3.5x length. Left mandible with fingerlike structures distal to mesal brush.

Pronotum scars darker, indistinct; narrow band of spines along anterior, remainder polygonal reticulate texture. Anterolateral corner produced into small triangular point; carina extending straight back from apex, curving very slightly dorsad at end. Dorsum densely covered with minute setae: one per polygonal cell; a few longer pale setae. Lateral face forming acute angle with dorsum, anterior 2/3 with scattered minute setae.

Mesonotum width about 3x length.

Pupa

Case with anterior opening slit strongly curved; posterior membrane flat with small central oval hole.

Segment 9 dorsum with band of many medium length fine hairs; terminal processes fairly stout, apex upturned, inner surfaces minutely spiny. Lateral fringe colourless, single row of hairs.

Mandibles with distal 1/3 curving inwards, right mandible tip more strongly hooked and strengthened. Labrum with two large setae in posterolateral area.

Material examined: 1 M larval sclerites and pupal exuviae, 99, 18.ii.88; **Victoria:**1 M larval sclerites and pupal exuviae, Yarra River O'Shannassy Rd, 21.ii.79, JD. Drawings based on specimen from Lilydale Falls.
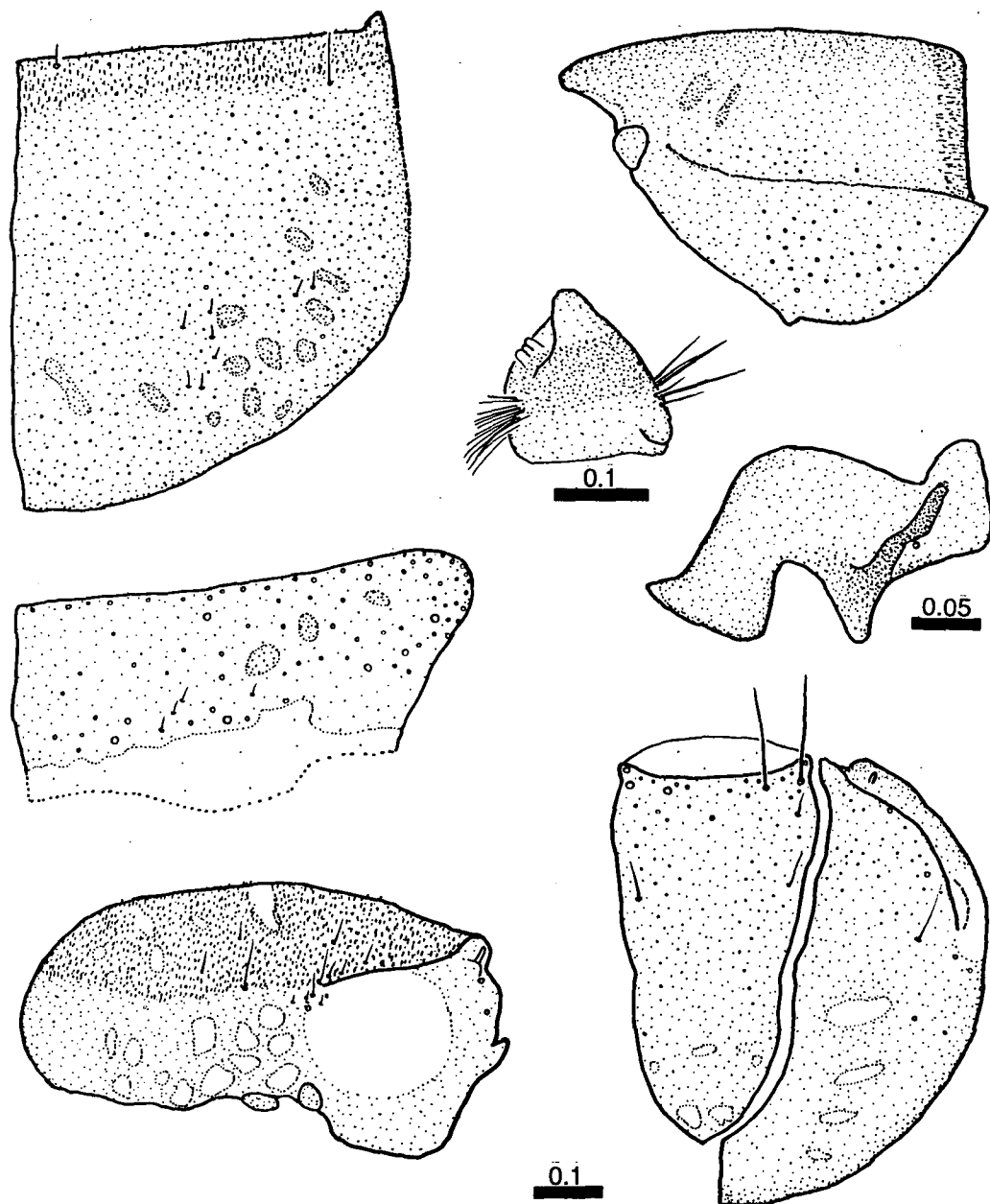
Figure 5.57. *Hampa patona* larva. **a, b:** pronotum dorsal, lateral; **c:** mesonotum; **d:** mandible, ventral; **e:** protrochantin; **f, g:** head lateral, dorsal.
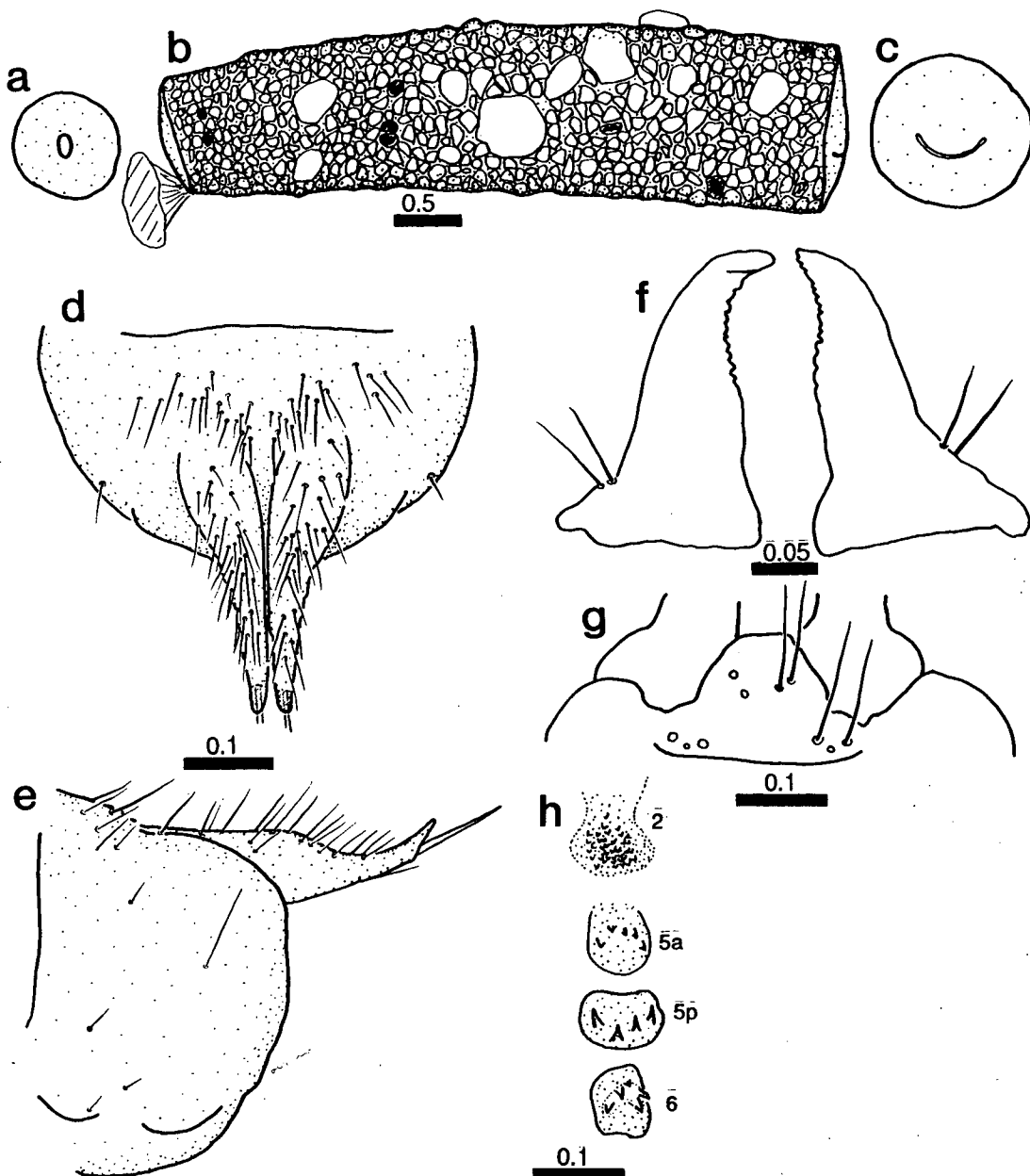
Figure 5.58. *Hampa patona* pupa. **a, b, c:** case posterior membrane, lateral case, anterior membrane; **d, e:** terminalia dorsal, lateral; **f, g:** mandibles ventral, labrum; **h:** hookplates.
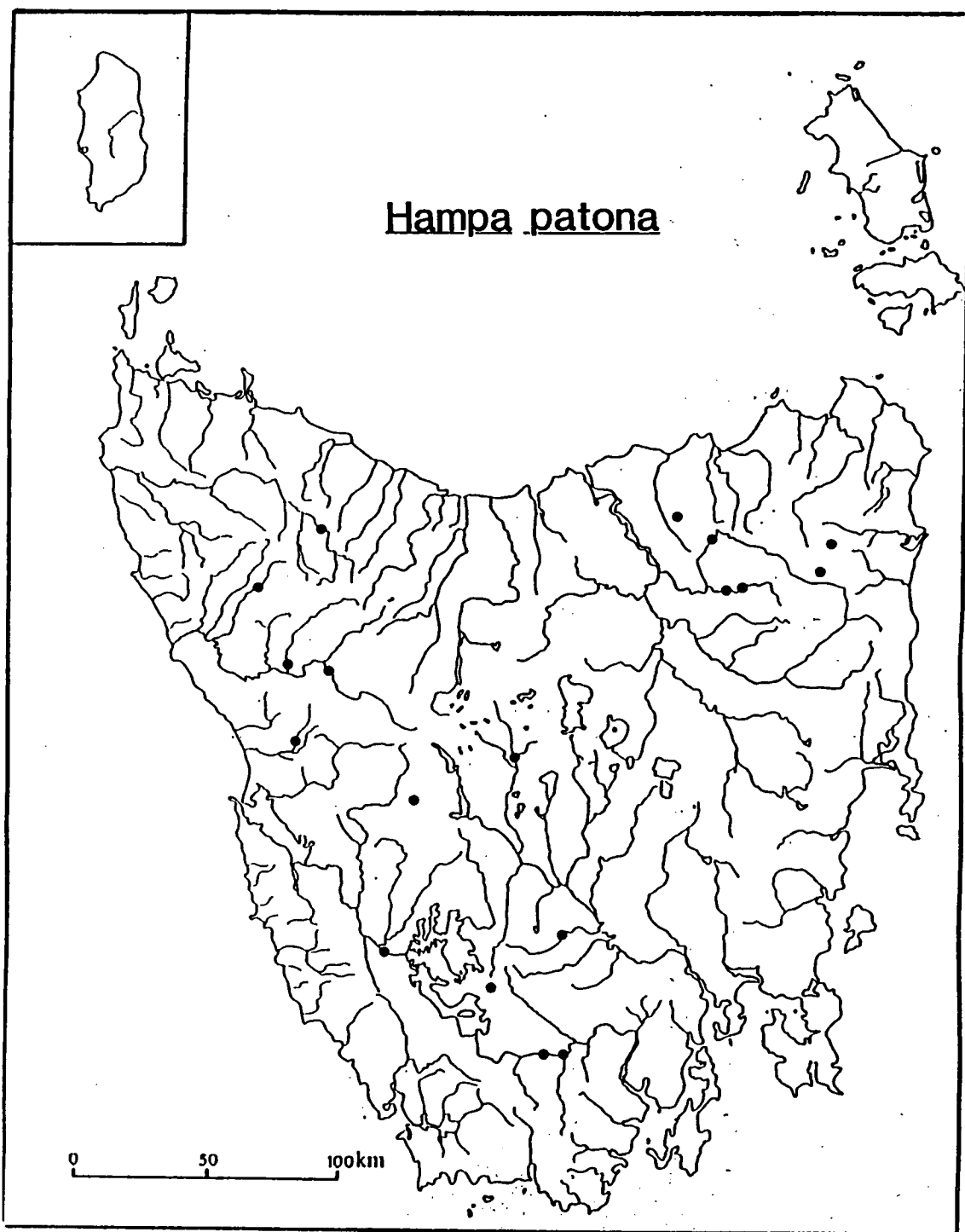
Hampa patona

Figure 5.59. Distribution of *Hampa patona*.

Distribution (Fig. 5.59). Tasmania and SE Australia; relatively few, widespread sites in Tasmania; adults numerous where collected, larvae not found.

Matasia satana Mosely
(Figs 5.60, 5.61)

Matasia satana Mosely, 1936, p. 411; Mosely & Kimmins, 1953, p. 42; Neboiss, 1977, p. 101.

Larva

Case stout, very slightly dorsoventrally flattened at posterior in mature larva; entirely of silk or with bands of sandgrains, mostly on dorsal surface. Anterior margin slightly oblique with dorsal overhang; posterior opening circular-oval, in projection of membrane, slightly dorsad of centre.

Abdomen orange in fresh specimens; gills on segment 2 anterodorsal, lateral and ventral, on segment 3 anterodorsal and ventral. Lateral abdominal spicules lacking on segment 8, segment 7 with 3 single spicules anteriorly, segments 2-6 with irregular band of about 24-32 single spines, 1-4 wide, narrowest at ends.

Tergite 9 largely unpigmented, two pairs of small muscle scars; posterior margin bow-shaped, 4 pairs of setae on posterior margin. Anal proleg lateral sclerites with few setae: in addition to large setae, a transverse row of shorter stout setae; small humps dorsad to large setae near median edge of sclerite, tiny bifid spicule laterad to hump. Ventral sclerite unpigmented.

Head dorsal scars thin, width about 10-15x length, only slightly paler, distinct by being spine free. Head laterally with 20-30 medium length pale setae between eye and anterior margin. Laterally, many medium length pale setae between eye and anterior margin.

Left mandible with pair of flat transparent structures arising from centre, distal to them a pointed process.

Pronotum spinulose anterior of carina; scars paler and spine-free, width about 6x length; posterior margin irregularly pigmented. Anterolateral corner sharply pointed and produced forward of anterior margin; strong carina extending from anterolateral apex straight back, curving onto dorsum, turning anteriad near median suture, above muscle scar. Anterior margin with a few medium length fine setae, about 8 medium dark setae scattered on dorsum.

Mesonotum width about 3x length. Metanotum lacking any pigmentation, SA 1, 2 and 3 with 1, 2 and 1 setae respectively.

Pupa

Case ventral anterior margin filled in with silk, anterior opening straight, width about 1/3 of membrane diameter; posterior membrane with central projected vertical slit. Large ventral adhesive patch (not stalked) at each end of case.

Abdomen pigmented brown dorsally, covered with spicules. Anterior hookplates with 2-3 hooks and broad anterior extensions. Lateral fringe a broad band of hairs. Terminal processes smooth; dorsal hump between bases on segment 9 with long seta on each side and 3-5 fine setae laterally.

74

Figure 5.60. *Matasia satana* larva and pupa. **a, b:** larval case posterior membrane, lateral case; **c:** larva, lateral; **d, e, f:** tergite 9 and anal legs posterior view, ventral, dorsal; **g, h, I:** pupal case posterior membrane, lateral case, anterior membrane; **J, k:** terminalia dorsal, process enlarged; **I:** mandibles; **m:** labrum; **n:** hookplates.

a

b
0.5

c
0.5

d
0.2

e

f

g

h
0.5

i

j
0.1

k
0.05

l

m

n
5a

5p

6
0.1
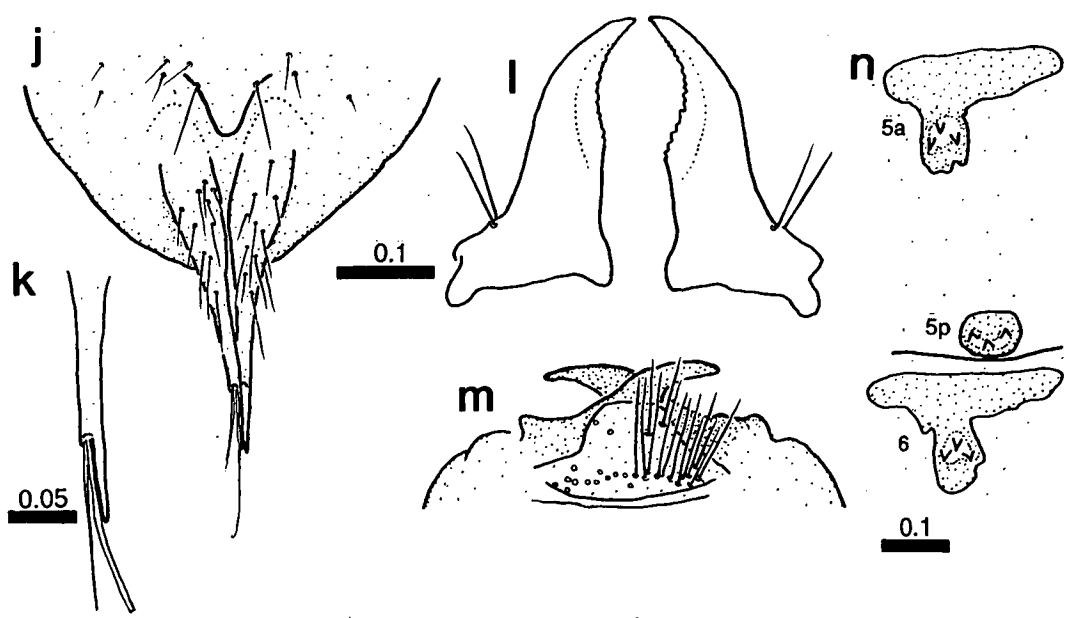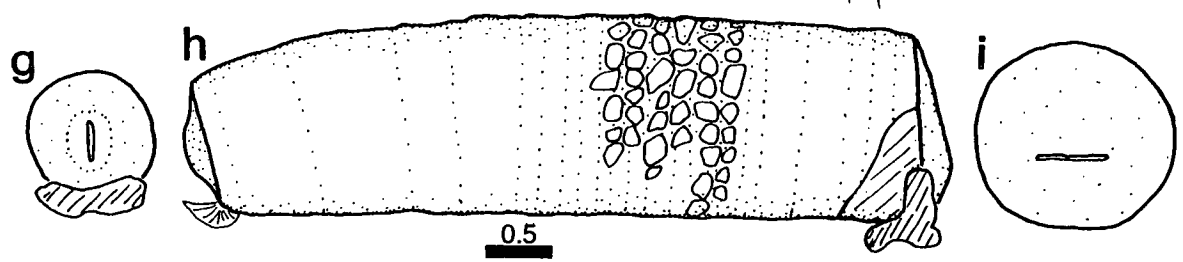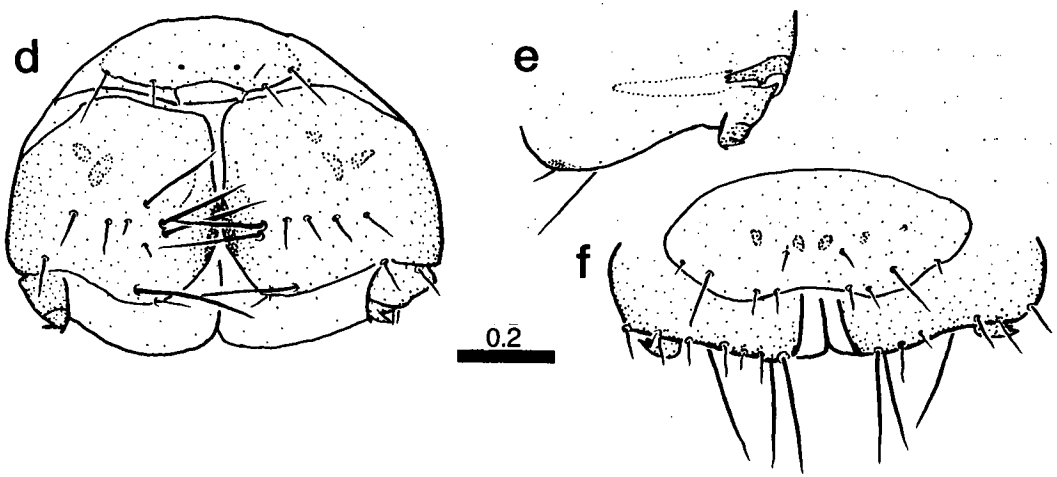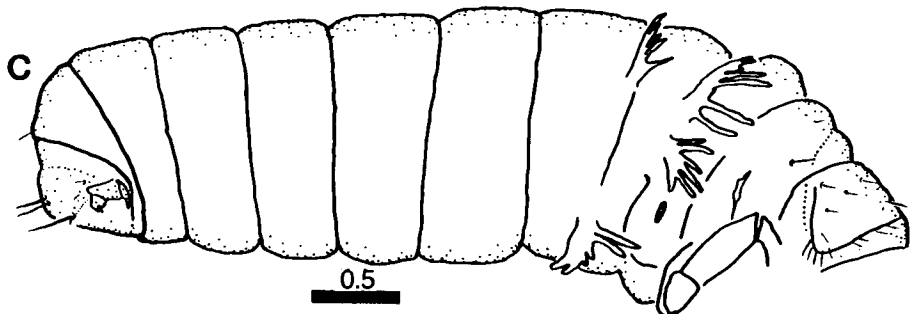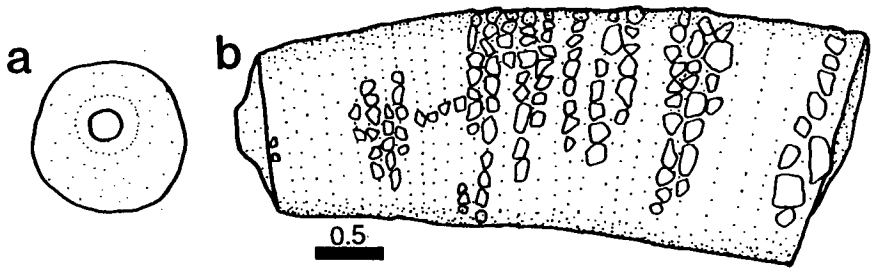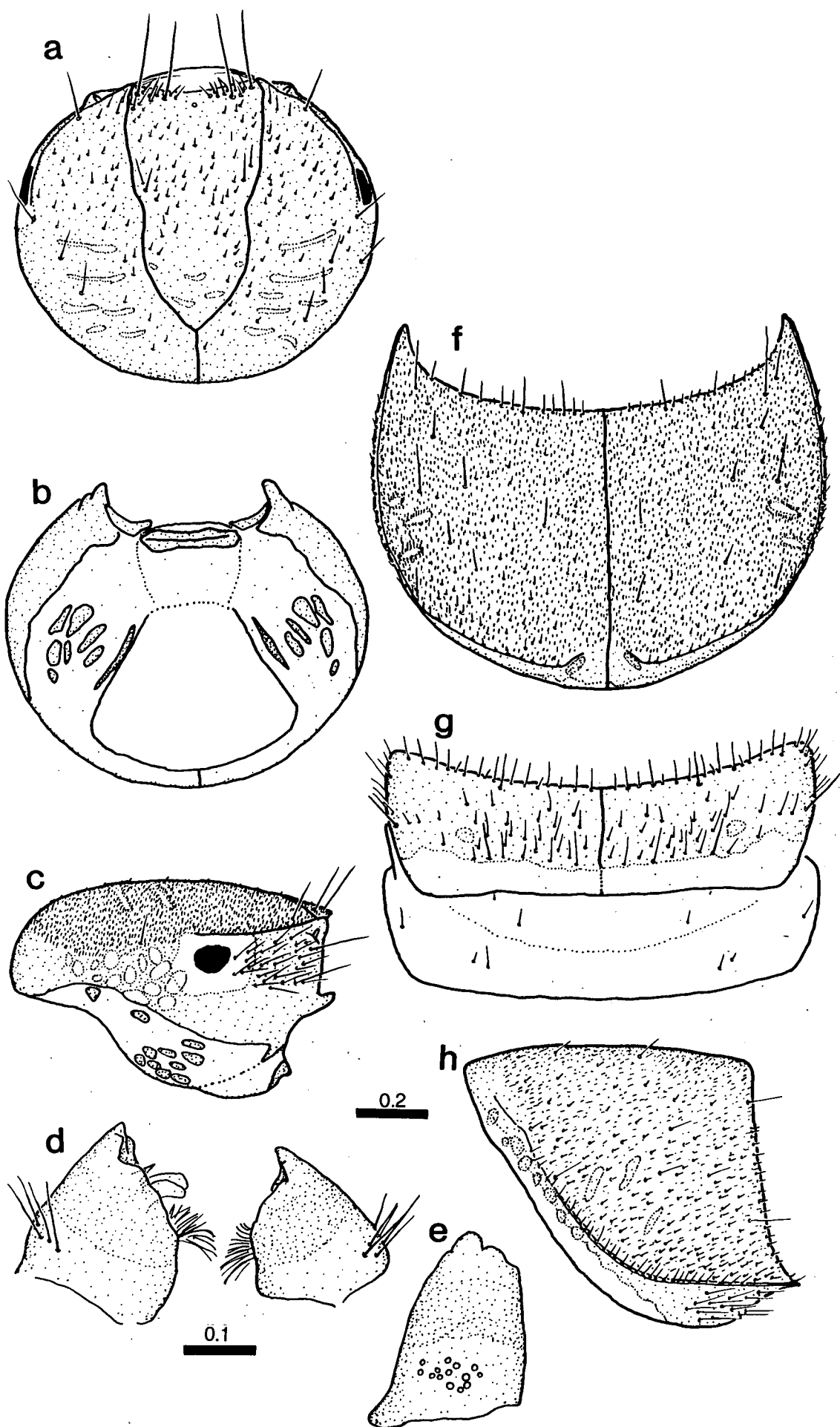
Figure 5.61. *Matasia satana* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e:** mandibles dorsal, outer face (setae not shown); **f, g, h:** pronotum, meso- and metanotum, pronotum lateral.
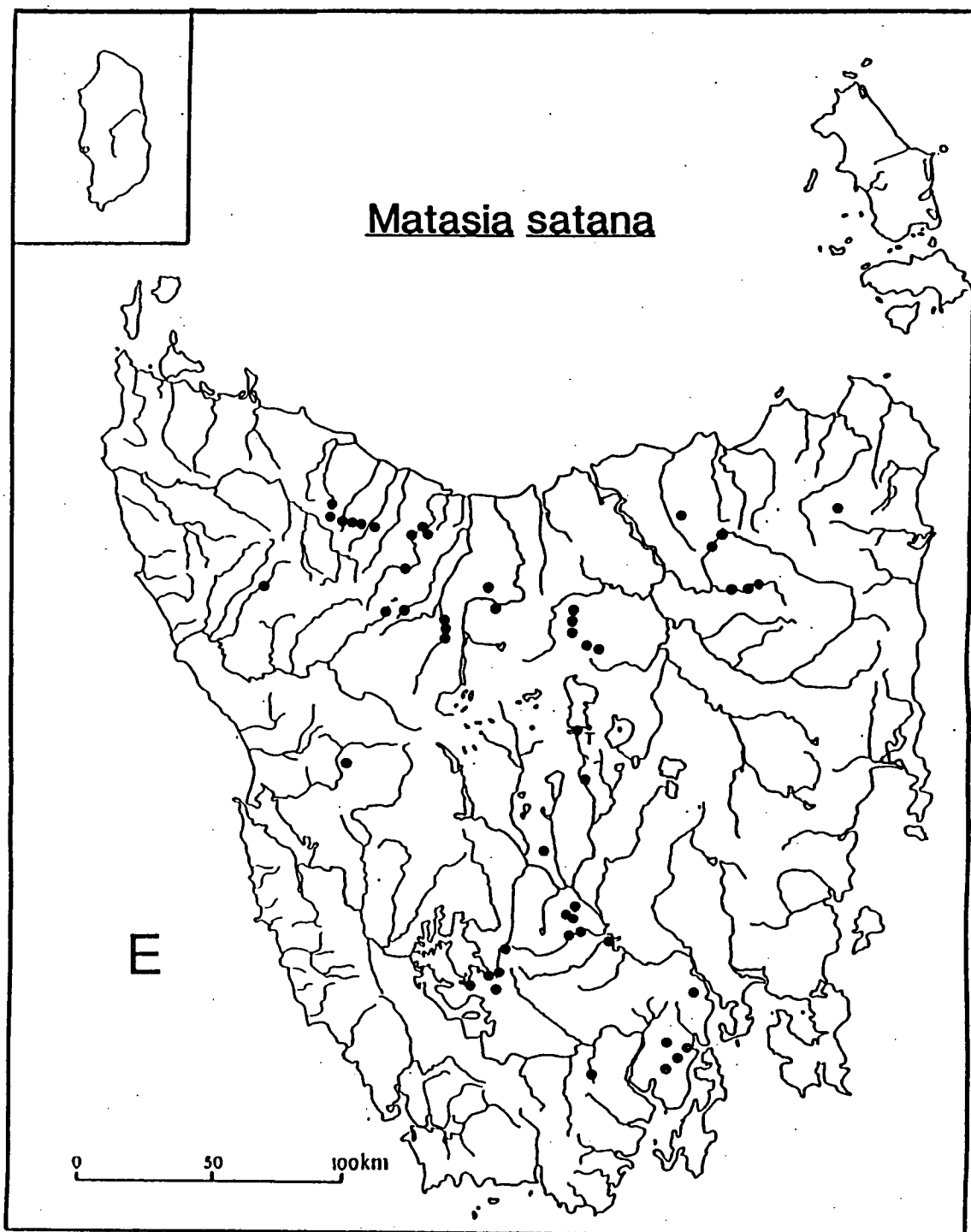
Figure 5.62. Distribution of *Matasia satana*.

Labrum with about 14 long setae in each posterolateral area. Mandibles equally hooked.

Remarks

Pupates in large dense aggregations under and on sides of rocks, usually in crevices, right up to the water line so cases may be above water if levels drop.

Material examined: cleared: 3L 229, 25.viii.88; 4L 170, 25.viii.88; other: 6L 180, 5.x.87; 2L 246, 18.viii.88; 1L 18, 21.ix.88; 3L 20, 21.ix.88; 2L 30, 21.ix.88; 28L 229, 22.x.87, 25.viii.88; 1L 233, 14.x.87; 15L 170, 25.viii.88; 5L 219, 30.iv.87; 3L 230, 6.x.87. Drawings based on specimens: 2L 229, 25.viii.88; 1P 230, 6.x.87 em. 23.x.87.

Distribution (Fig. 5.62). Endemic; widespread except for mid-east area; usually numerous where collected.

5.3.2

Family **HELICOPHIDAE** Mosely (1953)

Genus **Alloecella** Banks

Alloecella Banks, 1939, p. 481; Mosely & Kimmins, 1953, p. 142; Neboiss, 1977, p. 96.
Type species: *Alloecella grisea* Banks.

Larva

Case differing between species; slightly curved and tapered, constructed of sandgrains or sandgrains and plant material.

Abdominal gills absent; lateral hair fringe absent, segment 8 with lateral row or band of bifid spicules and single spines, segments 3-7 with lateral band of single spicules. Segment 1 dorsal hump low, with sclerotised transverse band; lateral humps prominent, pointed, with oval sclerite of spines and longitudinal sclerite, terminal black seta and small seta 1/2 way along posterior edge.

Tergite 9 unpigmented or with transverse band of brown patches or pale muscle scars; posterior row of about 10 pairs of setae, 2 pairs long. Anal prolegs fairly slender, lateral sclerite mostly unpigmented; with up to 4 long posterior setae, 1 very stout; dorsal accessory hook of anal claw raised; ventral oval sclerite narrow, pale brown or unpigmented.

Head in dorsal view round or tapering anteriorly; dark golden-brown, regular polygonal reticulate texture; dorsal scars small, slightly darker, may be indistinct; eye bulging slightly, surrounded by pale area. Several long dark setae arising from dorsum, several behind eye. Carina present in some species.

Frontoclypeus broad anteriorly, 3 pairs of lateral setae; each anterolateral corner with a pale curved seta and 2 long brown setae, central non-setose pit.

Antennae very small, about half way between pale area around eye and anterior margin of capsule.

Head with 2 long dark setae laterally near anterior margin; area of scars posterior to eye; 2 small setae ventral to scars. Ventral head mostly unpigmented, dark scars in posterior half, a short spiny seta and non-setose pit anterior to scars on each side;

pigmented bands along occipital margins. Apotome triangular, broad anteriorly, length equal to anterior width, anteriorly sclerotized and brown; genae almost abutting.

Mandibles slightly longer than wide, left longer and with deeper mesal concavity than right; each with mesal brush, shorter distally; 2 outer basal setae, 2 apical teeth.

Labrum rounded quadrate; mid row of 3 pairs of stout pale setae and pair on each anterolateral margin, slight concavity in anterior margin with short dense brush, stout seta each side just posterior to margin; long ventral brushes.

Pronotum same colour as head, polygonal reticulate texture; anterolateral corner angle obtuse. Lateral carina weak, extending from posterior. Dorsum with sparsely scattered minute setae in some species. Anterior margin smooth, straight or curved forward slightly, folded under anterolaterally giving appearance of dark band; lateral face setose.

Mesonotum completely sclerotised, irregular pigmented areas centrally on each side and anterolaterally; posterior margin slightly or greatly extended posteriorly to form unpigmented hemisphere. Few-many anterior setae, mid pair of long setae, and 1 fine seta.

Metanotum mostly or entirely membranous, divided by transverse fold, pair of minute setae on anterior margin. SA 1 with 1-3 setae, sometimes sclerite; SA 2 with 1 long and 1-2 minute setae; SA 3 with 4-5 setae, sometimes sclerite.

Legs even dark gold, setose, increasing in length and slenderness posteriorly; mid- and hindlegs with fleshy pleural humps; all with clear dorsal femoral setae. Hind tibia bent, broadened by lateral flattening. Protrochantin well developed, not fused to propleuron; tip more or less rectangular with anterodorsal angle produced into small point, anteroventral corner rounded.

Each testis with four large round lobes.

Pupa

Case formed by modification of larval case, anterior closure with outer thin membrane covering inner membrane with transverse slit.

Fore- and midleg tarsi with dense fringe of hairs on both edges. Hookplates golden brown with pale band around dark hooks, anterior plates on segments 3-6 oval, broad anterior margin indistinct, with 3-5 hooks; posterior plates on segment 5, rounded quadrate, as wide as long, 3-4 hooks on posterior margin.

Mandibles broad basally, tapering, length and degree of curve varying with species; inner distal 1/2 with small serrations, each with two outer basal setae. Labrum hemispherical, anterior margin papillate, 2-4 long dark setae in each posterolateral area, mid transverse row of about 3 each side, 4-7 in anterolateral area.

Lateral abdominal fringe extending from posterior margin of segment 6 to posterior 2/3 of segment 8. Segment 9 slender, with dorsal transverse row of 3-5 pairs of setae, ventral slit with lateral longitudinal rows of 4-5 setae, M with lateral flat-faced humps; terminal processes slender at base, not strongly sclerotized, tapering to slender apex, a few setae dorsally, apices extending well beyond bases of terminal clear setae.

Key to larvae of Tasmanian *Alloecella* species.

1.-Frontoclypeus margins curved outwards in anterior half; anterior width 2x posterior width ....*A. pilosa*
[cylindrical sand case]
-Frontoclypeus margins straight in anterior half; anterior width < 2x posterior width 2

2.-Pronotum lateral carina a fold only...............*A. grisea* [sand case]
-Pronotum lateral carina a straight ridge .... *A. longispina*
[sand and plant case]

Key to pupae of *Alloecella* species.

1.-Mandibles tapering from base; terminal processes dorsally smooth, toothed apically.. *A. grisea*
-Mandibles tapering from 1/2 way along; terminal processes papillate dorsally and apically.. 2

2.- Foreleg hair fringe sparse; labrum with > 3 pairsanterior setae; terminal processes straight................................... *A. pilosa*
-Foreleg hair fringe dense; labrum with 2 pairs anterior setae; terminal processes turned up................................. *A. longispina*

Alloecella grisea Banks

Alloecella grisea Banks, 1939, p. 481; Neboiss, 1977, p. 97;

Alloecella warneria Mosely in Mosely & Kimmins, 1953, 144; Jacquemart, 1965, p.13; Neboiss, 1974c, p. 14.

Larvae and pupae of *Alloecella grisea* are described and figured by Drecktrah (1984).

Distribution (Fig. 5.63). Tasmania and SE Australia; widespread within Tasmania; may be numerous where collected.

Alloecella longispina Jacquemart
(Figs 5.64, 5.65)

Alloecella longispina Jacquemart, 1965, p. 14; Neboiss, 1977, p. 97.

Larva

Case a curved tapering dorsoventrally flattened cylinder, of small sandgrains with projecting plant material covering dorsum, making cased larva very cryptic. Anterior margin oblique, overhanging dorsally; posterior membrane oblique, extending anteriorly on ventral side, transverse oval or oblong opening in posterior end of membrane.

Abdomen dorsoventrally flattened; lateral spicules on segment 8 a row of about
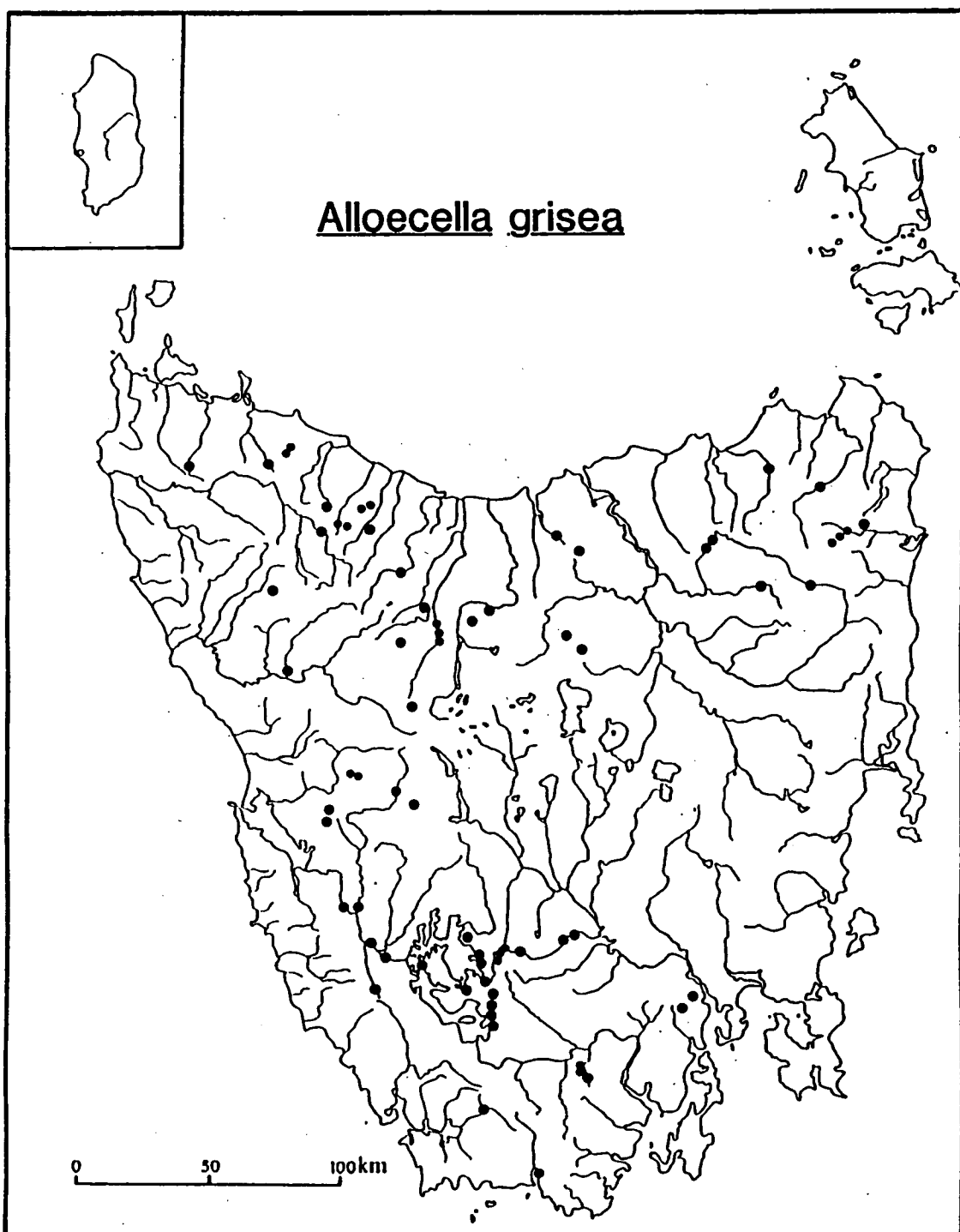
Figure 5.63. Distribution of *Alloecella grisea*.

Figure 5.64. *Alloecella longispina* larva and pupa. **a, b:** larval case lateral, ventral; **c:** larva lateral; **d, e:** anal legs and tergite 9 dorsal, ventral; **f, g, h:** pupal case anterior ventral, posterior ventral, anterior membranes (outer membrane moved to show inner); **i:** hookplates; **j, k, l:** ♂ terminalia dorsal, ventral, process lateral; **m:** mid or foreleg fringe; **n:** mandibles and labrum.

a b c d e f g h i j k l m n

1 0.5 0.2 1 0.5 2 5a 5p 6 0.1 0.1 0.5 0.1
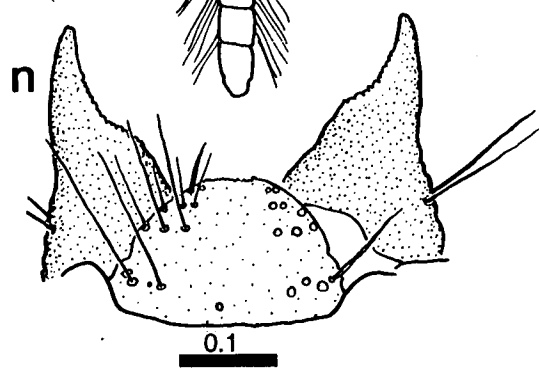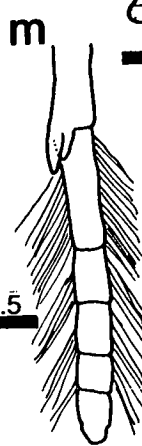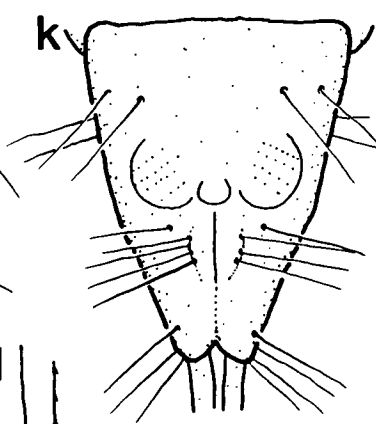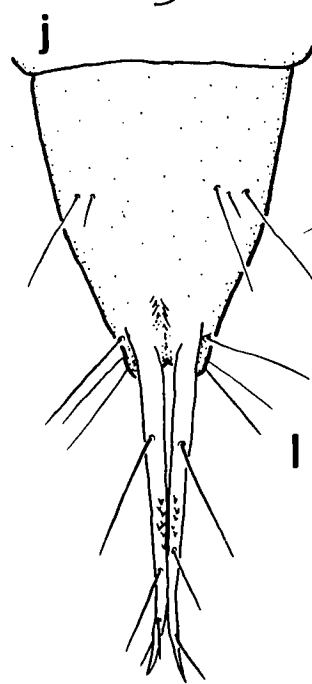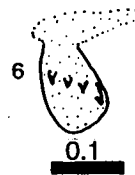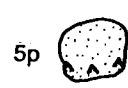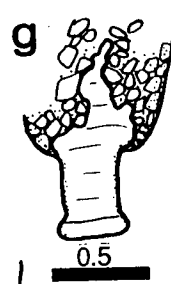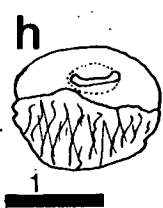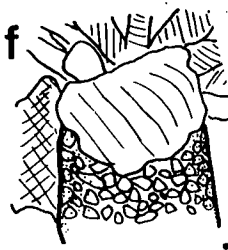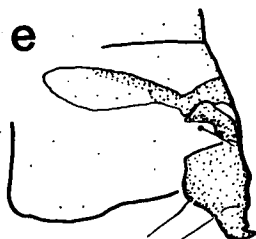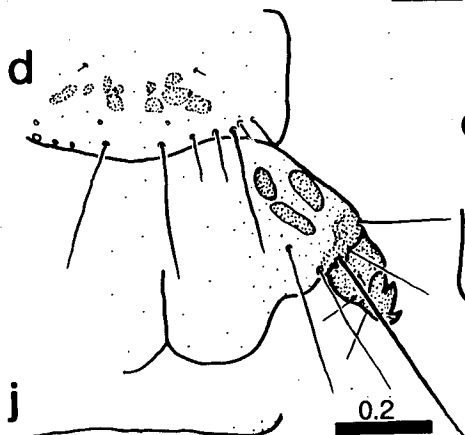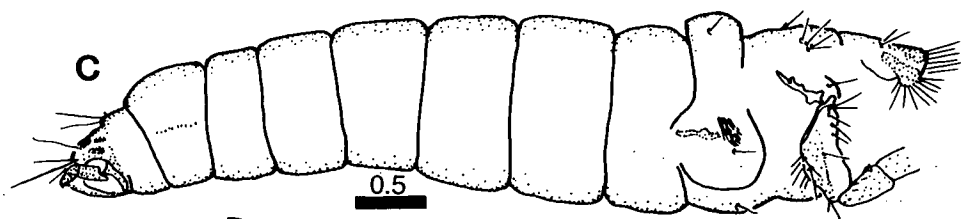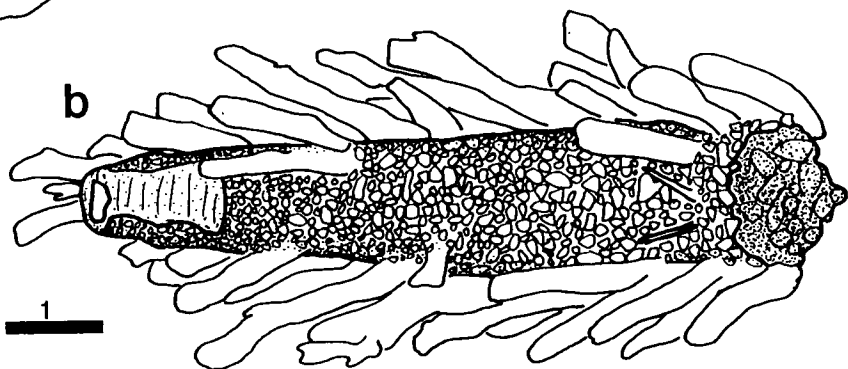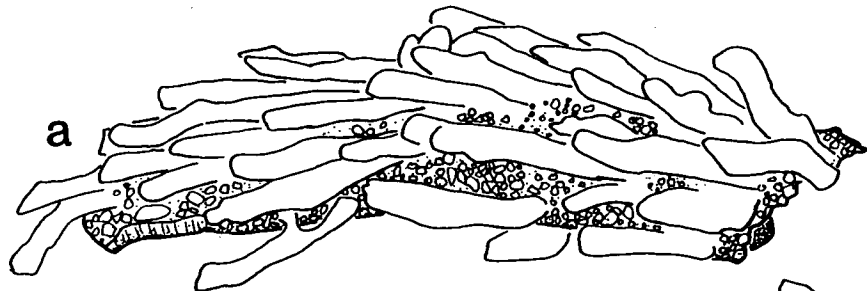
Figure 5.65. *Alloecella longispina* larva. **a, b, c:** head dorsal, ventral, lateral; **d:** mandibles, dorsal; **e, f, g:** pronotum, meso- and metanotum, pronotum lateral; **h:** protrochantin; **i:** hindleg (R).

a

b

c

d

0.1

e

f

g

h

0.2

i

0.2
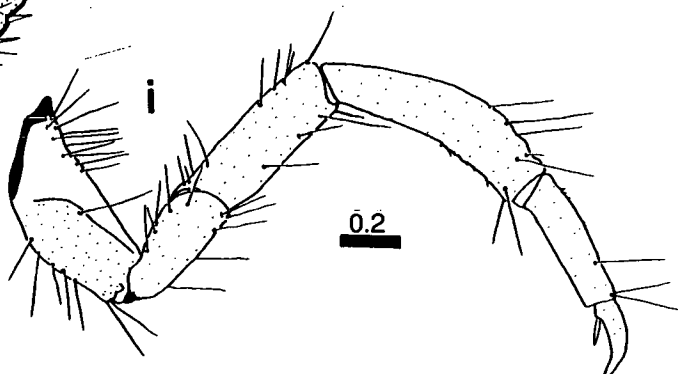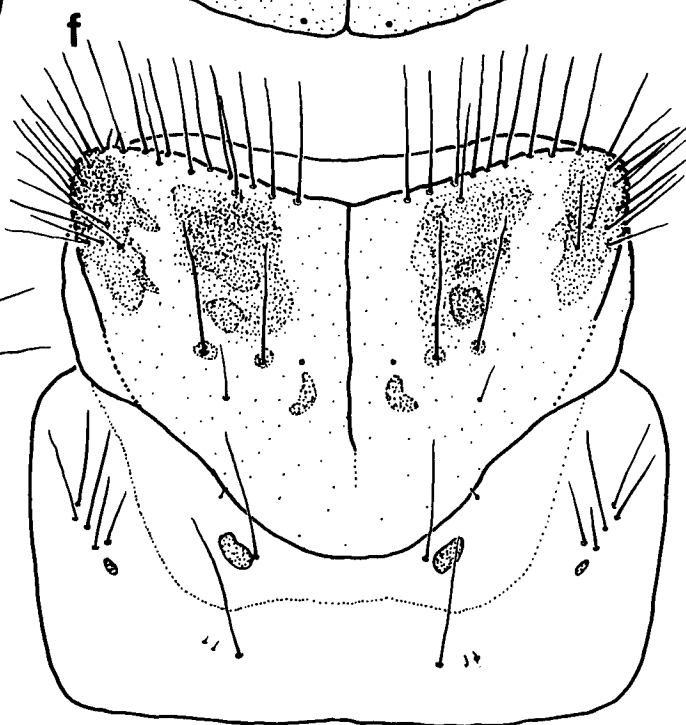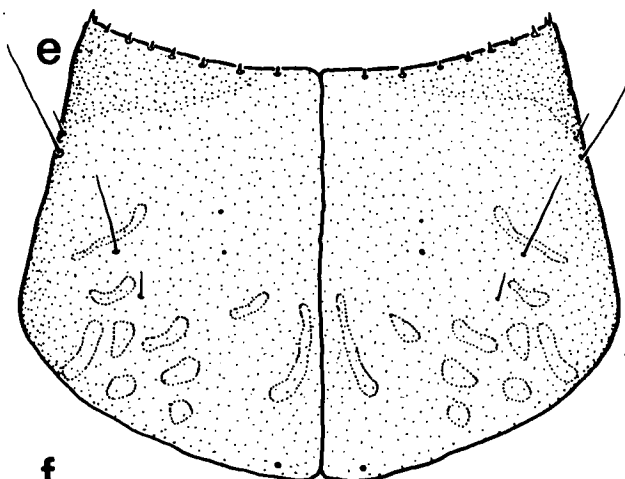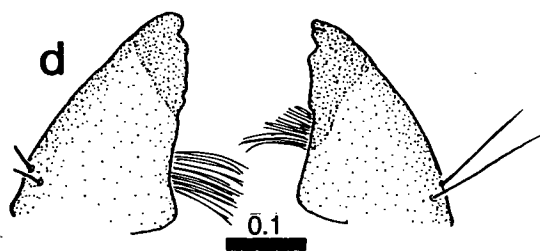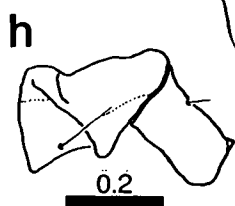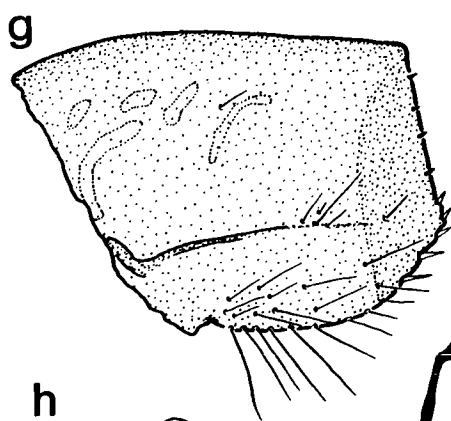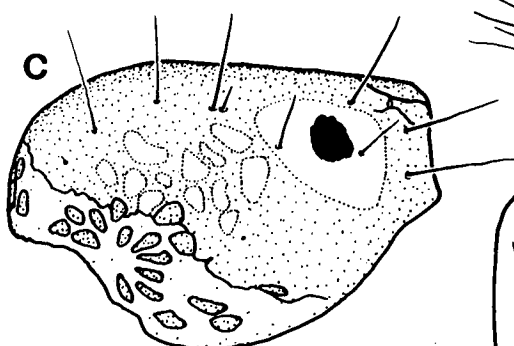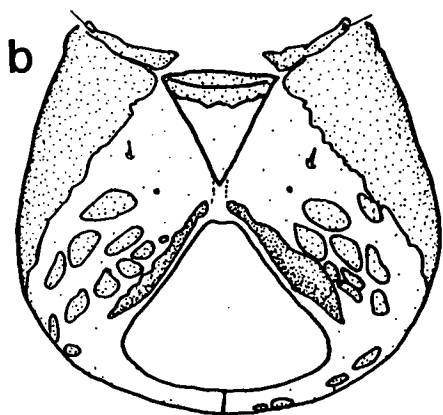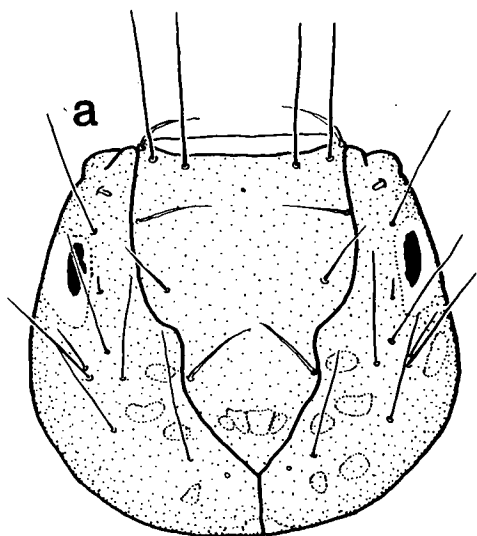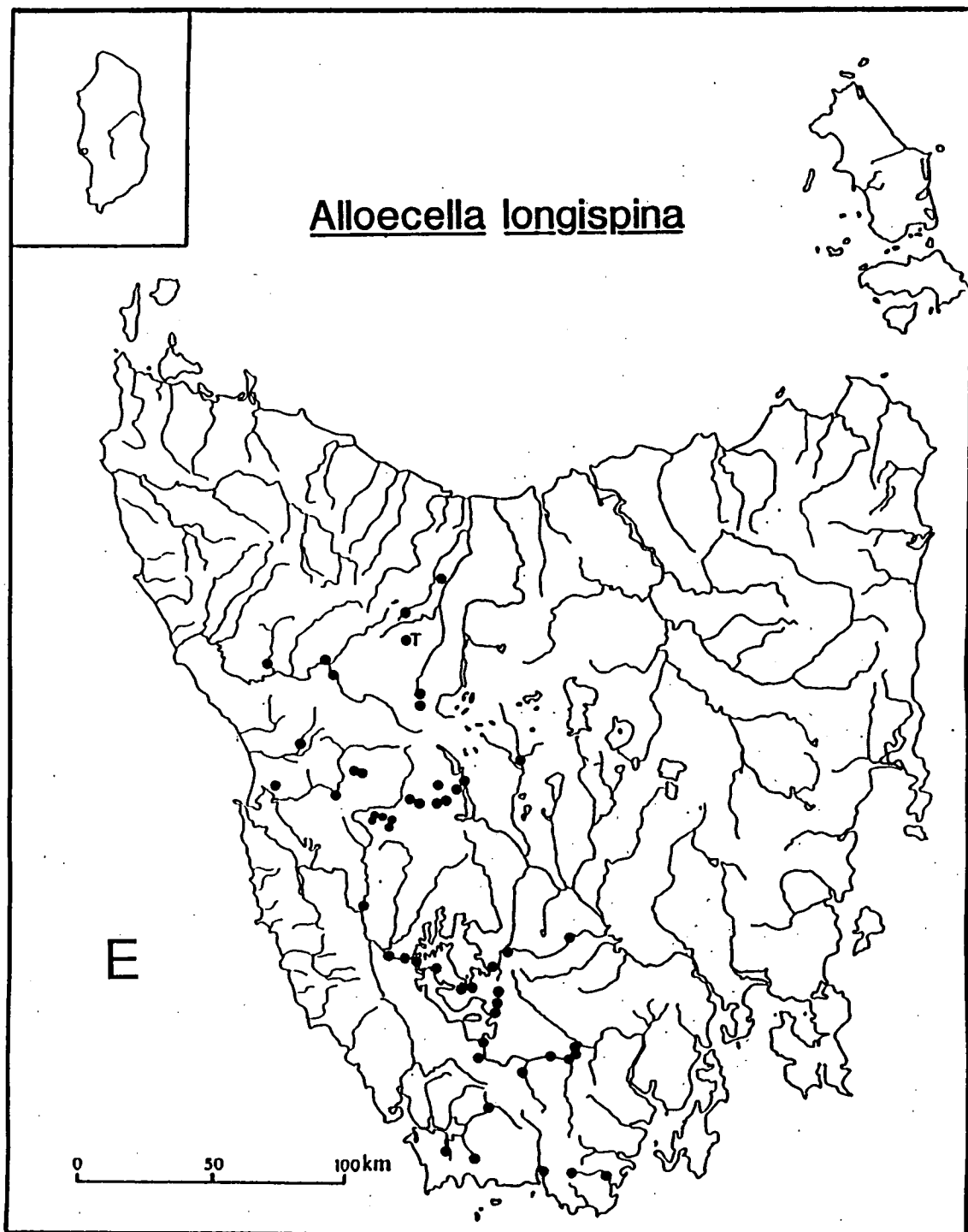
Figure 5.66. Distribution of *Alloecella longispina.*

28 bifid spicules and about 10 single at posterior end, on segments 3-7 band of many single spicules up to 5 wide; segment 2 lacking spicules. Tergite 9 with transverse band of pigmented patches. Anal proleg ventral sclerites pale brown.

Head tapering anteriorly; scars small, rounded, width usually not more than 2x length; no carina; a few long setae scattered on posterior half of dorsum laterad to scars. Ventral apotome anterolateral corners very pointed.

Pronotum in dorsal view broader posteriorly; 2 long pairs of setae on dorsum. Anterior margin with regular row of about 7 pairs of very short, stout setae, slightly longer setae laterally. Anterolateral corner angle obtuse, with stout setae, lateral face setose. Weak carina extending from posterolateral margin about 1/2 way to anterolateral corner; a group of about 4 medium setae at anterior end. Mesonotum anterior margin slightly concave, posterior margin extended; anterior regular row of long setae. Irregular pigmented areas anterolaterally and in centre of each half of dorsum. Metanotum SA1 with single long seta and lateral rounded sclerite; SA 2 with long seta and 2 minute; SA 3 with group of 5 long setae and small sclerite.

Pleural humps with 2 small dorsal setae and single long one.

Pupa

Case posterior membrane a cylindrical tube with thickened margin, projecting from posterior of case. Anteriorly, a thin flexible outer membrane covering thin inner membrane; slit in inner membrane with wider and upturned ends, on dorsal side of membrane. Adhesive stalked discs anteriorly.

Dorsum of pupa with longitudinal rows of sclerotized spots on each side of segment. Dorsal surface of terminal processes with minute pointed flat scales; apices papillate, turned up and slightly out.

Mandibles short, about as long as wide; outer margins slightly curved.

Remarks

Pupates attached amongst liverwort or moss.

Material examined: cleared: 1L 139, 19.ix.88; 2L 150, 27.x.87; 2P 204, 17.xii.87; other: 2L 166, 13.xi.87; 2L 134, 19.ix.88; 2L 150, 11.i.88; 2L 39, 22.ix.88; 2L 151, 27.x.87; 2L 233, 20.x.88; 4L 9, 20.xi.87; 1L 41T, 22.ix.88; 1L 261, 19.ix.88; 1L 164, 14.x.87; 3L 145, 29.i.88; 1P 259, 1.xi.88 em. 16.i.89.

Drawings based on specimens: 1L 139, 19.ix.88; 1L 150, 27.x.87; 1P 204, 17.xii.87.

Distribution (Fig. 5.66). Endemic; widespread in the west; cryptic, apparently not numerous where collected.

Alloecella pilosa Neboiss
(Figs 5.67, 5.68)

Alloecella pilosa Neboiss, 1977, p. 98.

Larva

Case cylindrical, curved, tapered, of relatively large quartzite sandgrains; translucent white. Anterior and posterior margins slightly oblique. Two longitudinal dorsal rows of larger stones sometimes present. Posterior membrane oblique, with
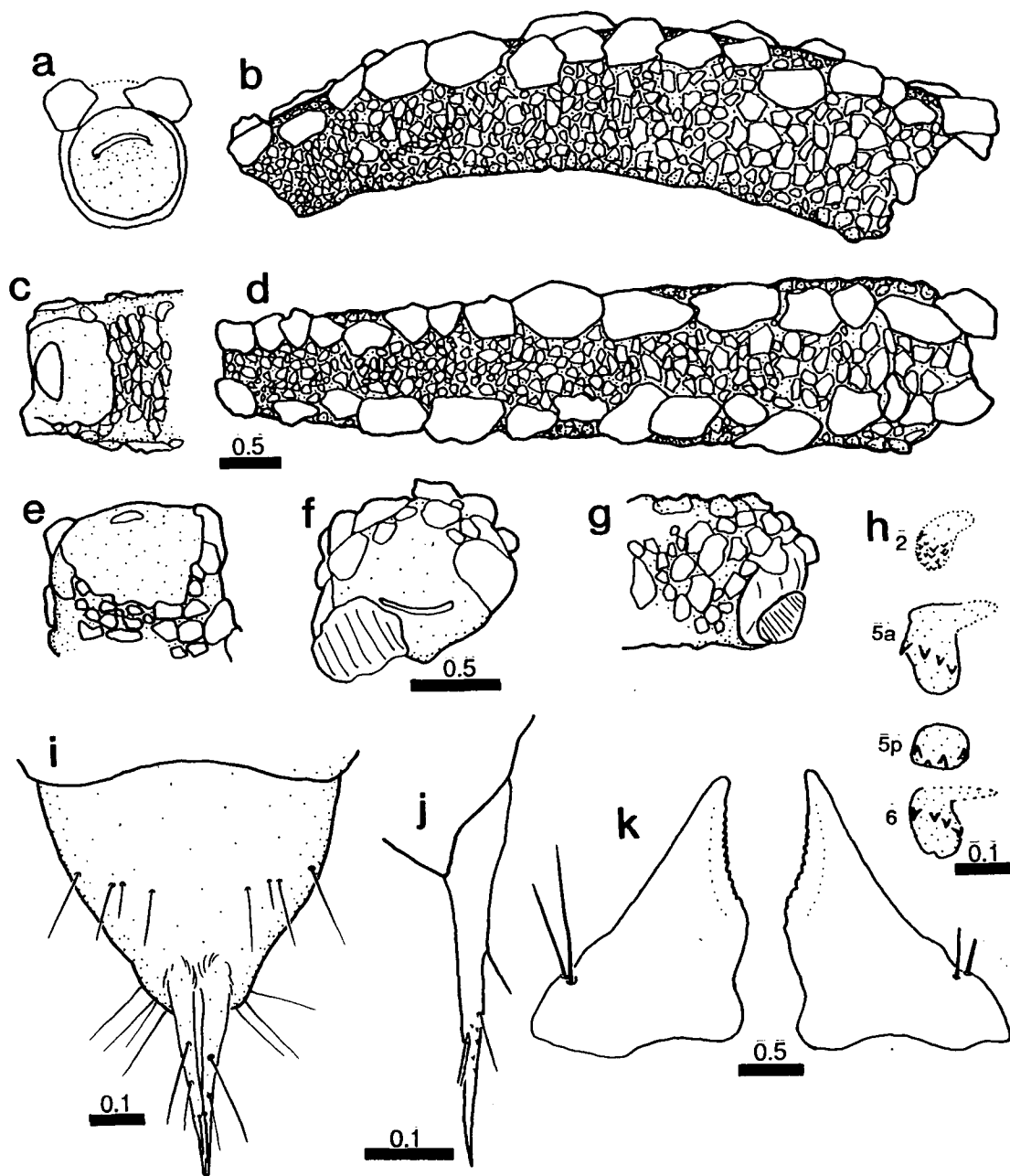
Figure 5.67. *Alloecella pilosa* larva and pupa. **a, b, c, d:** larval case posterior membrane, case lateral, posterior ventral, case dorsal; **e, f, g:** pupal case posterior ventral, anterior membrane, anterior lateral; **h:** hookplates; **i, j:** terminalia dorsal, lateral; **k:** mandibles.

Figure 5.68. *Alloecella pilosa* larva. **a, b, c:** head dorsal, ventral, lateral; **d, e, f:** pronotum, meso- and metanotum, pronotum lateral; **g:** protrochantin.

a

b

0.2

c

d

e

f

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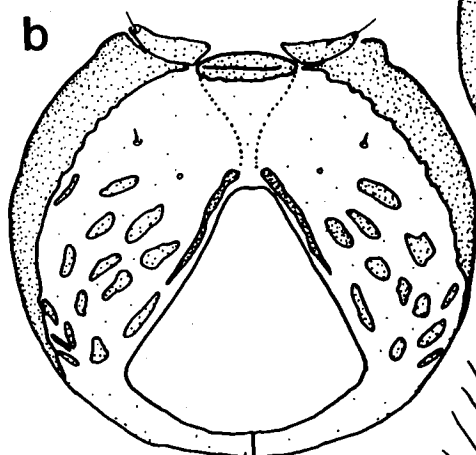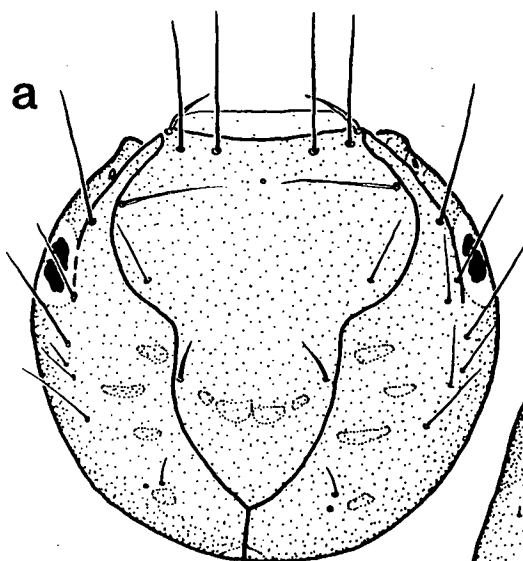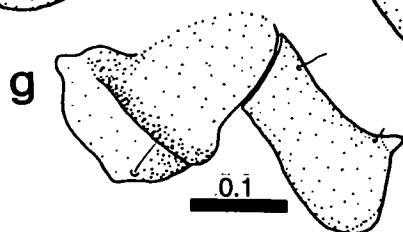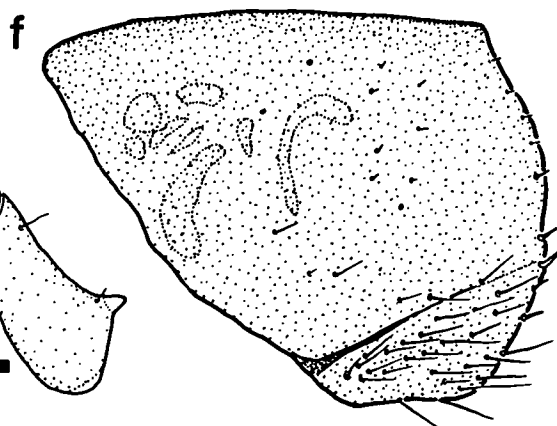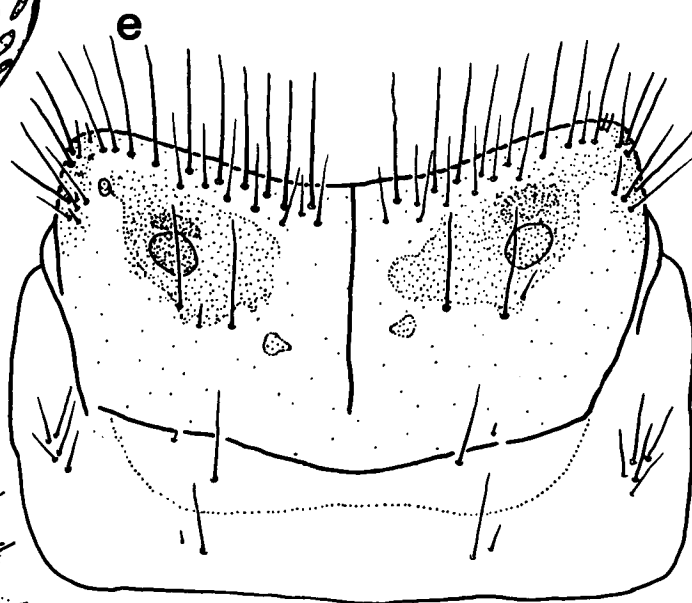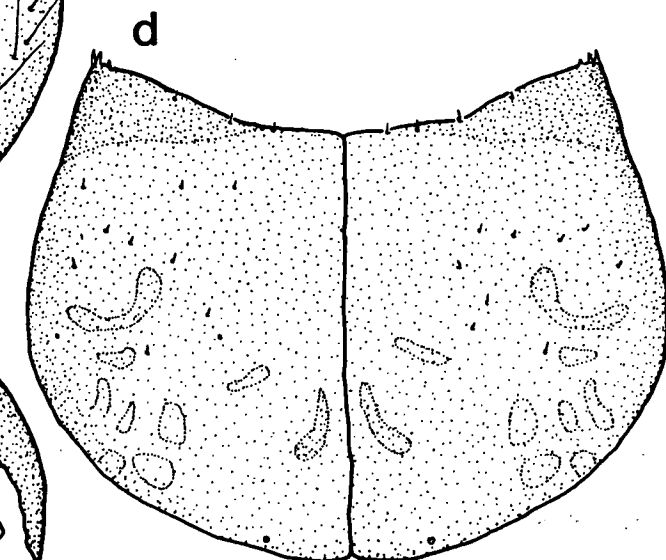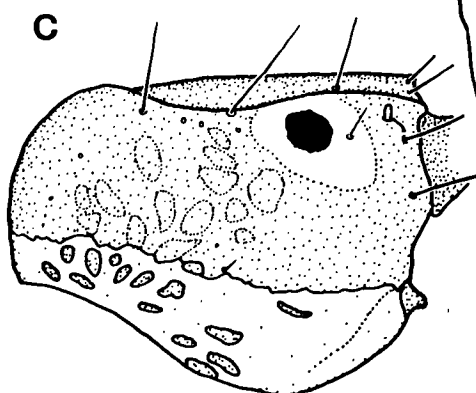
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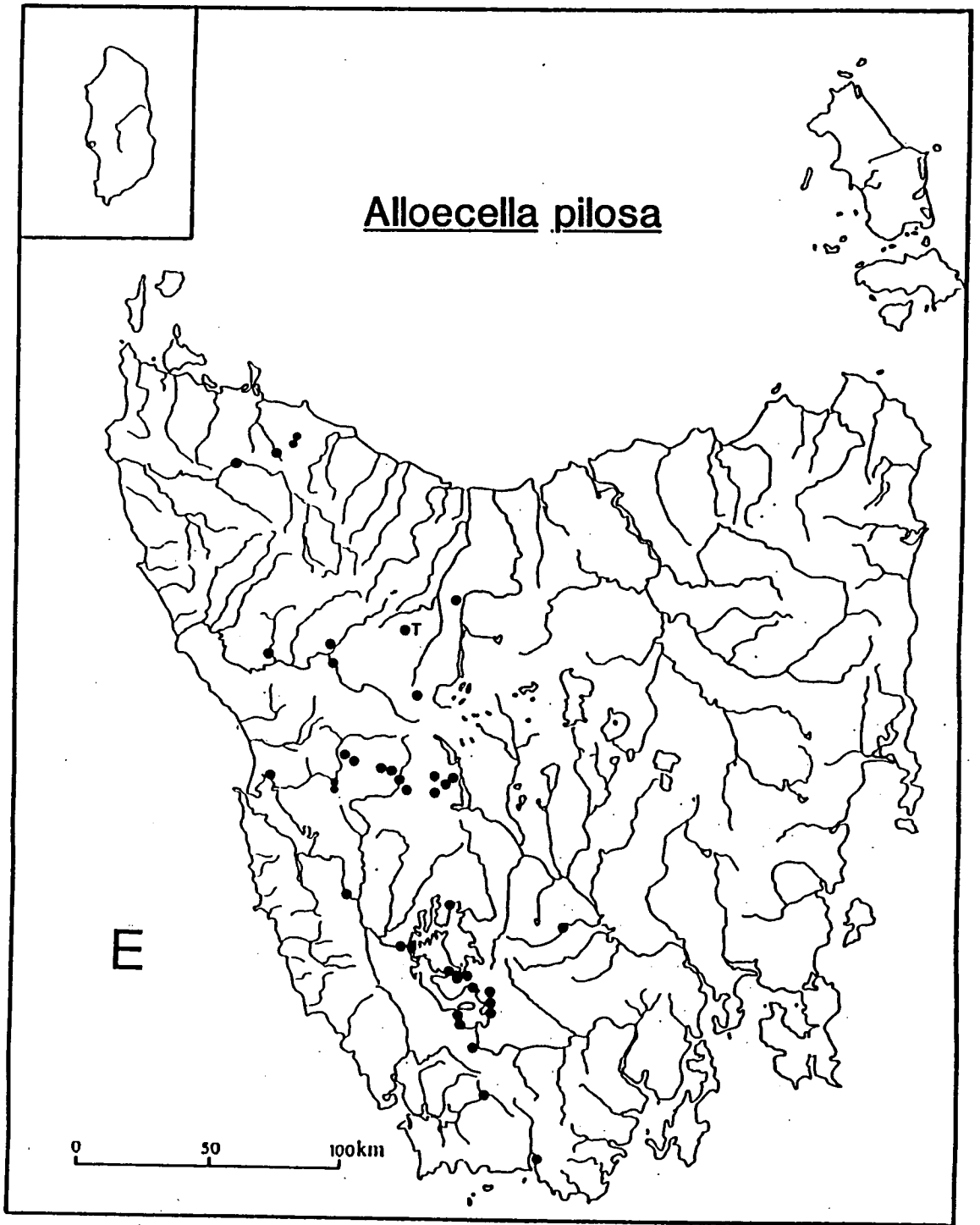
Figure 5.69. Distribution of *Alloecella pilosa*.

hemispherical opening resembling a downward-curved transverse slit from end-on; dorsal membrane overhanging.

Abdomen cylindrical, green; lateral spicules on segment 8 a single row of about 20 bifid spicules, segments 3-7 with band 1-3 wide of about 60 single. Ventral bands of minute elongate spicules on segments 3-7. Tergite 9 unpigmented; ventral sclerite of anal prolegs unpigmented.

Head round in dorsal view, width of scars about 3x length. Strong carina extending from anterior margin to behind eye; posterolateral margin of head capsule raised into bump on each side. Frontoclypeus very broad anteriorly, margins curved out. Ventral apotome anterior margin slightly convex.

Pronotum with dorsal sparsely scattered minute setae. Anterior margin curving slightly forward laterally, forming median concavity. About 5 pairs of widely spaced minute setae on margin, becoming stout and short at anterolateral corner. Anterolateral angle very obtuse, no distinct corner, angle on lateral margin; weak carina extending from posterior margin about 2/3 towards anterolateral corner; lateral face densely setose with medium length setae.

Mesonotum wider than long, irregular areas of pigmentation in centre of each sclerite and anterolaterally; 2 rows of long setae just behind anterior margin, posterior row less stout. Metanotum membranous, short; transverse fold bow-shaped; SA 1 with single seta; SA 2 with 2, long and short; SA 3 with 4-5 long setae.

Pupa

Case with loose stones and domed membrane anteriorly, membrane white with curved slit below centre; posterior membrane oblique, opening of larval case reduced to small oval. Ventral anterior adhesive disc.

Terminal processes smooth, apical margins papillate.

Mandibles short, just longer than wide; outer margin straight, inner distal margin only slightly curved.

Remarks

Pupates under rocks, in rock crevices and amongst moss.

Material examined: cleared: 4L 164, 14.x.87, 1.ix.88; 1L 10, 20.xi.87; 1L 167, 14.x.87; 1P 9, 20.xi.87; 3P 164, 14.x.87; other: 2L 133, 19.ix.88; 1L 142, 19.ix.88; 25L 164,14.x.87, 1.ix.88; 1L 139, 19.ix.88; 1L 109, 20.ix.88; 2L 10, 20.xi.87; 7L 169, 14.x.87, 1.ix.88; 6L 41T, 22.ix.88; 4L 259, 18.viii.88; 4L 136, 20.ix.88; 10L 167, 14.x.87; 3L 9, 20.xi.87, 3P 136, 27.x.87; 1P 10, 20.xi.87. Drawings based on specimens: 2L 164, 1.ix.88; 1P 164, 6.x.87.

Distribution (Fig. 5.69). Endemic: widespread in the west; may be numerous where collected.

Genus **Helicopha** Mosely

Helicopha Mosely in Mosely & Kimmins, 1953, p.148; Neboiss, 1977, p. 94.

Type species: *Helicopha astia* Mosely.

Although adults of *Helicopha* were collected during this study, no larval associations were made.

Distribution. Fig. 5.70. The known distribution of *H. astia* has been greatly
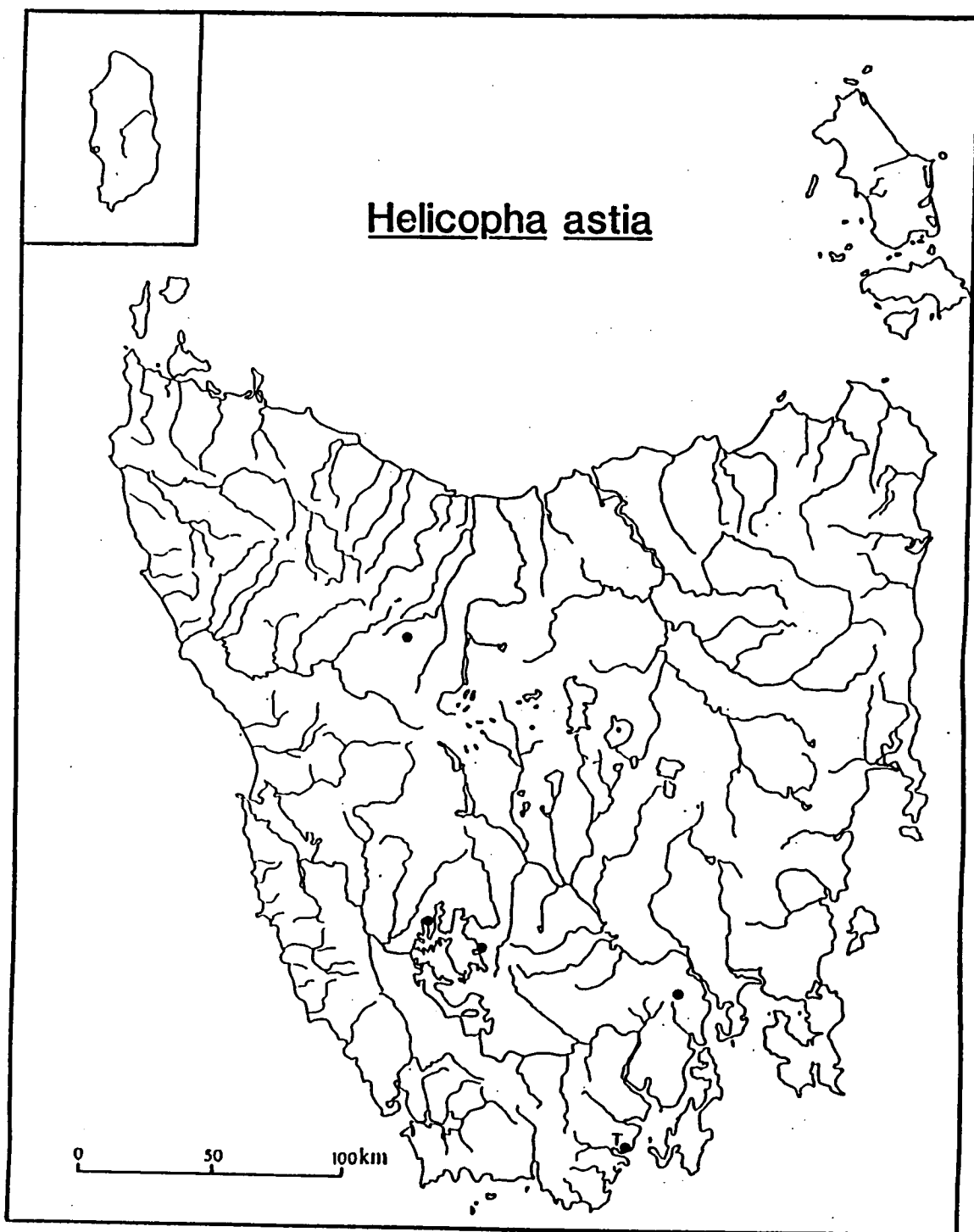
Helicopha astia

Figure 5.70. Distribution of *Helicopha astia*.

expanded from the only previous Tasmanian record at Hythe in the southeast (Neboiss 1977).

5.3.3

Family **CALOCIDAE** Ross (1967)

Neboiss, 1977, p. 89.

Larva

Abdominal lateral fringe absent; segment 8 with lateral row of distinct bifid spicules; ventral bands of minute elongate spicules, no dorsal patches. Tergite 9 pigmentation pale or lacking, posterior row of 5-6 pairs of setae; anal claw with single dorsal accessory hook and about 3 long setae directed inwards; lateral sclerite palely pigmented.

Head ventrally lacking some or most pigmentation; apotome short, genae abutting. Eye bulging distinctly; antennae small, situated just anterior to eye. Frontoclypeus with 1 clear curved and 2 long brown setae in each anterolateral corner.

Mandibles short and stout, each with 2 outer basal setae, long mesal brushes, a few apical teeth; dorsal margin of left bladelike, right with blunt tooth. Labrum rounded quadrate, transverse row of 3 pairs of stout pale setae and central non-setose pit, stout seta on anterolateral margin; anterior margin not indented; long ventral anterolateral brushes.

Metanotum with transverse fold between SA 1 and 2; SA 1 with transverse row of about 8 medium length setae; SA 3 with group of about 8-9 setae.

Protrochantin fused to propleuron, narrow, tapered and upturned to pointed tip.

Pupa

Abdominal gills absent; lateral fringe on segments 6-8 or 7-8. Anterior hookplates roughly oval, anterior margins indistinct, 2-3 hooks; posterior plates rectangular, 3-4 hooks.

Anal opening slit with group of about 7 laterally directed setae each side. Labrum rounded quadrate, slightly broader basally, 2-3 setae in each posterolateral corner. Mandibles each with 2 long outer basal setae, inner distal margin with small serrations.

Midlegs with dense hair fringe on one edge only.

Key to larvae of Calocidae species studied.

1.-Frontoclypeus anterior width >2x wider than posterior
.... *Caenota plicata* [plant panel case]

-Frontoclypeus anterior width ≤ 1.5x posterior width
.... 2

2.-Pronotum smooth, without large anterior setae; head dorsal scars
        narrow.. *Tamasia variegata*
                                                          [sand case]
    -Pronotum spinulose, anterior row of large setae; head dorsal scars   width
        about 2-4 times length.............................*Caloca saneva*
                                                          [sand case]

Genus **Caenota** Mosely

Caenota Mosely in Mosely & Kimmins, 1953, p. 61; Neboiss, 1977, p. 92.
Type species: *Caenota plicata* Mosely.
        Only one species in Tasmania.
                    Caenota plicata Mosely
                        (Figs 5.71-5.73)
Caenota plicata Mosely in Mosely & Kimmins, 1953, p. 61; Neboiss, 1977, p. 92.
Larva
        Case dorsoventrally flattened, dorsal and ventral surfaces each of two regular
rows of roughly circular panels of bark or leaf; anterior panels slightly overlaying
posterior ones, making the case curve; dorsal rows offset from ventral ones. Dorsal
anterior overhang of about 1/2 a panel-width, silk lining extending to anterior edge. No
posterior membrane. Transversely adjacent panels usually of the same material.
        Abdomen slightly dorsoventrally flattened; small single gills present: on segment
2 anteroventral, posterolateral and ventral; on segment 3 anterolateral and ventral.
About 50 lateral spicules on segment 8, on segments 3-7 a row of about 30 single.
Segment 1 lateral hump prominent, with large oval area of very dense spines.
        Tergite 9 sclerite single, pigmentation pale; posterior row of 5 pairs of setae, 2
pairs long. Anal proleg lateral sclerite mostly unpigmented; densely setose with large
dark setae in posterior area; ventral sclerite a pale brown bar, broadening medially.
        Head round in dorsal view, very dark brown, dorsal muscle scars golden and
distinct, small and thin; regular polygonal reticulate texture. Distinct carina absent, but
slight ridge on dorsum along anterior lateral margins of frontoclypeus. Frontoclypeus
very broad anteriorly; about 4 irregular apical scars; 3 lateral pairs of setae: mid pair at
widest point stout and short, posterior pair small.
        Head laterally with 2 long setae near anterior margin; area of scars behind eye.
Ventral head lacking median pigmentation, dark scars near occipital margin and pale
scars in pigmented area; anterior to scars a pair of non-setose pits, 1 each side of
pigmentation line.
        Pronotum scars indistinct, median scar longitudinal, elongate, elongate scar
diagonal to it, posterolateral scars rounded; anterior margin with row of small fine
setae and regular row of large setae alternately pale and dark; mid transverse band of
dark setae, a few fine setae anterior to band. Anterolateral corner rounded, angle
square; lateral carina lacking, anterolateral area folded under.
        Mesonotum entirely sclerotised and pigmented palely; scars small, in oval pattern

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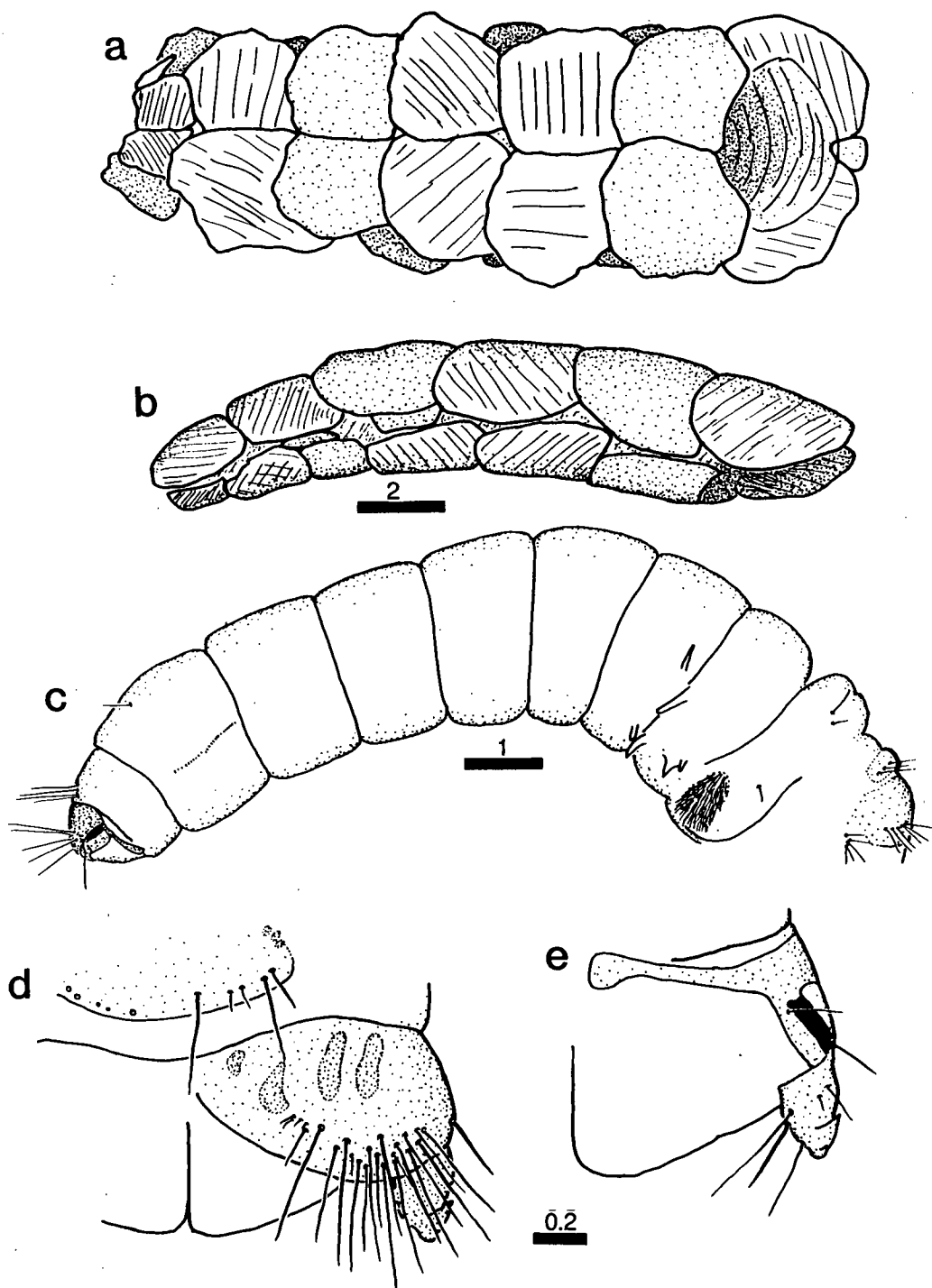
Figure 5.71. *Caenota plicata* larva. **a, b:** case ventral, lateral; **c:** larva, lateral; **d, e:** anal legs dorsal, ventral.

Figure 5.72. *Caenota plicata* larva. **a, b, c:** head dorsal, ventral, lateral; **d:** protrochantin; **e, f, g:** pronotum lateral, pronotum dorsal, meso- and metanotum; **h:** mandibles, dorsal.

a

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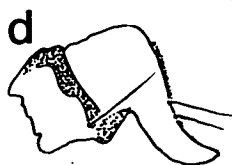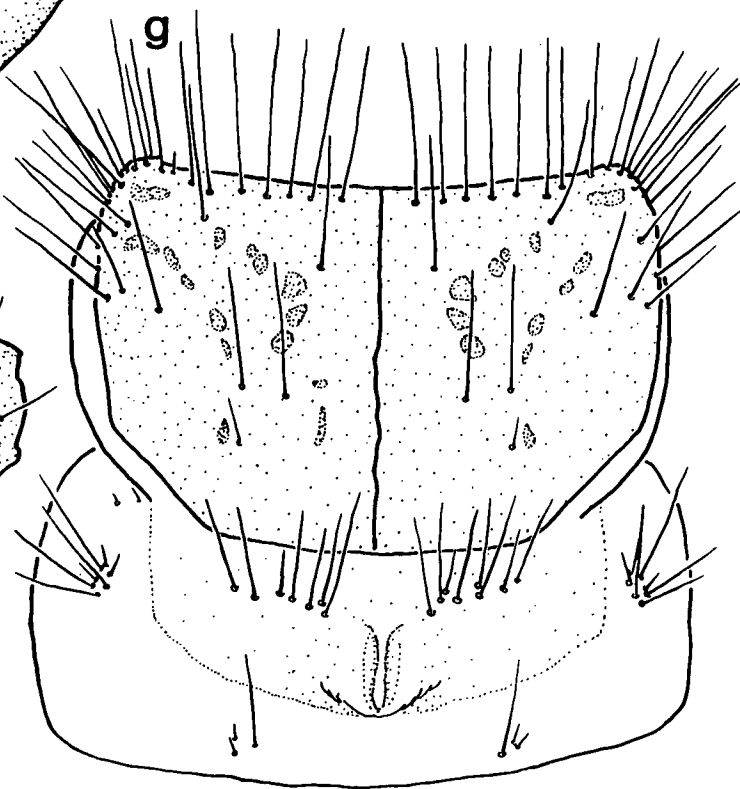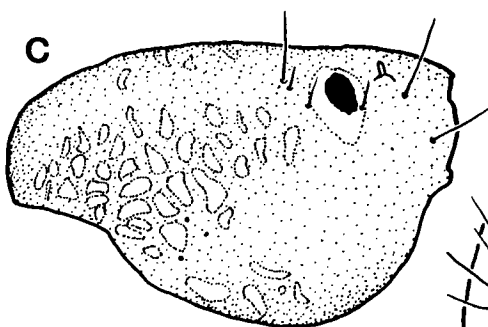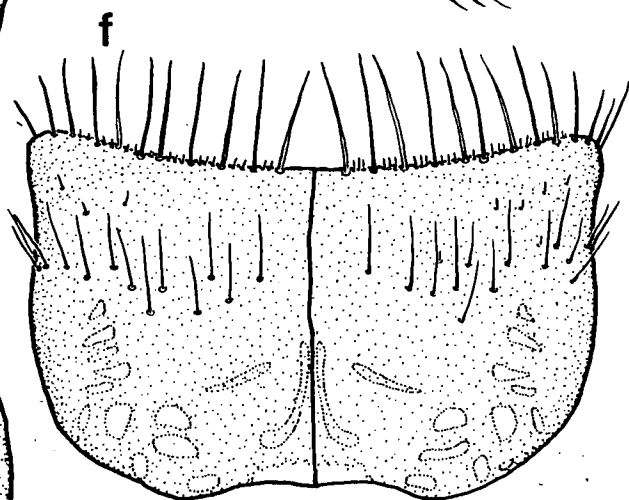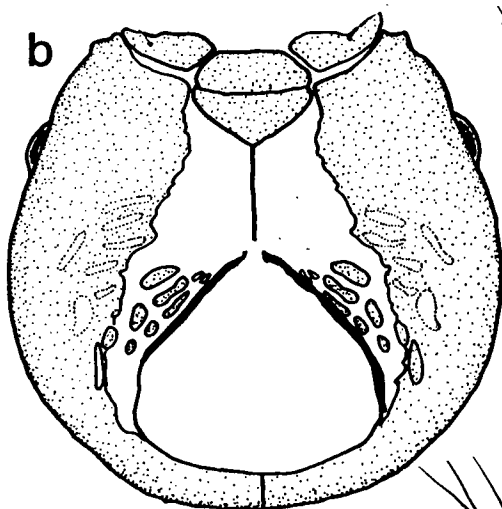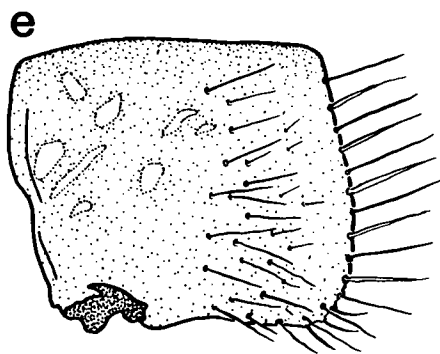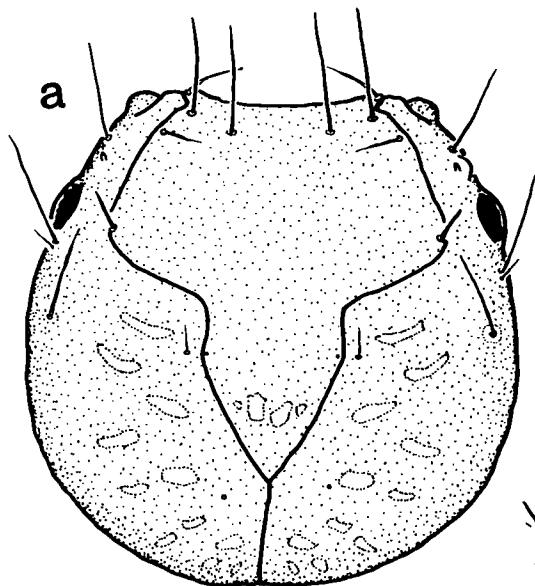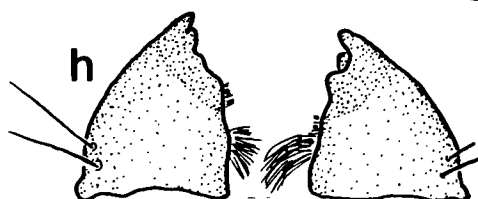
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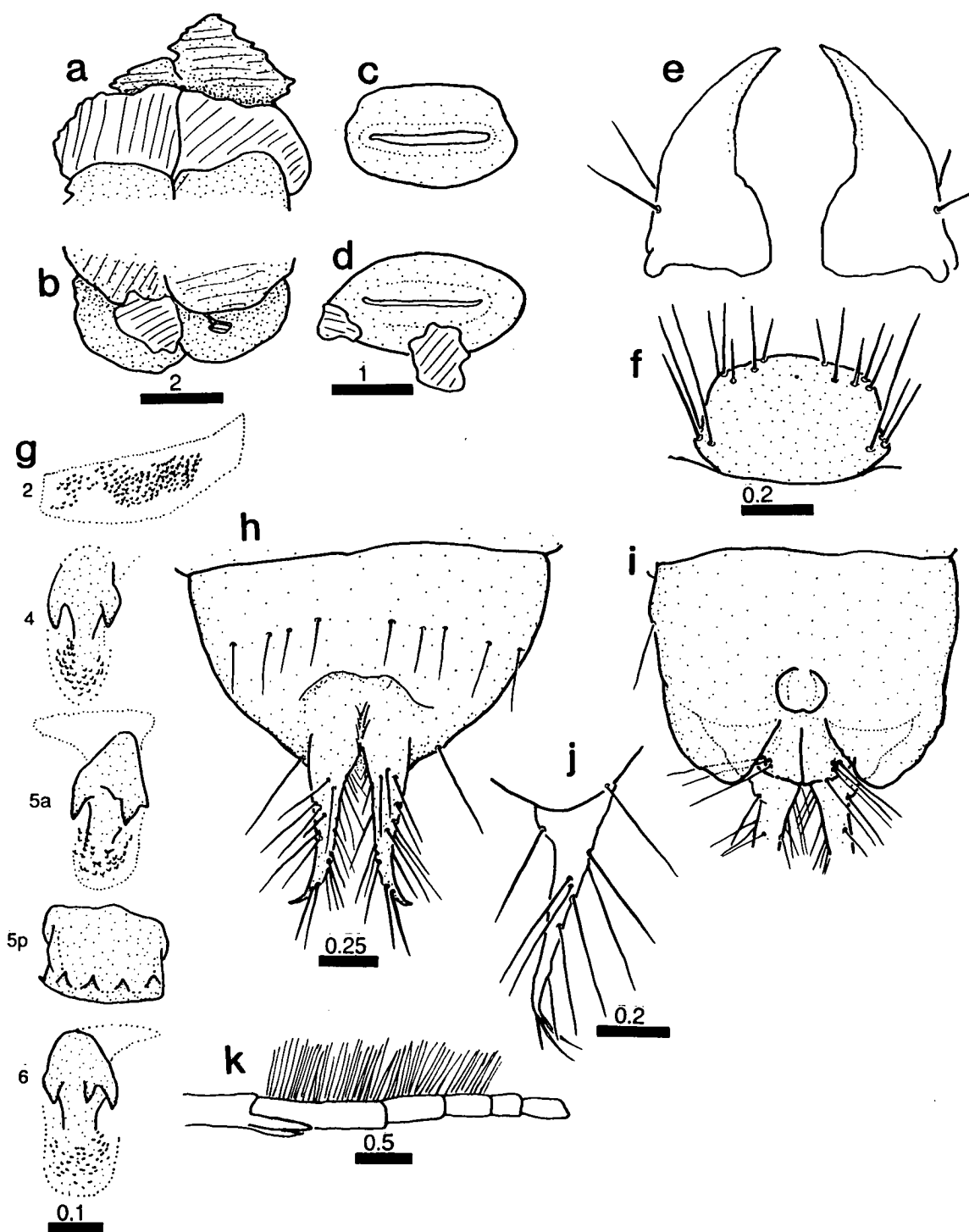
Figure 5.73. *Caenota plicata* pupa. **a, b, c, d**: case anterior ventral, posterior ventral, anterior membrane, posterior membrane; **e**: mandibles; **f**: labrum; **g**: hookplates; **h, i, j**: ♂ terminalia dorsal, ventral, process lateral; **k**: midleg fringe.
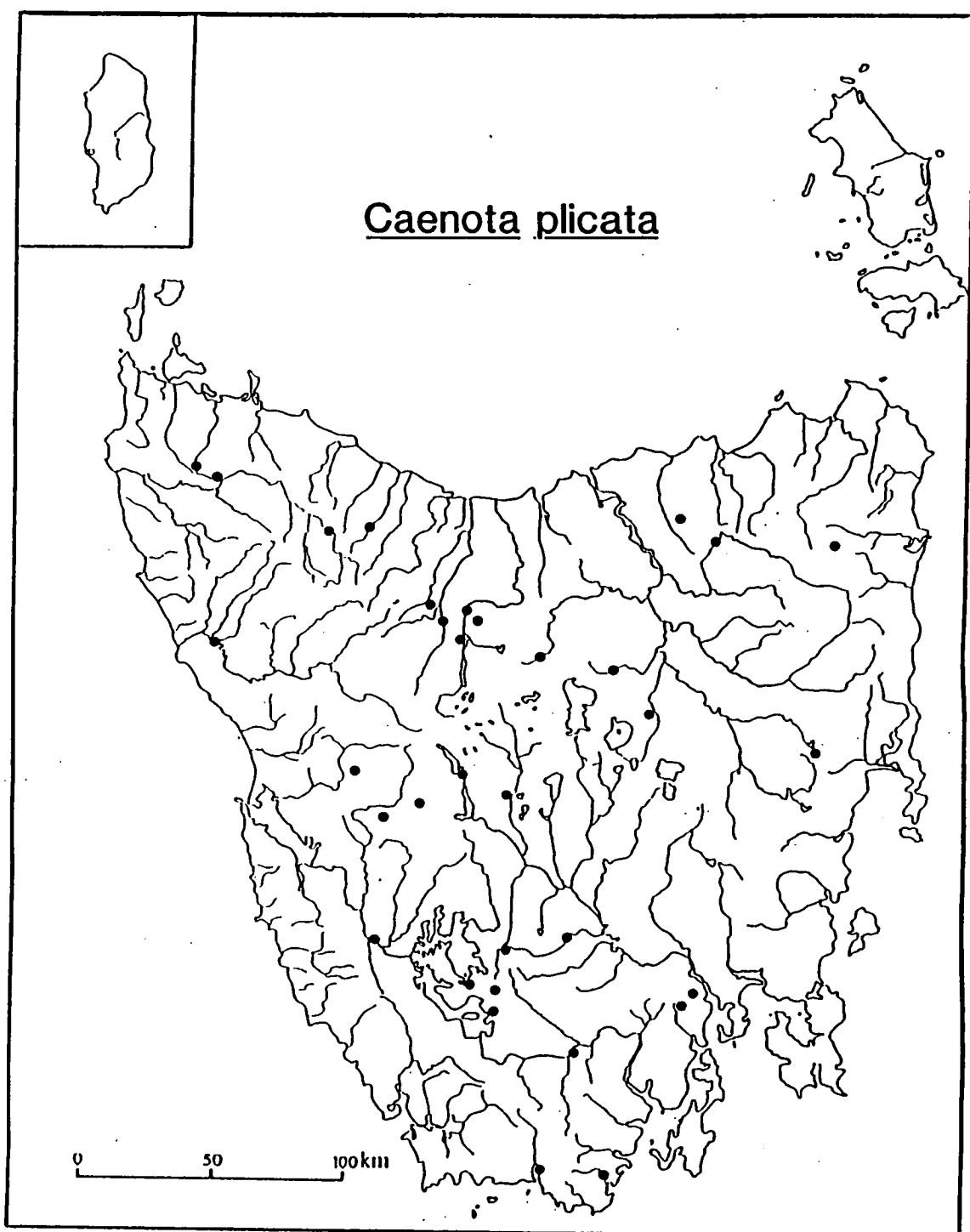
Figure 5.74. Distribution of *Caenota plicata*.

on each side; anterior margin with regular row of long dark setae, anterolateral area densely setose, 2 central pairs of long dark setae. Mesonotum with a central hump with longitudinal ridge sclerite, pigmentation very pale; SA 2 with 1 long and 2-3 small setae.

Protrochantin anterior margin with dense minute setae, 2 longer setae.

Pupa

Case constructed from larval by addition of perpendicular membranes to anterior and posterior; both oval with central transverse slit. Several small stalked adhesive discs posteriorly.

Segment 2 with anterior low hump, minutely toothed, width about 3x length. Dorsum of segment 9 with transverse row of 5-6 pairs of dark setae; ventrally in M, central round hump and large lateral fleshy processes. Terminal processes not heavily sclerotized, length $\leq$ length of segment 9; tapering evenly to apex, apices pointed and curved slightly out and up; margins smooth; setose dorsally, pair of thick dark setae arising subapically from inner margin.

Labrum with about 5 pale, stout, short setae in each anterolateral area. Mandibles stout, basal width about 1/2 length; broad basally then constrict almost 1/2 way along, tapering and curving to pointed apices.

Remarks

Found in litter accumulations in streams and rivers, usually in slower flowing sections. Pupates under rocks or on other substrates such as sticks.

Material examined: cleared: 5L 223, 9.vii.87; other: 20L 223, 8.vi.87; 2L 70, 18.xi.88; 1L 169, 1.ix.88; 2L 99, 23.iii.87; 5L 219, 30.iv.87; 3L 13, 17.ix.86; 1L 193, 16.ii.88; 2L 282, 11.xi.87; 2L 64, 22.xi.87; 5L 223, 5.viii.87; 2L 133, 31.x.88; 1P 171, 7.xii.87; 2P 223, 25.viii.87. Drawings based on specimens: 2L 223, 9.vii.87; 1P 223, 3.i.87.

Distribution (Fig. 5.74). Tasmania and SE Australia; widespread within Tasmania; may be numerous where collected.

Genus **Caloca** Mosely

Caloca Mosely in Mosely & Kimmins, 1953, p. 153; Neboiss, 1977, p. 90;

Tismana Mosely in Mosely & Kimmins, 1953, p. 65. Synomymised by Neboiss 1977.

Type species: *Caloca straminea* Mosely.

Caloca saneva (Mosely)

Tismana saneva Mosely in Mosely & Kimmins, 1953, p. 65; Jacquemart, 1965, p. 3; Neboiss, 1977, p. 91.

Larvae and pupae are described and figured by Neboiss (1979).

Distribution (Fig. 5.75). Endemic; fairly widespread but few localities; apparently not numerous where collected.

Remarks

Terrestrial, collected amongst leaf litter (Neboiss 1977), also from cave wall near entrance (S. Eberhard pers. comm.). Adults have been collected flying during the day outside a cave entrance, where it was cool and damp.
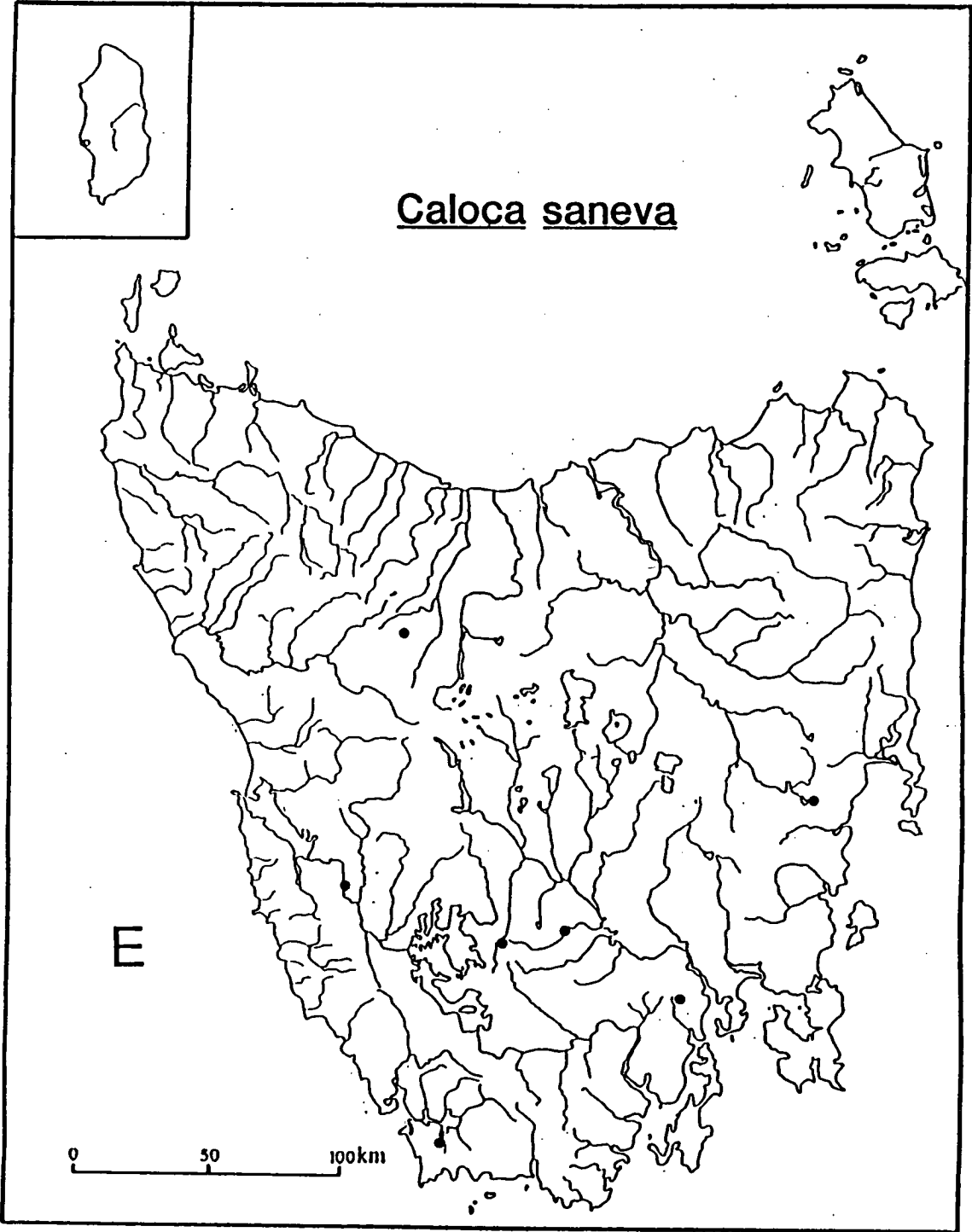
Figure 5.75. Distribution of *Caloca saneva*.

Larvae were not associated with adults for any other Tasmanian *Caloca* species.

Caloca tertia Mosely
Caloca tertia Mosely in Mosely & Kimmins 1953, p. 156.
Distribution (Fig. 5.76). The distribution of *Caloca tertia* has been expanded from the previously known range, at Mt Wellington.

Genus **Tamasia** Mosely
Tamasia Mosely, 1936, p. 399; Mosely & Kimmins, 1953, p. 56; Neboiss, 1977, p. 93.
Type species: *Tamasia variegata* Mosely.
Only one species in Tasmania.
Tamasia variegata Mosely
(Figs 5.77-5.79)
Tamasia variegata Mosely, 1936, p. 401; Mosely & Kimmins, 1953, p. 57; Jacquemart, 1965, p. 5; Neboiss, 1977, p. 93.
Larva

Case of irregularly arranged sand grains; cylindrical, curved and slightly tapering posteriorly; anterior margin straight; posterior margin straight, membrane with pointed projections into circular opening.

Abdomen cylindrical, gills absent; segment 8 with single lateral row of about 60 bifid spicules, segments 3-7 with row of 40-60 single on posterior of segment. Segment 1 dorsal hump low, lateral hump with oval sclerite of spines. Tergite 9 without visible sclerite. Anal prolegs ventral sclerite unpigmented, straight bar.

Head dark brown, dorsal scars golden and distinct, anterior ones thin; dorsum and upper lateral areas densely spinulose; few large setae. Strong carina extending from anterior margin of head capsule to anterior of eye. Frontoclypeus only slightly wider anteriorly than posteriorly, anterior lateral margins almost straight. Ventral head mostly lacking pigmentation, anterior to scars on each side a non-setose pit and small pale seta.

Mandibles longer than wide, length variable.

Pronotum scars mostly dark, 1 median elongate and 1 diagonal; anterior 2/3 densely covered with short setae, less dense laterally; anterior margin curving forwards near anterolateral corner; entire margin with row of very short stout brown curved setae, lengthening at corner. Anterolateral corner projected slightly forward, angle obtuse, marginal very stout dark setae. Strong carina extending from corner straight back for about 2/3 of pronotum length, before turning dorsad at end; regular row of medium length setae along carina. Lateral face flat, with scattered pale setae.

Mesonotum entirely sclerotised, pigmentation even or posterior 1/4 pale; regular row of short-medium setae along anterior margin, anterior 2/3 with scattered setae; darker scars in central and anterolateral area. Metanotum SA 1 with median seta behind anterior row; SA 2 with single seta.

Pupa

Case closed anteriorly with dorsal flap folded down to meet extended ventral
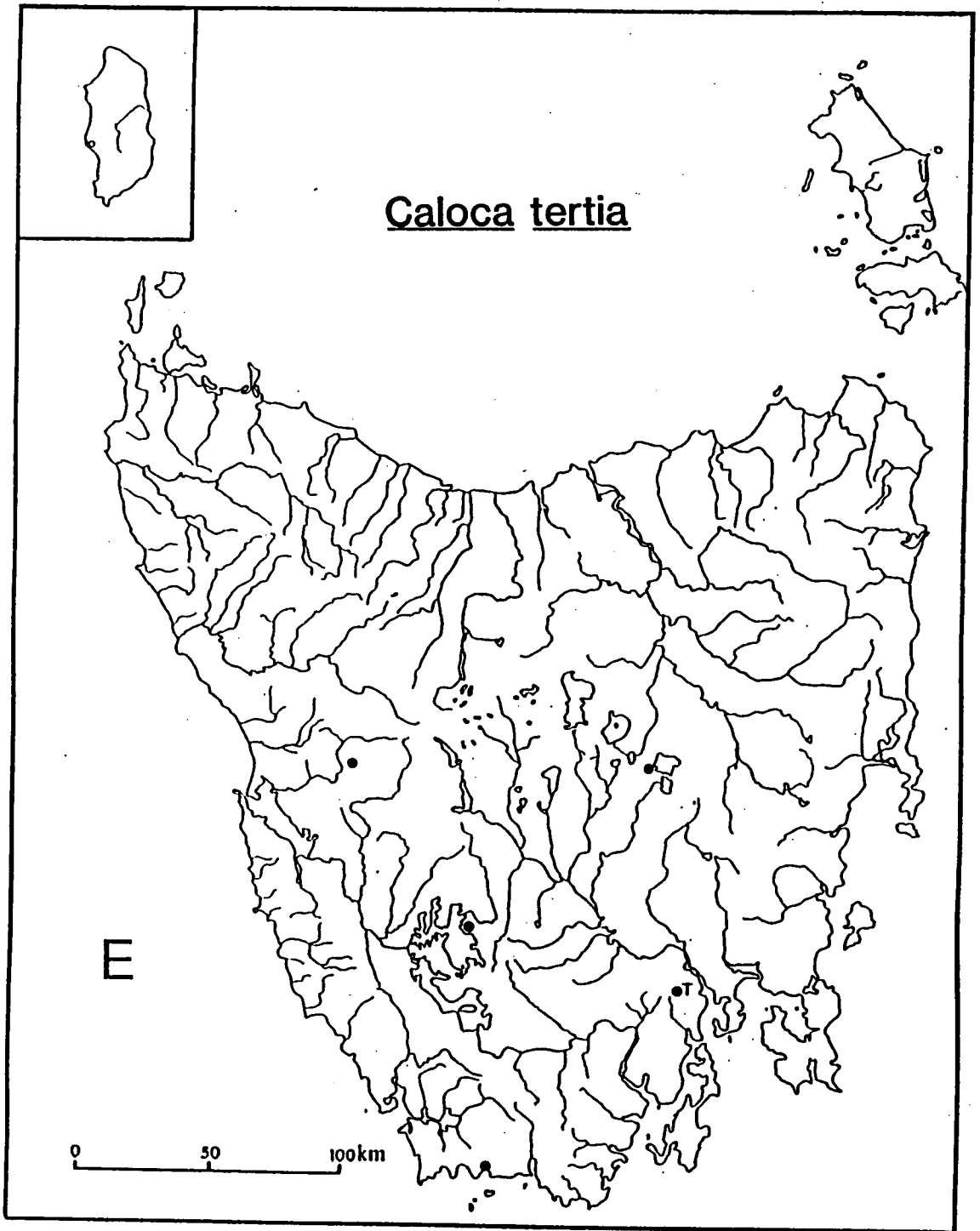
Figure 5.76. Distribution of *Caloca tertia*.
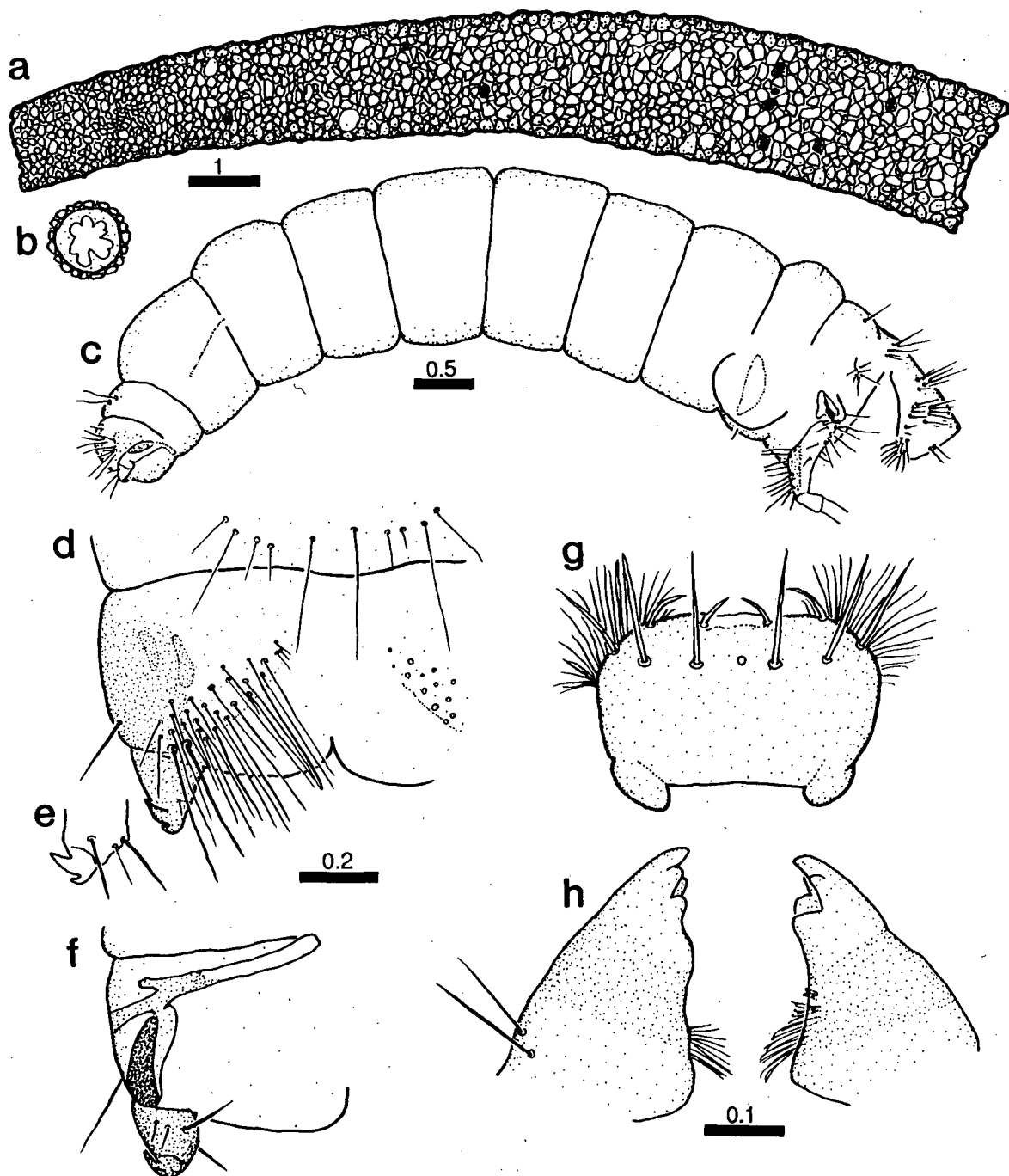
Figure 5.77. *Tamasia variegata* larva. **a, b:** case lateral, posterior membrane; **c:** larva, lateral; **d, e, f:** tergite 9 and anal legs dorsal, claw ventral, leg ventral; **g:** labrum; **h:** mandibles, dorsal.

Figure 5.78. *Tamasia variegata* larva. **a, b, c:** head dorsal, lateral, ventral; **d, e:** pronotum, meso- and metanotum; **f:** protrochantin; **g:** pronotum, lateral.

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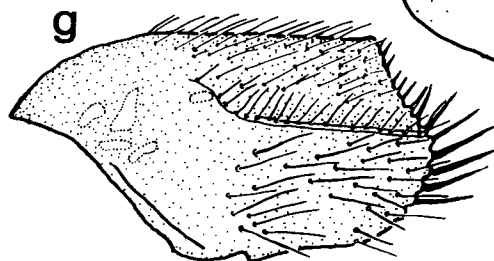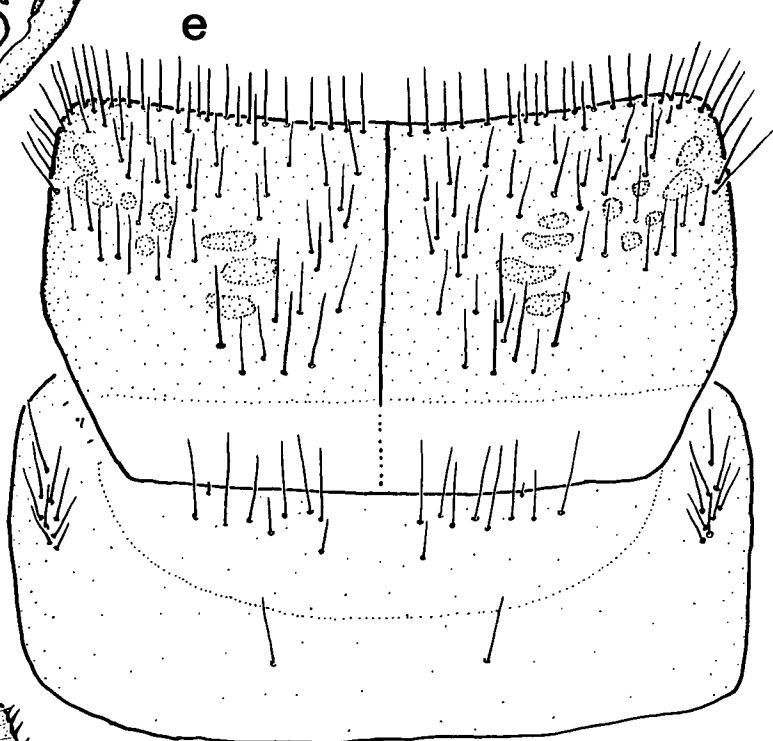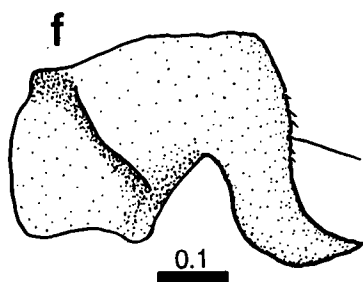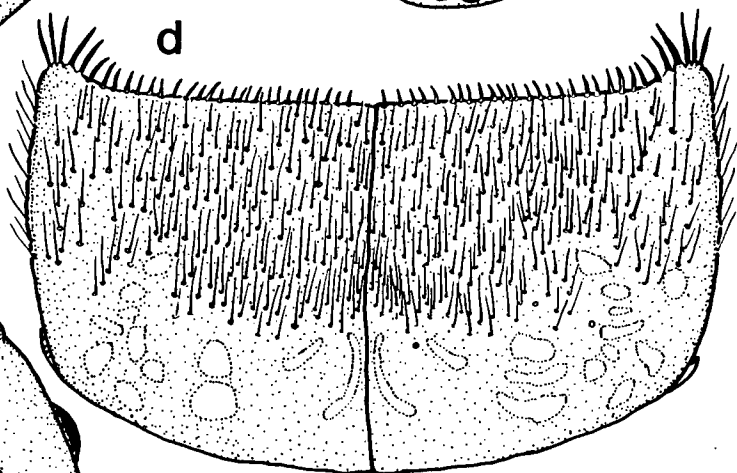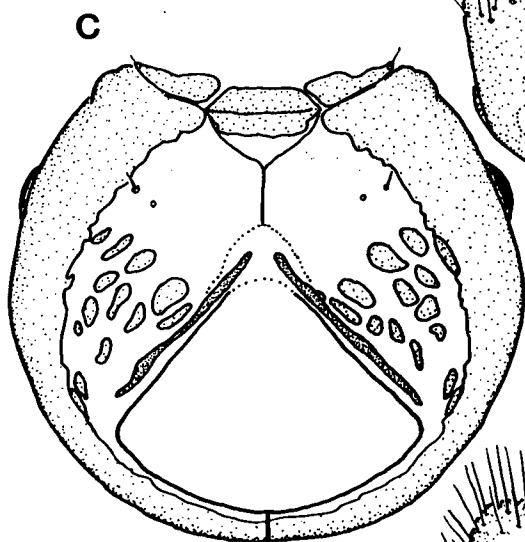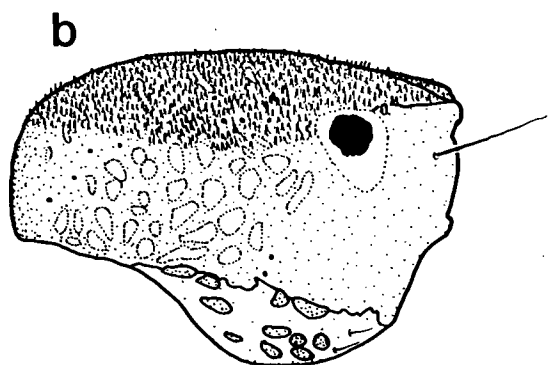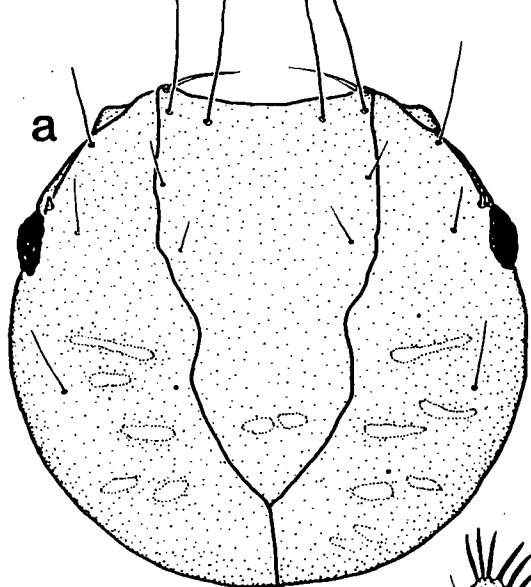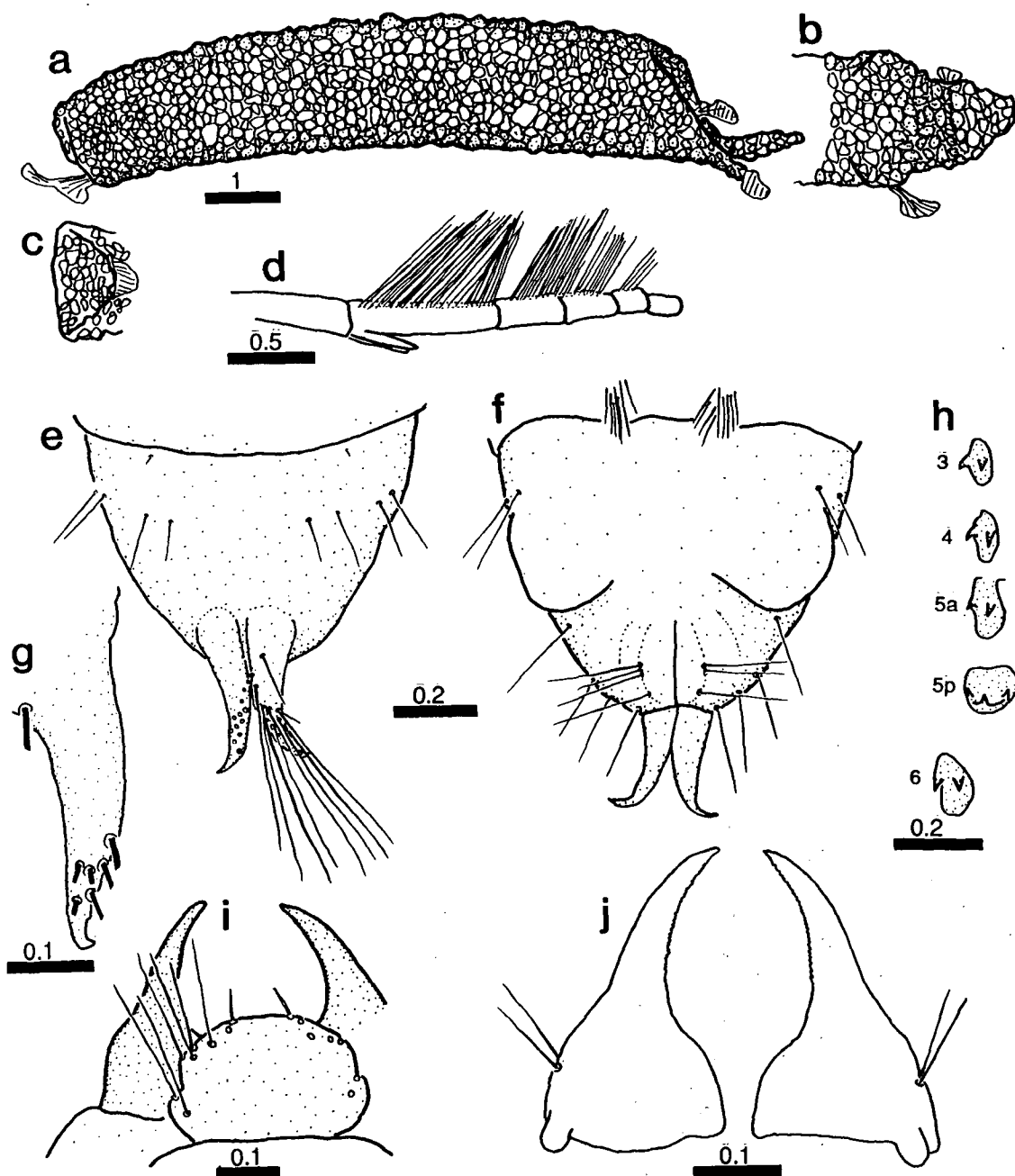
Figure 5.79. *Tamasia variegata* pupa. **a, b, c:** case lateral, anterior dorsal, posterior ventral; **d:** midleg fringe; **e, f, g:** ♂ terminalia dorsal, ventral, process lateral; **h:** hookplates; **I:** labrum; **J:** mandibles, ventral.

margin, flap turning up distally leaving narrow ventral opening; posterior closure a dorsal triangular flap folded down, posteroventral membrane with transverse slit, membrane only just exposed. Several adhesive discs anteriorly, large ventral disc posteriorly.

Segment lacking toothed hump. Terminal processes short and stout, apices tapering and curved out and up; distal dorsal area with dense stout long black setae forming brush.

Mandibles very broad at base (bulbous), strongly constricted to slender distal 2/3, curved and tapered to apices; inner margin minutely serrate. Labrum wider basally, lateral margins "stepped in"; about 6 stout long setae in each anterolateral area.

Remarks

Found in leaf litter, sand and root mats, in slower flowing regions of streams and large rivers. Pupates in crevices in wood or rocks, or in roots.

Material examined: 5L 132, 27.x.87; 2L 250, 22.ii.88; 2L 279, 2.xi.87; 1L 257, 4.xi.87; 2L 64, 22.xi.87; 1L 22, 1.ix.88; 1L 233, 25.viii.88; 2L 92, 5.ii.88; 5L 229, 25.i.88; 3L 193, 16.ii.88; 2L 281, 11.xi.87; 1L 181, 3.vii.87; 5L 223, 4.ix.87; 1P 216, 26.xi.87; 3P 14, 21.xi.87; 2P 281, 11.xi.87; 1P 278, 2.xi.87 em. 25.xi.87; 1P 257, 4.xi.87. Drawings based on specimens: 1L 259, 3.vii.87; 1L 223, 4.xi.87; 1P 29, 21.ix.88.

Distribution (Fig. 5.80). Tasmania and SE Australia up to Qld; widespread in Tasmania; often numerous where collected.
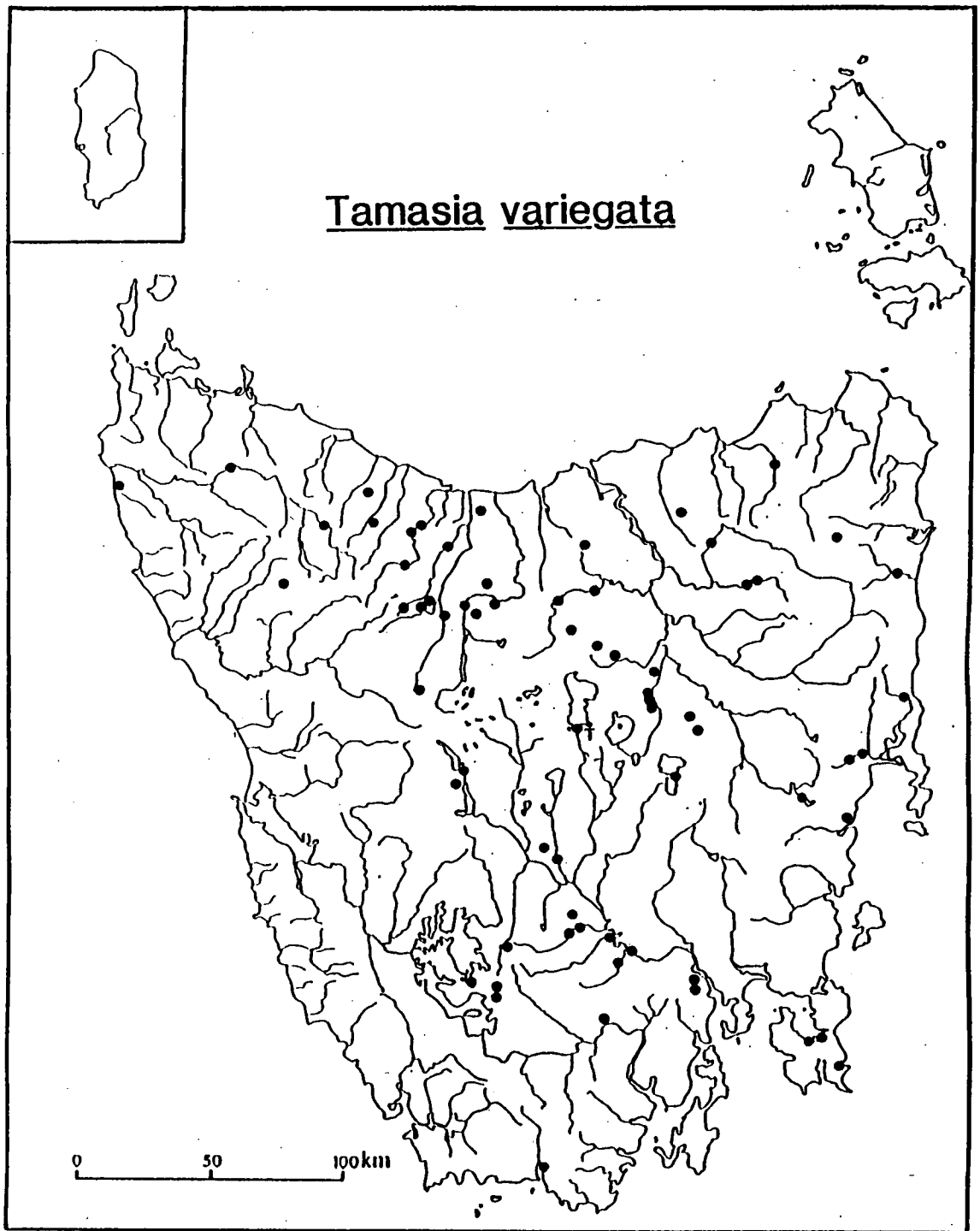
Figure 5.80. Distribution of *Tamasia variegata*.

5.4 DISCUSSION

5.4.1 Taxonomy

These keys and descriptions allow specific identification of immatures of Tasmanian Conoesucidae for the first time. For Helicophidae and Calocidae, however, larvae were not associated with adults for all species, and therefore keys are incomplete. Larvae are known for all three Tasmanian genera of Calocidae, but the larvae of *Helicopha* remain unknown.

The recent key to families by J. Dean & D. Cartwright (pers. comm.) is workable for all the identified Australian larvae. The separation of Conoesucidae from Calocidae and Helicophidae on the basis of ventral apotome shape is sound. However, the separation of Helicophidae from Calocidae on the basis of antennal position alone is inadequate, as this character state can be difficult to determine (*Pycnocentrella* from New Zealand does not appear to fit the key), and unidentified larvae from the mainland that key to Helicophidae/Calocidae have antennae near the anterior margin of the head capsule and thus do not fit the key. Additional characters found to separate Calocidae and Helicophidae in this study have been added to the key. Nevertheless, their separation remains somewhat unclear (see ch. 6), and the additional characters may prove not to be useful when larvae of more species are known.

Winterbourn & Gregson (1981) give a key to families for New Zealand species based on the single species of calocid and 2-3 species of helicophid occurring there, which is not useful for Australian representatives of these families. They separate Calocidae from Helicophidae and Conoesucidae on the basis of the larger accessory hook on the anal proleg claw in calocids, but in Australian Helicophidae this hook is also large and raised; also, Australian helicophids may not have the metanotal pigmented patches that Winterbourn & Gregson use to separate them from Conoesucidae, and they have only a single anteromedian seta on each side, not several as in New Zealand species.

The first key to Australian larvae of these families, which are not separated in the key of Williams (1980), was given by Drecktrah (1984), based on a few Australian larvae and New Zealand larvae described by Cowley (1978). Drecktrah separates Conoesucidae and Calocidae on the basis of antennal position, which does not hold for some undescribed mainland larvae, and the number of setae on SA 1, which does not hold for *Conoesucus norelus*. The lateral band of spicules in *Alloecella grisea*, which Drecktrah suggests may separate Helicophidae from the other families, is not characteristic of the helicophids: *Alloecella pilosa* and *A. longispina* both have a single row of spicules, like most calocids and conoesucids.

The only other published information on Australian larvae of these families is by Neboiss (1988), who gives brief family descriptions of larvae. Again, these are based on limited information, and are inaccurate for some characters. Some conoesucid species have more than two metanotal anteromesal setae (*C. norelus* has many spine-like setae; others have up to 3 small setae in addition to easily visible setae); *Lingora*

spp. have a sparse band of lateral spicules on segment 8 two wide, rather than a "lateral row". In Calocidae, gills are present in at least *Caenota plicata*. Some helicophid species lack the head carina described by Neboiss, metanotal sclerites may be absent, segment 8 lateral spicules may be a single row, a tergite 9 sclerite is present, its pigmentation varying with species.

The diagnostic characters so far established for families and genera will be tested when more larvae are associated with described adults, and more new species are discovered.

5.4.2 Distribution.

The science of biogeography aims to elucidate the geographical distributions of organisms, and the historical and biological factors which have caused them (Simpson 1978). The phylogenetic relationships and patterns of distribution of the organisms are examined in relation to the geological history of the regions where they occur (Platnick & Nelson 1978), and ecological factors must also be considered, to avoid spurious historical explanations (Endler 1982). The following discussion of the biogeography of the groups studied, particularly of worldwide distribution, is based on the limited information available, which is not sufficient for detailed rigorous analysis.

Within Australia.

Like several other animal groups, the Trichoptera studied show high Tasmanian endemicity at the species level, with 14 of 17 conoesucids, 2 of 3 helicophids and 1 of 3 calocids being endemic. Endemicity of all Tasmanian Trichoptera is about 75% (Neboiss 1977), and some other groups found to show high endemicity include Plecoptera (Hynes & Hynes 1980, Hynes 1989), Ephemeroptera (Campbell 1981), Diptera (Zwick 1977), terrestrial amphipods (Friend 1980, 1987), freshwater crustacea (Williams 1974a), burrowing crayfish *Engaeus* (Horwitz 1990) and Psephenidae (Davis 1985). Reasons for this high endemicity are likely to include Tasmania's isolation from the Australian mainland, and unique ecological conditions resulting from climatic and physical characteristics. Generic endemicity is much lower, which may indicate the broad timescale of speciation events in relation to isolation events, i.e. genera differentiated before there was any barrier between Tasmania and the mainland.

Bass Strait has been a barrier to many groups for a long time, despite repeated land connection. It was dry several times during the Pleistocene, when periods of glaciation caused lowering of sea level (Galloway & Kemp 1981, Blom 1988, Hope 1989). The climate during these periods was dry, and during the last connection which ended about 10,500 years B.P. (Blom 1988, G. J. Jordan pers. comm.), the Bassian Isthmus was arid (Hope 1978, 1984) and conditions likely to be unfavourable for aquatic and forest-dependent animals (Hynes & Hynes 1980, Friend 1987). Although De Deckker (1986) has suggested that a chain of lakes along the coast at the height of the last glacial provided a refuge for much of the aquatic biota, such habitat would have been unsuitable for species dependent on cool, fast water, such as those studied. However, even a flooded Bass Strait is not an effective barrier to all insect species, e.g. pest species such as noctuid moths and locusts migrate across it (Drake *et al.*

1981).

Despite the Bass Strait barrier, there are some shared species in the groups studied. Either they originated in Tasmania or the mainland, and subsequently dispersed across Bass Strait or the isthmus, or they were formerly widespread in the two areas and have maintained their specific identity since separation. No evidence on speciation rates or dispersal ability is available to support either possibility. The phylogenetic analysis (ch.6) does not include mainland species and therefore does not give information on the affinities of the shared species, which could indicate direction of possible dispersal.

Ecology seems to be an important factor in the endemicity of these Trichoptera, since most of the endemic species are restricted to the west of the state (see following discussion). Tasmania's climate and geology results in conditions not found elsewhere. For example, the rivers of western Tasmania with high, constant flow have no equivalent on the mainland (Hughes 1988). Friend (1987), however, concluded that ecology may make only a small contribution to endemism, as more vagile groups have relatively low endemism (Friend 1980).

The known range of most species has been greatly expanded by this study. Species fall into two groups with respect to distribution: species widespread within Tasmania, and those occurring only in western areas (west of the line shown in Fig. 5.81).

Ten of the 14 endemic conoesucid species are western; the three non-endemics are all widespread. The two endemic species of *Alloecella* are western; the non-endemic *A. grisea* is widespread. The two calocids extensively collected are non-endemic and widespread. The endemic *Caloca saneva* is also widespread, but since larvae of *Caloca saneva* are terrestrial (Neboiss 1979), they were generally not collected. Detailed study of these families on the mainland may reveal the occurrence of some widespread Tasmanian endemics (e.g. *Conoesucus fromus*) there.

This pattern within Tasmania can be explained in terms of ecological factors (Endler 1982), as distributions correlate with abiotic patterns. The physical and climatic characteristics of Tasmania, and previous environments, have been described by Friend (1987). Division of the state into western and eastern areas can be made on the basis of rainfall (Fig. 5.81), geology (Dept of Mines 1976), topography (Williams 1974b), water chemistry (Buckney & Tyler 1973, Bowling *et al.* 1986) and temperature (Davies 1965, Tasmanian Year Book 1985). A classification of rivers based on flow characteristics broadly coincides with rainfall distribution (Hughes 1988). Many biotic patterns reflect this discontinuity, e.g. vegetation-type (Fig. 5.82) and distribution of many animal taxa, including freshwater plankton (Ling *et al.* 1989, Shiel *et al.* 1989), terrestrial amphipods (Friend 1987), burrowing crayfish *Parastacoides* (A. M. M. Richardson pers. comm.) and the Trichoptera studied.

Western species are generally not found in the eastern highlands (Ben Lomond and north-eastern mountains), despite the rainfall being high enough to support *Nothofagus* forest and availability of apparently suitable habitats. However, there is
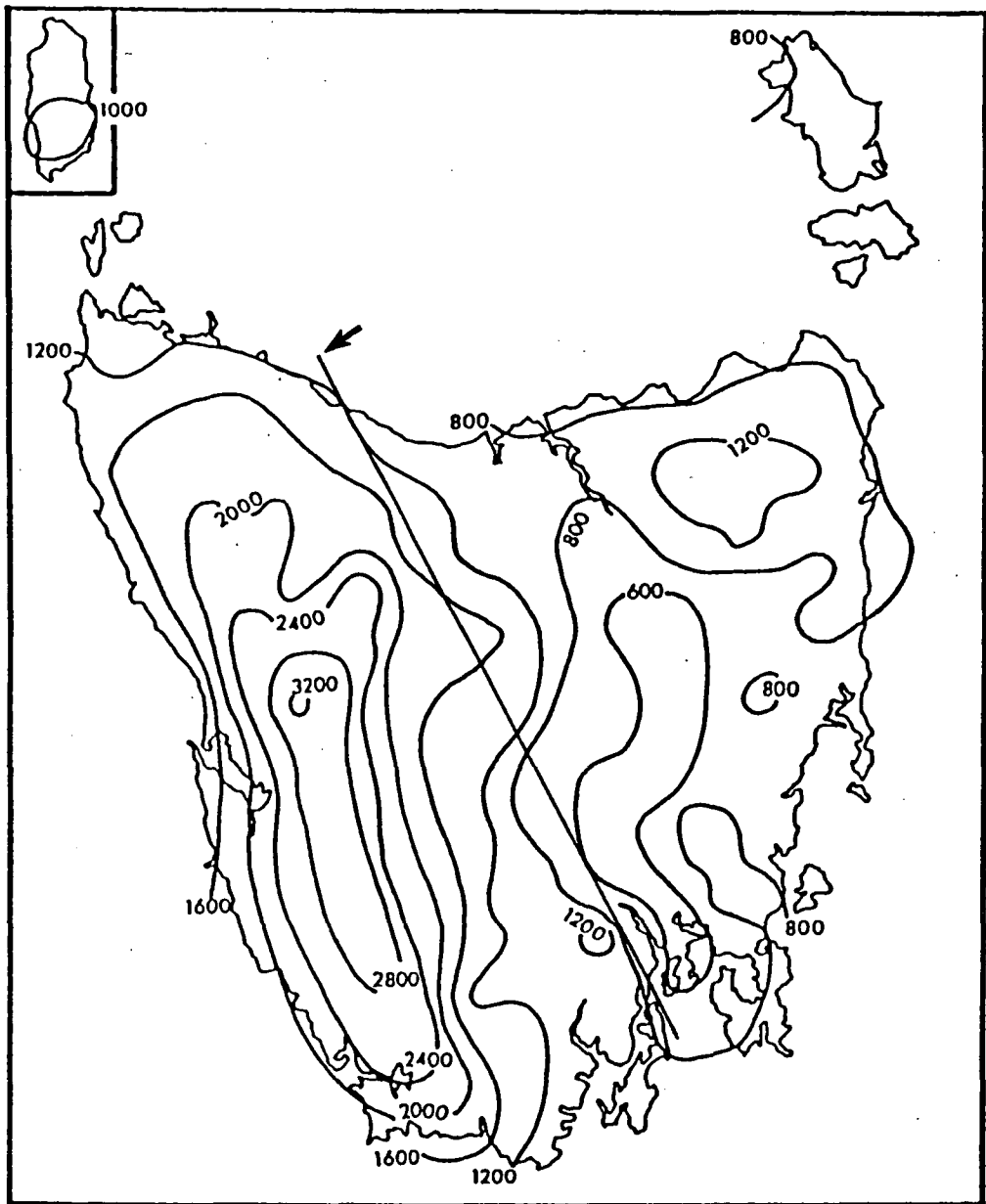
Figure 5.81. Rainfall map of Tasmania (from Tasmanian Year Book 1985), showing the approximate division of the state into western and eastern areas.

Figure 5.82. Distribution of vegetation types in Tasmania (modified from Davies 1965).
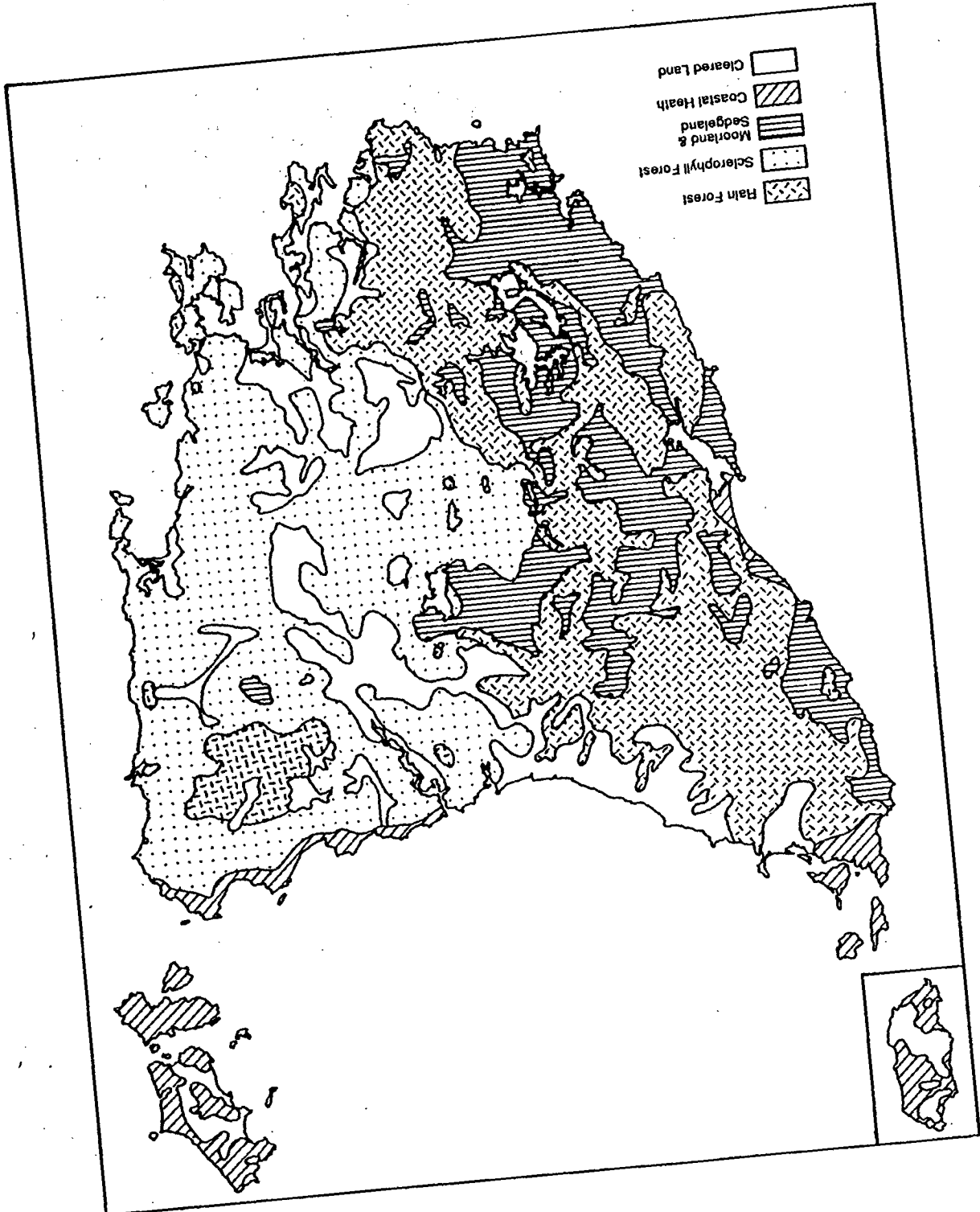
palynological evidence that the eastern rainforest is of post-glacial origin (Macphail 1975, 1979), and that at the height of the last Pleistocene glaciation (from about 20,000-17,000 years BP (Hope 1989)), large areas of Tasmania, including the north-east and central west, were covered with very open woodlands, grasslands and composite shrubs, and heathlands. Eastern coastal areas had open eucalypt forest (Hope 1984). A band of lowland rain forest remained in the west.

With warming and increased rainfall after about 10,000 years BP, the western forests spread to higher altitudes, but rain forest did not appear in eastern Tasmania until about 8,600 BP, presumably due to the time taken for migration from western refuges (Hope 1989). Thus, despite possible eastern refuges for some alpine and rainforest plants (Macphail & Moscal 1981), it seems likely that there were no eastern refuges for many aquatic and forest dependent groups, and that the western species (or their ancestors) survived the last glaciation in western lowland forest remnants and have not been able to colonise the eastern rainforest since. Either conditions in the east are not suitable, or the animals have low vagility. The apparently very low vagility of the Trichoptera studied is somewhat surprising, considering their winged stage, but most Trichoptera are not strong fliers, and their habit of sheltering in vegetation from wind would reduce the probability of passive wind dispersal.

Aquatic species occurring in the eastern lowlands must be tolerant of the lower and less predictable rainfall there (Davies 1975) compared with the high, consistent rainfall in the west. In addition, the western topography results in generally high gradient (fast flowing) streams and rivers. The high proportion of endemic Conoesucidae and Helicophidae which occur only in the west suggests that they cannot survive in the potentially intermittent, warmer, slower flowing streams of the eastern lowlands, and that the dry Midlands form a barrier to their dispersal into the eastern highlands. All the non-endemic species studied are widespread within Tasmania, and other trichopterans common to both Tasmania and the mainland are found mainly in the east (Neboiss 1977).

The effect of recent influences on present distributions is difficult to assess. Human activity has altered habitat by land clearance, damming of rivers, and creation of rocky riffles by road building. Distribution in some aquatic groups seems to be influenced by the type of riparian vegetation, due to adult requirements (e.g. Psephenidae (Davis 1985)). This may not directly influence some Trichoptera though, as several species mated and laid eggs in the laboratory soon after emergence and without feeding. Nevertheless, vegetation type is likely to affect stream conditions and larval populations (e.g. Behmer & Hawkins 1986).

The distributions of the Trichoptera studied correlate with the presence or absence of gills, at least in the genus *Conoesucus*, in which the widespread species (*C.fromus* and *C. norelus*) and three undescribed mainland species have gills. The only "western" *Conoesucus* with gills is *C. notialis*, in which the gills are minute.

Conoesucidae, Calocidae and Helicophidae occur in the south-east of mainland Australia, and *Coenoria* (Conoesucidae) extends to Cape York (Neboiss 1987). There are several undescribed species which do not occur in Tasmania. Although south-

western Australia is included in the Bassian faunal province by Spencer (1896, cited in Neboiss 1981a), these families are absent, which is likely to be due to the harsh summer rainfall deficit (Davis 1982). The detailed taxonomic, phylogenetic, distributional and ecological data required for biogeographical analysis of their distribution in Australia as a whole is not presently available.

Worldwide distribution.

The families studied have their closest relatives in New Zealand (Conoesucidae, Helicophidae, Calocidae) and Chilean South America (Helicophidae) (Flint 1979, pers. comm.). A close relationship between South American Anomalopsychidae and Australian Antipodoeciidae has been demonstrated in this study (ch. 6). Other trichopteran families with typical trans-antarctic distributions are Hydrobiosidae, Leptoceridae (*Triplectides*), Philopotamidae, Kokiriidae, Oeconesidae, Tasimiidae and Philorheithridae (Neboiss 1977, Flint 1983). Flint remarks that the Trichopteran fauna of the Chilean Subregion is more similar to that of Australia and New Zealand than to other regions of South America Flint (1974), and that any area of *Nothofagus* forest would have a Chilean-type fauna (Flint 1983). Other aquatic insect groups with a similar trans-antarctic distribution include Ephemeroptera, Plecoptera, Mecoptera and Diptera (Winterbourn 1980).

Thus, entire sections of stream insect communities on the Gondwanan fragments have resemblances and affinities to each other, suggesting origin from a common ancestral fauna. This pattern seems best explained in terms of vicariance of an ancestral Gondwanan fauna (Winterbourn 1980). For the group studied, a common ancestor in Gondwana can be postulated, but without phylogenetic and distributional data from all the relevant areas, and information on the timing of speciation in relation to geological and climatic changes (derived from fossil or molecular evidence), any explanation of their origin and subsequent evolution and change in distribution must remain speculative.

The complete absence of fossils in the group studied means that there is no additional support for any of several alternative explanations. However, changes in the ancestral group are likely to have occurred around the time of major geological changes in the southern hemisphere, as fossil evidence indicates that the order arose in the Triassic (about 225-180 mya) (Ross 1967, Hennig 1981), and Ross (1967) suggests that the progenitors of most families may have been in existence 100-150 mya, well before the split of Gondwanaland. This diversification coincides with the origin of angiosperms in about the early Cretaceous (141-100 mya) (Doyle 1984, Truswell 1987).

Geological evidence shows that Tasmania and New Zealand were in close proximity while part of Gondwanaland (Lawver & Scotese 1987), and a dispersal route to South America occurred via Antarctica. New Zealand was isolated by 80-60 million years ago (mya) (Crook 1981), and the Tasman Sea reached its present size by 55-57 mya (Kamp 1986, Stock & Molnar 1987). Australia began to separate from Antarctica about 55 mya (Crook & Belbin 1978), and by 50 mya the Southern Ocean

was a pronounced seaway (Coleman 1980). The Drake Passage between South America and Antarctica was open by 29.3 mya and of oceanic depth by 23.5 mya (Barker & Burrell 1977), ending dispersal from Antarctica and enabling establishment of the circum-antarctic current.

During this time, conditions on the southern continents were suitable for aquatic fauna inhabiting cool streams. Since more than 100 mya up to about 20 mya when the establishment of the circum-antarctic current led to cooling, Antarctica probably had a cool-temperate climate and gymnosperm-*Nothofagus* flora which was also present in South America, New Zealand and Australia (Winterbourn 1980, Hill 1990). Expansion of the Antarctic ice sheet in the late Miocene and associated increasing dryness in Australia led to contraction of the forest (Kemp 1981). Although Antarctica was thought to have become ice covered about 12 mya, recent fossil evidence shows that it may have been at least partly ice-free as recently as 3 mya (R. S. Hill pers. comm.).

When considering species distributions in relation to the sequence of Gondwanaland breakup, closer relationships might be expected between South American and Australian taxa than either with New Zealand. However, the present distribution of Conoesucidae and Calocidae is in Australia and New Zealand (although there is some uncertainty about Calocidae-refer to Taxonomic History, section 1.2). This distribution is also found in some stonefly groups (Campbell 1981) and terrestrial amphipods (A. M. M. Richardson pers. comm.). Assuming that this is not a taxonomic artifact for the Conoesucidae and Calocidae (which is possible considering the somewhat unstable classification of the group studied, and the need for further study of South American species), this distribution could be explained in several ways. The families may have originated from widespread ancestral taxa in the area of Gondwanaland including Australia and New Zealand, and failed to disperse the 6000 km to South America (R.J. Carpenter pers. comm.). In this case, the present distribution would be expected to include New Caledonia, unless subsequent extinction has occurred. Although the present distribution could be relictual, there is no apparent reason for extinction in South America. Alternatively, the Conoesucidae could have arisen in either Australia or New Zealand after their separation from Antarctica, and subsequently dispersed across the Tasman Sea. Such long-distance dispersal does occur (e.g. Wise 1983), and the prevailing westerly winds bring butterflies to New Zealand (Fox 1973); however, there is no direct evidence for this occurring in Trichoptera.

Clearly, more data are needed on the distribution, ecology and phylogenetic relationships of Conoesucidae, Calocidae, Helicophidae and Antipodoeciidae before the historical biogeography of these southern hemisphere families can be more fully elucidated.

CHAPTER 6. PHYLOGENETIC ANALYSIS

6.1 INTRODUCTION

The aim of the cladistic analysis undertaken in this study was firstly to determine, on the basis of evidence from immatures, whether established generic and family taxa of Conoesucidae, Calocidae, Helicophidae and Antipodoeciidae are monophyletic. Specifically, this will test the validity of the familial status of Helicophidae, Calocidae and Antipodoeciidae, which are poorly defined, and of the genera *Hampa*, *Matasia* and *Lingora*, which may be congeneric (A. Neboiss, pers. comm.). The small sericostomatoid family Anomalopsychidae (from South America) is also included in the analysis in order to clarify the status of this anomalous family.

The second aim was to deduce the phylogenetic relationships of these taxa. If the present classification reflects the phylogeny, there will be no difference between the phylogeny derived in this analysis and that implicit in the present classification (Fig. 6.1). Therefore, it is expected that confamilial genera and species will be shown to be more closely related to each other than to other taxa; at present there is no resolution of these taxa at the family level. The existing classification is based on intuitive analysis of adult characters, therefore this cladistic analysis based on larval and pupal characters will test its strength, and further resolve relationships.

Although attempts have been made to justify separation of the evolutionary process from the cladistic approach (Platnick 1979, Nelson 1989), these have been criticised by several authors (Charig 1982, Ridley 1986, de Queiroz & Donoghue 1990a). Arguments that cladistic methods can be applied without the underlying principle of common descent (Platnick 1979, 1982; Nelson & Platnick 1981; Patterson 1982) ignore the issue of how the methods were formulated, and the power of this principle to explain the patterns of living things in space (biogeography), time (biostratigraphy) and form (de Queiroz & Donoghue 1990a).

Therefore, in this study it is assumed that the taxa are related by common descent, resulting in the observed pattern of character distribution. No assumptions need to be made about any particular model of the evolutionary process. Thus, character states designated as "plesiomorphic" are considered to be ancestral states, rather than simply the more general states (cf. Barnard 1984). There is a correct phylogenetic tree, which analysis seeks to approximate as closely as possible from available evidence.

The preferred distribution of synapomorphies is determined by the criterion of parsimony, whereby homoplasy (convergence, reversal and parallelism in character state evolution) is minimised, so that the optimal cladogram (and, by inference, phylogenetic tree) is that with the fewest character state changes (Felsenstein 1983): the tree that minimises the number of steps also minimises the number of "extra" steps (homoplasies) needed to explain the data (Swofford & Olsen 1990).

The location of the common ancestor (root of the tree) can be identified by the use of characters for which polarity has been established *a priori* (e.g. Schultz 1990),
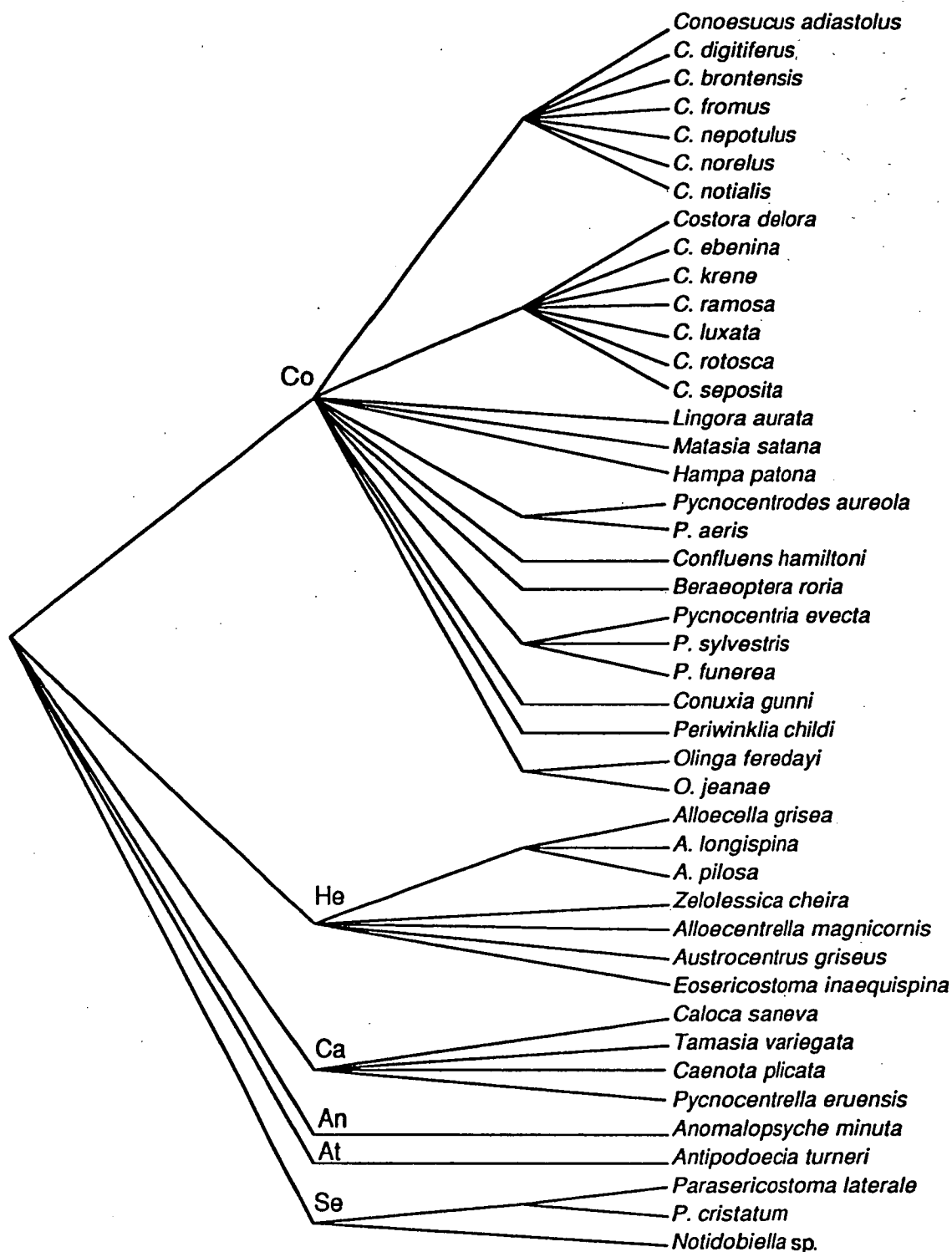
Figure 6.1. Phylogeny of the taxa included in phylogenetic analyses, as represented by the current classification.
Co = Conoesucidae; He = Helicophidae; Ca = Calocidae; An = Anomalopsychidae; At = Antipodoeciidae; Se = Sericostomatidae.

thereby implying a hypothetical ancestor. Of several methods for determining character polarity (Stevens 1980), the method of outgroup comparison is generally preferred (Stevens 1980, Watrous & Wheeler 1981). Polarity is assigned such that the character state shared between the outgroup and the ingroup is the ancestral state, and the state unique to the ingroup is the derived state.

However, such *a priori* specification of character polarities is not prerequisite to the use of cladistic analysis or parsimony methods (Swofford & Olsen 1990). Rather, all that is required to obtain rooted trees from parsimony analysis is to include in the data set one or more taxa designated as the outgroup: the location at which the outgroup joins the unrooted tree implies a root with respect to the ingroup.

The outgroup chosen must be such that the ingroup is monophyletic, i.e. the outgroup must not belong to the taxa under study (Richardson *et al.* 1986, Swofford & Olsen 1990). Ideally the outgroup should include several species, as distantly related to each other as possible, subject to being as close to the group under study as possible (Richardson *et al.* 1986).

There is not sufficient basis for clearly establishing character polarities *a priori* in this study, due to the instability and poor resolution of the higher classification of Trichoptera, and the paucity of information on immatures. Therefore, trees are rooted by including an outgroup in the analysis. Choosing an appropriate outgroup at family level is difficult, as all the existing phylogenies of Trichoptera families (Ross 1967, 1978, Schmid 1980, Weaver 1983; Figs 1.1-1.3) leave the relationships of sericostomatoid (*sensu* Weaver & Morse 1986) families unresolved. For this analysis, sericostomatids are designated as the outgroup, since this family is distinct from the taxa under study (see Taxonomic History, 1.1.2).

6.2 MATERIALS AND METHODS
Taxa included in analyses.

Analyses were carried out on two data sets. The first included data from the Tasmanian conoesucid, helicophid and calocid taxa studied in detail, plus species in these families from New Zealand and South America, and Antipodoeciidae and Anomalopsychidae. The second data set included only the Tasmanian taxa studied in detail. Tasmanian taxa were analysed separately because the character state data for them was more complete.

Many species of Conoesucidae, Helicophidae and Calocidae, including Australian mainland species, were omitted from this analysis as their immatures are unknown or unassociated with adults. The existence of undescribed mainland genera (A. Neboiss pers. comm.) means that unidentified larval material from the mainland cannot even be assigned to genus.

The taxa included in the analysis and sources of character state data are listed in Table 6.1.
Choice of characters.

Initially as many characters as practicable were scored for each taxon (Appendix

Table 6.1. Species included in cladistic analysis, their distribution, and source of character data. Distributions are abbreviated as in Table 1.1.

specs. = specimens examined; dr. = drawings

SPECIES	DISTRIBUTION	REFERENCE
Conoesucidae		
Conoesucus adiastolus sp.n.	TA	this study
C. brontensis	"	"
C. digitiferus	"	"
C. fromus	"	"
C. nepotulus	"	"
C. norelus	"	"
C. notialis sp. n.	"	"
Costora delora	TA, AUse	"
C. ebenina	" "	"
C. krene	TA	"
C. ramosa	"	"
C. luxata	"	"
C. rotosca	"	"
C. seposita	"	"
Lingora aurata	"	"
Matasia satana	"	"
Hampa patona	TA, AUse	"
Pycnocentrodes aureola	NZ	specs., Cowley (1978)
P. aeris	"	"
Confluens hamiltoni	"	"
Beraeoptera roria	"	"
Pycnocentria evecta	"	"
P. sylvestris	"	Cowley (1978)
P. funerea	"	"
Conuxia gunni	"	"
Periwinkl`a childi	"	specs.
Olinga feredayi	"	"
O. jeanae	"	Cowley (1978)
Helicophidae		
Alloecella grisea	TA, AUse	this study,
		Drecktrah (1984)
A. longispina	TA	"
A. pilosa	"	"
Zelolessica cheira	NZ	specs., Cowley (1978)
Alloecentrella magnicornis	"	Cowley (1978)
Austrocentrus griseus	SAm	specs.
Eosericostoma inaequispina	"	"
Calocidae		
Caloca saneva	TA	specs., Neboiss (1979)
Tamasia variegata	TA, AUse	this study
Caenota plicata	" , "	"
Pycnocentrella eruensis	NZ	specs., Cowley (1978)
Anomalopsychidae		
Anomalopsyche minuta	SAm	specs., Flint (1981)
Antipodoeciidae		
Antipodoecia turneri	TA?, AUse	dr. (J. Dean pers. comm.)
Sericostomatidae		
Parasericostoma laterale	SAm	specs.
P. cristatum	"	"
Notidobiella sp.	"	"

4). Characters subsequently chosen for use in the analysis (Tables 6.2 and 6.3) were those which could be clearly defined, (character states were not ambiguous); were characteristic of the species (showed no intraspecific variation of state); and were informative (not uniform and not autapomorphic for one species). Characters observable only in cleared specimens are indicated in Table 6.2 by (C). In total 115 characters (79 larval, 36 pupal; 66 binary, 49 multistate) were used.

Case characters (other than material type) were included, as they meet the criteria given above, and there is strong evidence that case type is genetically determined (Cummins 1964, Wiggins 1977); the case and larva have evolved together as a functional unit. Therefore, case characters should not be discounted as being under strong environmental influence.

Character states for taxa were determined from the Tasmanian material studied, the description of *Alloecella grisea* larvae and pupae by Drecktrah (1984), museum specimens from New Zealand and South America (Appendix 5), descriptions of New Zealand taxa (Cowley 1978), and for *Antipodoecia*, drawings by J. Dean (pers. comm.).

Analyses were conducted using both larval and pupal character states, larval states only, and pupal states only, to determine the degree of congruence of phylogenetic trees based on the different life stages. For analysis of taxa using only pupal characters, 9 taxa for which data on pupae (except cases) were unavailable were omitted.

Rooting trees.

For an initial analysis of all taxa, the sericostomatid species for which data were available (*Parasericostoma laterale, P. cristatum* and *Notidobiella* sp.) were designated collectively as the outgroup. However, the resultant trees could not be rooted such that the ingroup was monophyletic; either *Notidobiella* or *Parasericostoma*, but not both, were suitable as the outgroup.

Finding trees.

The computer program PAUP (Phylogenetic Analysis Using Parsimony; David Swofford, Uni. of Illinois; version 3.0L) was used to find the most parsimonious distribution of characters.

No *a priori* assumptions were made concerning the state transformations allowed or the probability of transformation in multistate characters, or about the relative importance of characters, therefore all characters were unordered (i.e. any state can transform directly to any other) and equally weighted.

As the entire data set (44 taxa, 115 characters) was too large to run with the branch-and-bound algorithm, the heuristics algorithm (which sacrifices the guarantee of optimality in favour of reduced computing time (Swofford & Olsen 1990)) was used to search for optimal trees. The exhaustive search option is not feasible for data sets of more than 10 taxa, so was not used.

Trees are represented by the 50% Majority Rule consensus tree, which includes groups occurring in 50% or more of trees, and gives the best resolved tree of the

Table 6.2. Larval characters and states used in analysis. For morphological terminology refer to Figs 5.1-5.2.
Char. no. = Character number in data set (missing numbers are characters in the program data set which were not included in final analyses); char name= character name in raw data set (Appendix 6).

character	char no.	char name	0	1	2	3	4	5
CASE:								
Material arrangement	2	2	spiral	panels/plates	irregular			
	3	2a	no projections	projecting bits				
Case shape	4	3	cylinder	d-v flattened				
	5	4&5	strongly tapered & curved	slight taper & curve	straight			
Case size cf. larva	6	6	just longer	same/smaller	much longer			
Case anterior margin	7	7	straight/slight obl.	strongly oblique				
Post. closure membrane	8	8	flat	cone	dome	oblique	absent	dors overhang
Post. closure opening	9	9	round	oval	slit	other		
	10	10	central	ventral	dors	terminal	subterminal	
ABDOMEN:								
Shape	11	11	cylindrical	d-v flattened				
Gills	12	12	absent	simple	branched			
	13	12a	on few segments	on all segments				
Segt 8 spicules (C)	14	16	row	band				
" 3-7 (C)	15	17	bifid & single	single only	bifid only	absent		
" 2 (C)	16	18	absent	present				
Tergite 9 sclerite	17	19	single	double				
	18	20	pigm. mostly	unpigmented	pigm. slightly			
" " post. setae	19	21	4 -7 pairs	many				
	20	21a	along post. margin	all over				
	21	22	1-2 pairs long	even sized				
Segment 1 ventral bulge	22	24	absent	present				
Lat. hump sclerite	23	26	small spiny oval	large spiny cresent	lacks spines			
longitudinal scler.	24	27	absent	present				
additional scler.	25	28	absent	present				
Elongate spicule areas (C)	26	29	dorsal & ventr.	ventral	absent			
ANAL PROLEGS:								
Lat. scler. pigmentation	27	30	pale	even brown/irreg.	median v. dark			
" orientation	28	32	dorsal	posterior				
Ventral sclerite	29	33	brown oval	bar (brown/pale)	oval pale			
Fleshy proc. mes. to claw	30	38	absent	present				
HEAD:								
Shape from dorsal	31	41	round	tapered/oval				
Texture	32	44	spiny	honeycomb	smooth			
Scar colour (C)	33	46	paler	darker	same			
Scar shape	34	47	w=2-4l	w much > 1				
Carina shape	35	49	around capsule	posteriad of eye	ant/1/2 to eye	absent		
Antennae position	36	51	anterior	1/2 way	near eye			
Minute dorsal setae (C)	37	53	absent	present				
other setae								
Lateral anterior setae	38	54	2	>2				
Frontoclypeus shape	39	55	ant w>>post w	ant w just > post w				
Frontoclypeus ant.lat. setae	40	58	2 long+clear curved	many				
Ventral pigmentation	41	62	median only lacking	mostly lacking				
Ventral dark scars	42	63	absent	present				
Lateral minute setae	43	65	absent	2	9 to 18			
Ventral apotome shape	44	66	triangular	quadrate tapering	long tri./oblong			
Genae separate	45	68	wide	abut				
Ventr. mandib. articulatn	46	69	prominent	not prom.				
No. mandib. basal setae	47	71	2	many				
Labrum dors. round brush	48	80	absent	present				
PRONOTUM:								
Texture	49	81	ant 2/3 spiny	spiny ant band	reticulate	shiny retic.		
Carina	50	84	absent	fold	pinched ridge, weak post.curve	ridge, strong post.curve	ridge, straight	
Ant-lat corner shape	51	90	obtuse	square	acute			
	52	90a	corner not fold under	folded under				
Ant-lat corner shape	53	91	round	square	pointed			
	54	92	not projected	projected	projects strongly			
Fine dorsal setae	55	94	absent	present				
Large dorsal setae	56	94a	absent	present				
Ant. large setae	57	96	absent	3 to 7	many			
	58	97a	v. stout setae absent	present				
MESONOTUM shape	59	99	square	triang.	w>1			
Pigmentation	60	100	entire	ant 2/3	other			
Ant. setae no. rows	61	101	one	two-four				
	62	103	fine	stout	both			
Setae shape	63	104	tips taper	tips spatulate				

cont....

Character							
Post. setae	64	105	pair	row or band			
Dorsal setae	65	106	absent	scattered all over	few median		
METANOTUM sclerites	66	108	absent	SA 1 only	SA 1&2	all SAs	SA 1&3
	67	108a	scler. spots	entire area scler.			
Setae SA1	68	109	0	1	1-2 lng+1-3smll	>3 long	v. many
SA2	69	110	0	1	0-3lng+1-3smll	>3long	many
SA3	70	111	0	1	1-3lng+smll	>3long	many
LEGS:							
Protrochantin shape	71	113	slender taper pointed	broad horn/rect./tri.			
	72	113a	small	large			
" fused to propleuron	73	114	suture	fused			
Pleural humps	74	115	small	large			
" setae	75	117	long setae	minute setae+long			
Hind tibia	76	118	cylindrical	bent and flattened			
OTHER:							
Testes no. lobes	77	122	4	2			
shape	78	123	round	long			
colour	79	124	white	clear	green		
Chromosome number (n)	80	125	22	25	32-40		

Table 6.3. Pupal characters and states used in analyses. For morphological terminology refer to Fig. 5.3
Char. no. = Character number in data set (missing numbers are characters in the program data set which were not included in final analyses).

character	char. no.	char. name	0	1	2	3	4
CASE							
Ant. membrane	81	P1	flat	domed	opening raised	oblique	absent
	82	P1a	inset	flush			
	83	P2	single	double			
Anterior opening	85	P3	curved slit	straight slit	oval	seive	
	86	P4	central	ventrad	dorsad		
Post. membrane	87	P6	flat	domed	opening projected	oblique	
Post. end of case	88	P6a	retained	removed	partly removed		
" opening	89	P7	circular	oval	slit	seive	
	90	P8	vertical	transverse			
	91	P9	central	dorsad	ventrad		
Adhesive discs	92	P10	anterior	posterior	both	absent	
	93	P11	ventral	all round			
	94	P12	one	several	many		
	95	P14	stalked	not stalked			
ABDOMEN							
Hair fringe: foreleg	96	P15	absent	dense 1 side	dense 2 sides	sparse 1 side	sparse 2 sides
midleg	97	P16	absent	dense 1 side	dense 2 side	sparse 1 side	sparse 2 sides
Post. hookplate shape	98	P21	w=1	w>>1			
no. hooks	99	P22	two-four	eight-15	3 to 7		
Ant. hookpl. no. hooks	100	P25	two-five	many			
Segt 2 toothed hump	102	P30	absent	present			
MOUTHPARTS							
Mandibles shape	103	P30a	taper from base	taper from ~1/2 way			
	104	P31	l>3w	l<2w			
" curve	105	P32	strong	slight			
R more strongly hooked	106	P36	yes	no			
Labrum shape	107	P38	subquadr	hemisph/cone			
" ant. setae	108	P39	2-3 pairs	> 3 prs			
" post-lat setae	109	P40	2 lrge prs	~6 prs	many		
TERMINALIA							
Male ventral humps	110	P42	lat. & central	lat. only	smooth		
Tergite IX setae	111	P44	4-6 prs	many	absent		
Processes shape	112	P46	apex str	turned up	turned up &/or out	in & up	
	113	P46a	pointed	round			
" distal overhang	114	P48	none	short	longer		
" clear terminal setae	115	P49	present	absent			
" other setae	116	P52	long	med			
" texture dors	117	P53	smooth	toothed	scales	papillate	
" " apical	118	P54	smooth	toothed	scales	papillate	

consensus options available.

Minimum length trees output by PAUP were transferred to MacClade (version 2.1, W. & D. Maddison, Harvard University) for comparison of character distribution in different trees.

6.3 RESULTS

The data matrix of character states for all taxa is given in Appendix 6.

All taxa.

Figure 6.2 shows the shortest tree, with the character states defining monophyletic clades. This tree was found by a branch-swap in MacClade of the 50% Majority Rule consensus tree from PAUP, and is 2 steps shorter. Of the families included in analysis, monophyly was demonstrated only for the Conoesucidae. The helicophid and calocid family groups are defined by convergent and plesiomorphic characters, rather than synapomorphies, and therefore have not been shown to be monophyletic. The helicophids and calocids are united into one clade which is defined by a single synapomorphy 44(0) for which two taxa show reversal.

A search using only larval characters was incomplete after several hours, so was stopped and a consensus tree calculated from 50 of the shortest trees found (length 418 steps). The 50% Majority Rule consensus tree is shown in Fig. 6.3. Analysis using pupal characters only was also not completed; a consensus was calculated from 53 trees of length 163 steps (Fig. 6.4).

The New Zealand conoesucid species do not constitute monophyletic groups; rather they are grouped amongst Australian species (Fig. 6.2) *Pycnocentria evecta* is grouped with *Costora* spp. (except *C. delora* and *C. ebenina*) on the basis of case characters states 5(0) and 6(2). *Pycnocentria sylvestris*, *P. funerea* and *Conuxia gunni* are grouped with *Costora delora*, on the basis of the synapomorphic character state 70(1) (single seta on metanoum SA 3).

Other New Zealand species are also grouped with Australian confamilials. *Pycnocentrella* is included with Australian calocids, as is *Alloecentrella*, whose family placement is somewhat uncertain (see Taxonomic History, 1.2).

Antipodoecia and *Anomalopsyche* are placed as sister taxa within a group of helicophids, united by their unique possession of single, large ventral head scars (42(1)). They share other distinctive features such as the posterior case membrane overhang, and very strongly projected pronotal anterolateral corners; however, definition of character states was inadequate to distinguish these features as unique to these species.

Synapomorphies defining clades are the same whether *Parasericostoma* or
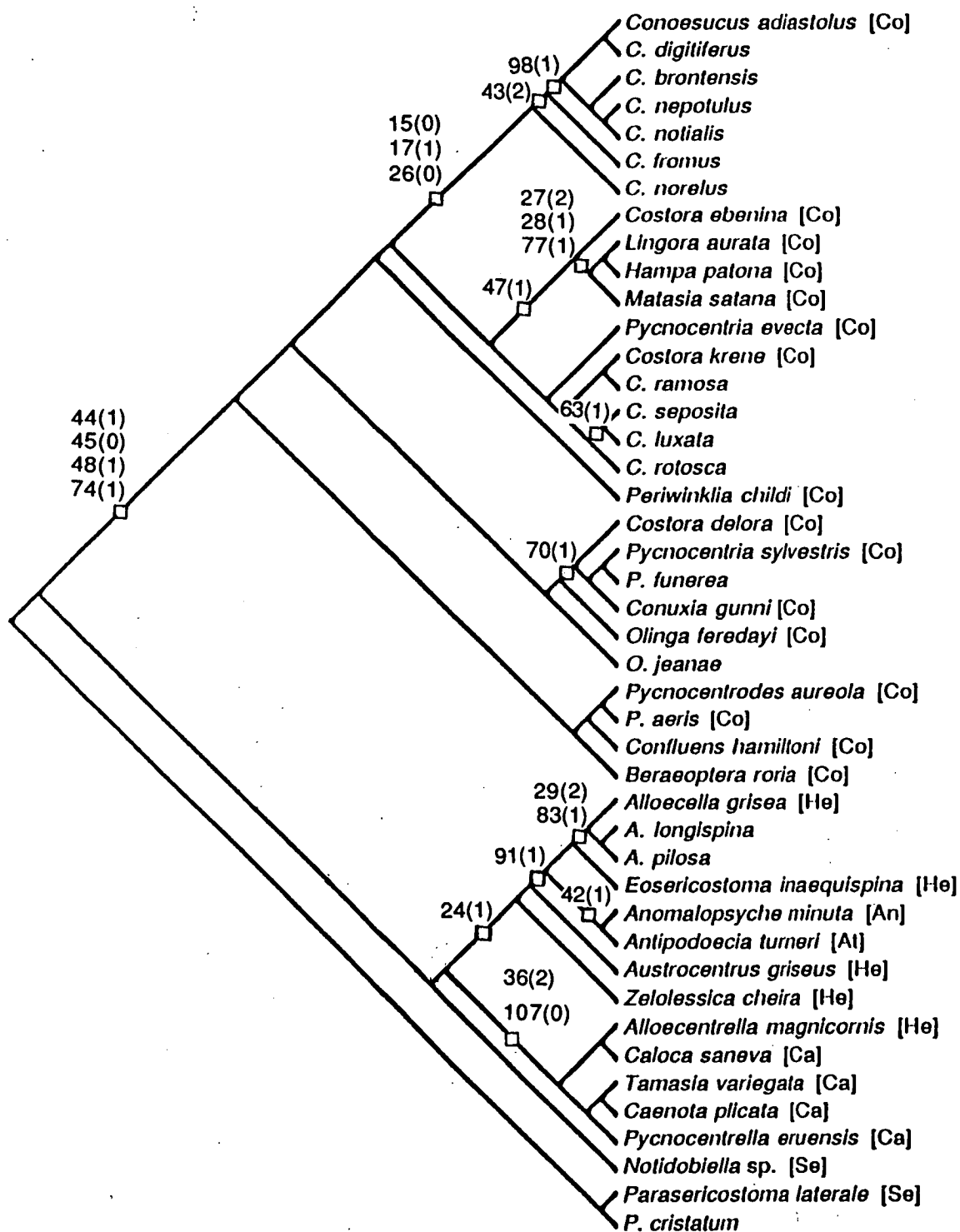
Figure 6.2. Shortest tree including all taxa, based on larval and pupal characters. Only synapomorphies are shown (□); characters for which some taxa show reversal or convergence are omitted. Numbers refer to characters listed in Tables 6.2 and 6.3.
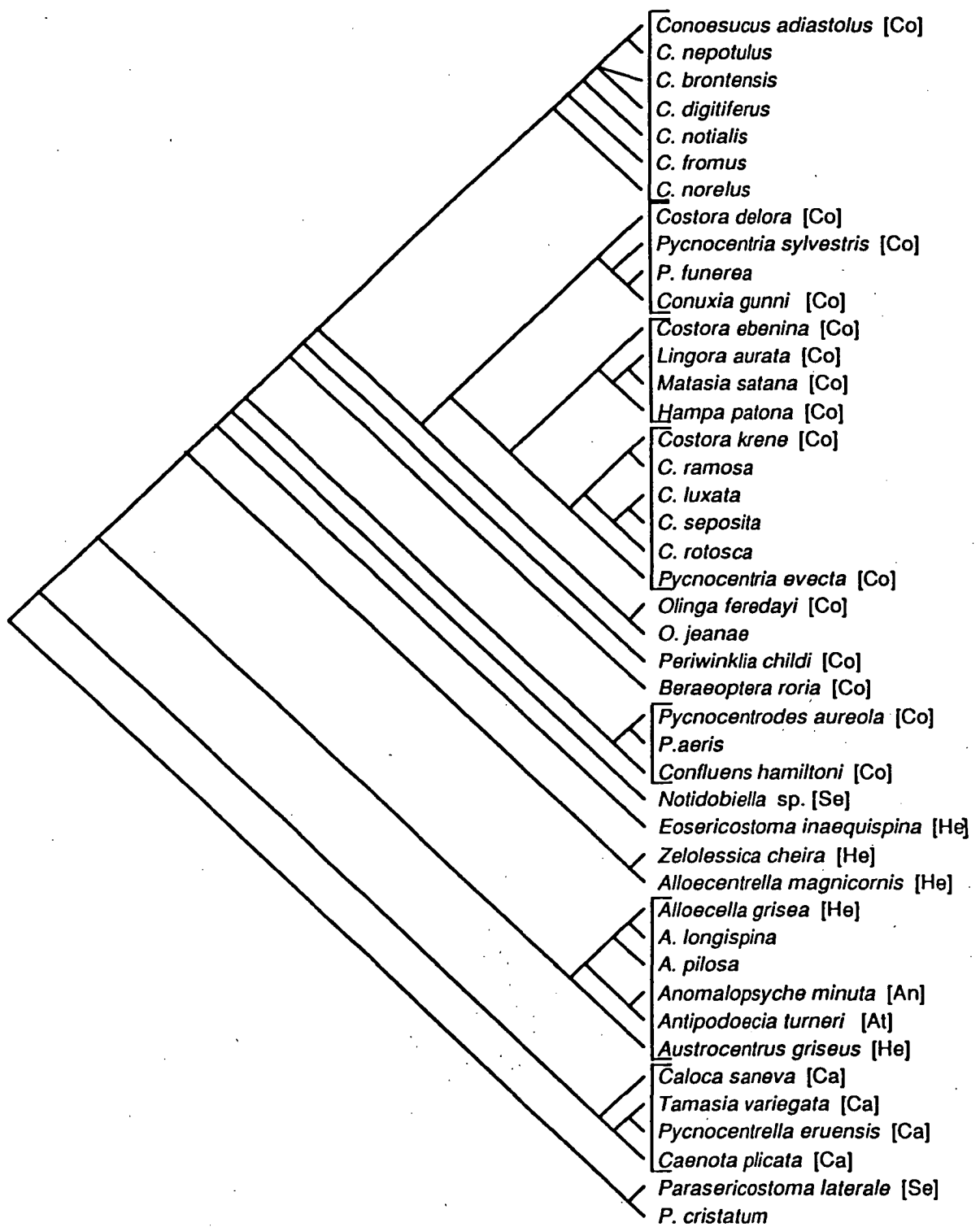
Figure 6.3. Consensus tree including all the taxa analysed, based on larval characters only. Clades congruent with those on the tree based on all characters (Fig. 6.2) are bracketed.
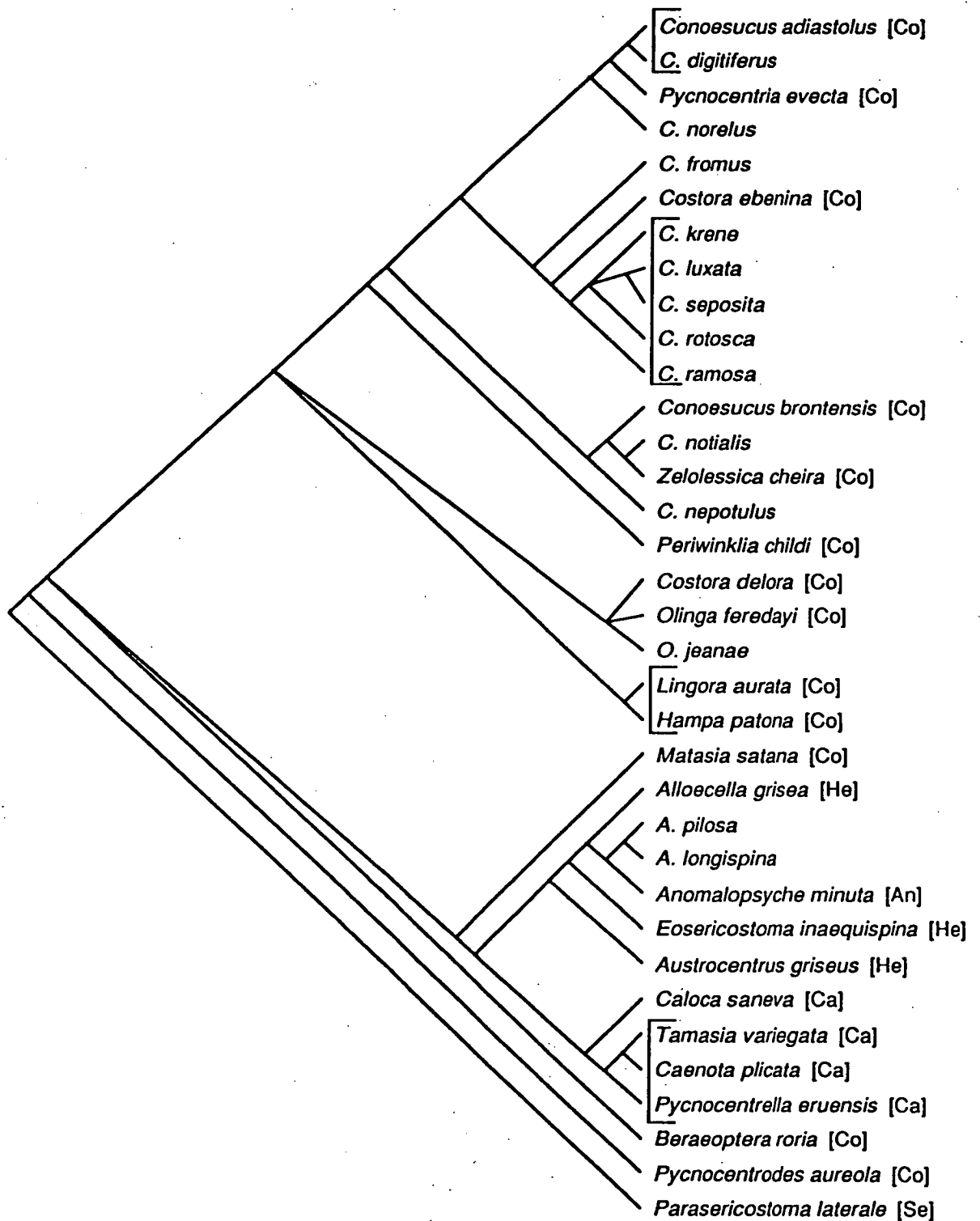
Figure 6.4. Consensus tree based on pupal characters only, including all the taxa analysed except 9 for which no data on pupae were available. Clades congruent with those on the tree based on all characters (Fig. 6.2) are bracketed.

Notidobiella is used as the outgroup: the characters for which polarity is influenced are homoplasious ones.

The consistency index (C.I.) of trees (Kluge & Farris 1979) is low (0.31); only 7 of the 79 larval characters and 3 of 36 pupal characters show no homoplasy, i.e. had a C.I. of 1 (Appendix 7) .

Tasmanian taxa.

A heuristic search including the 22 taxa studied in detail, using all characters, found 2 equally short trees of length 335 steps. The trees differ only in the position of *Costora delora*, placing it either as sister taxon to *Lingora+Hampa+Matasia*, or sister to *Conoesucus+ Lingora-Hampa-Matasia*. Synapomorphies defining clades are shown on the 50% Majority Rule consensus tree in Fig. 6.6. Current genera are shown to be well defined monophyletic groups, with the exception of *Costora*. *Lingora*, *Hampa* and *Matasia* also constitute a well defined monophyletic clade.

Inclusion of *C. delora* with other *Costora* (Fig. 6.7) adds 2 steps to the tree length by increasing the number of changes in characters 18 (tergite 9 pigmentation) and 46 (ventral mandibular articulation). Character state 18(2) is the only synapomorphy uniting *C.delora* with *Lingora+Hampa+Matasia*, whereas the clade including all *Costora* is defined by the synapomorphy of 79(2) (green testes), and also by the unique combination of character states 77(0) and 78(1) (four long testicular lobes). On the basis of subjective decisions about the relative value of these characters for revealing phylogenetic relationships, the placement of *C. delora* with other *Costora* is the preferred arrangement.

A search using only larval characters found 57 equally short trees, of length 212 steps. The 50% Majority Rule consensus tree is shown in Fig. 6.8. Unknown character states for *Hampa patona* (of which the whole larva is unknown) were predicted on the basis of this phylogeny, and are listed in Table 6.4.

The single shortest tree found by a search based on pupal characters only (Fig. 6.9) showed poor resolution. However, rearrangement of branches to form groups consistent with the current classification and trees based on all characters increased tree length by only four steps.

Both *Alloecella* and *Tamasia+Caenota* are shown to be monophyletic. However, these two possible outgroups to the Conoesucidae could be included in one clade without changing tree length. Synapomorphies defining conoesucid clades were the same whether Calocidae or Helicophidae were assigned as the outgroup.

The consistency index of the tree based on all characters was 0.51, with 27 of 79 larval characters and 13 of 36 pupal characters showing no homoplasy (Appendix 7).

6.4 DISCUSSION

This phylogenetic analysis has demonstrated the monophyly of all the current taxa of Tasmanian species of Conoesucidae, Helicophidae and Calocidae studied (with the possible exception of *Costora*, which is discussed below). Results support
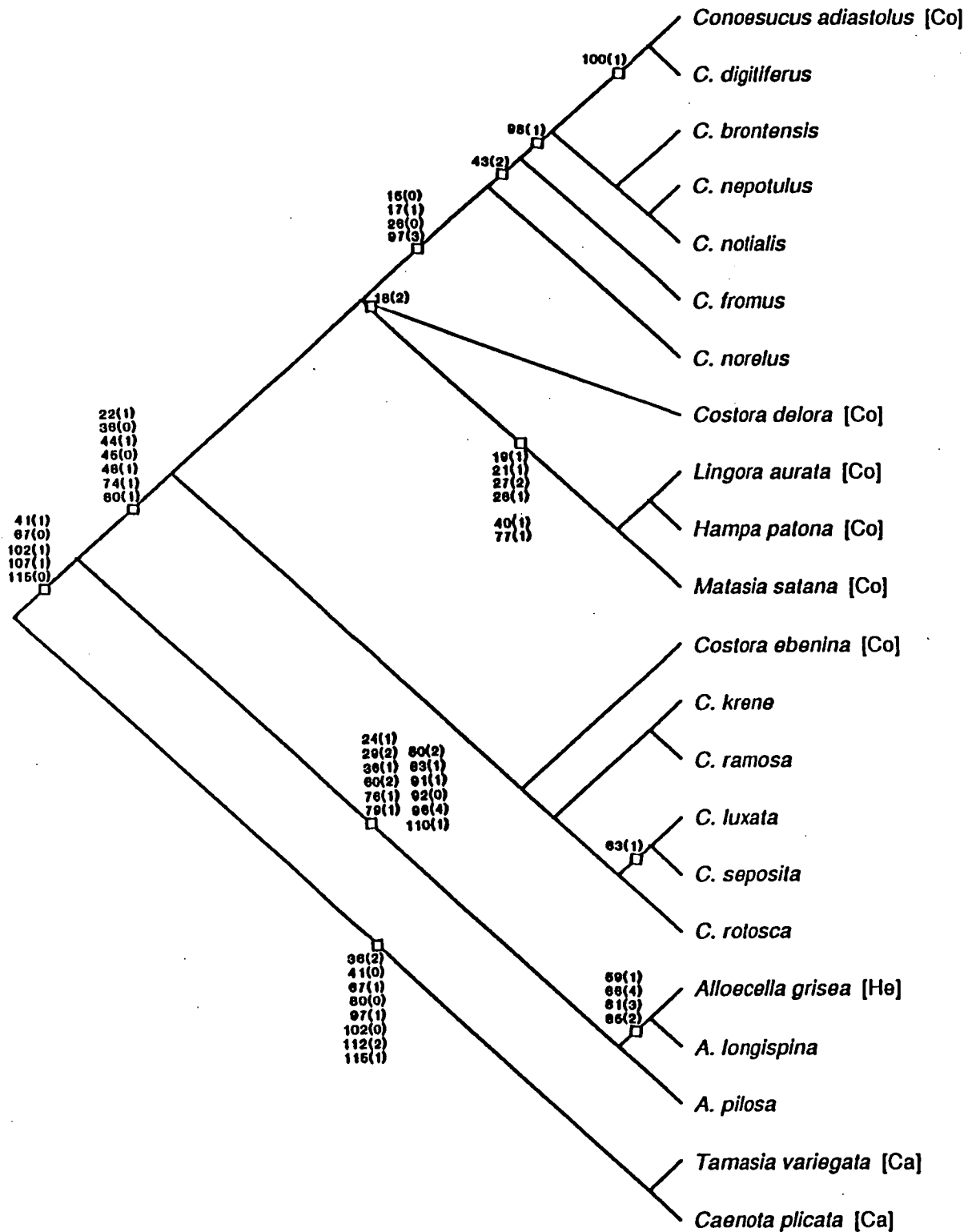
Figure 6.6. Consensus tree based on larval and pupal characters, including only the Tasmanian taxa studied in detail. Synapomorphies are shown (□); numbers refer to characters listed in Tables 6.2 and 6.3.
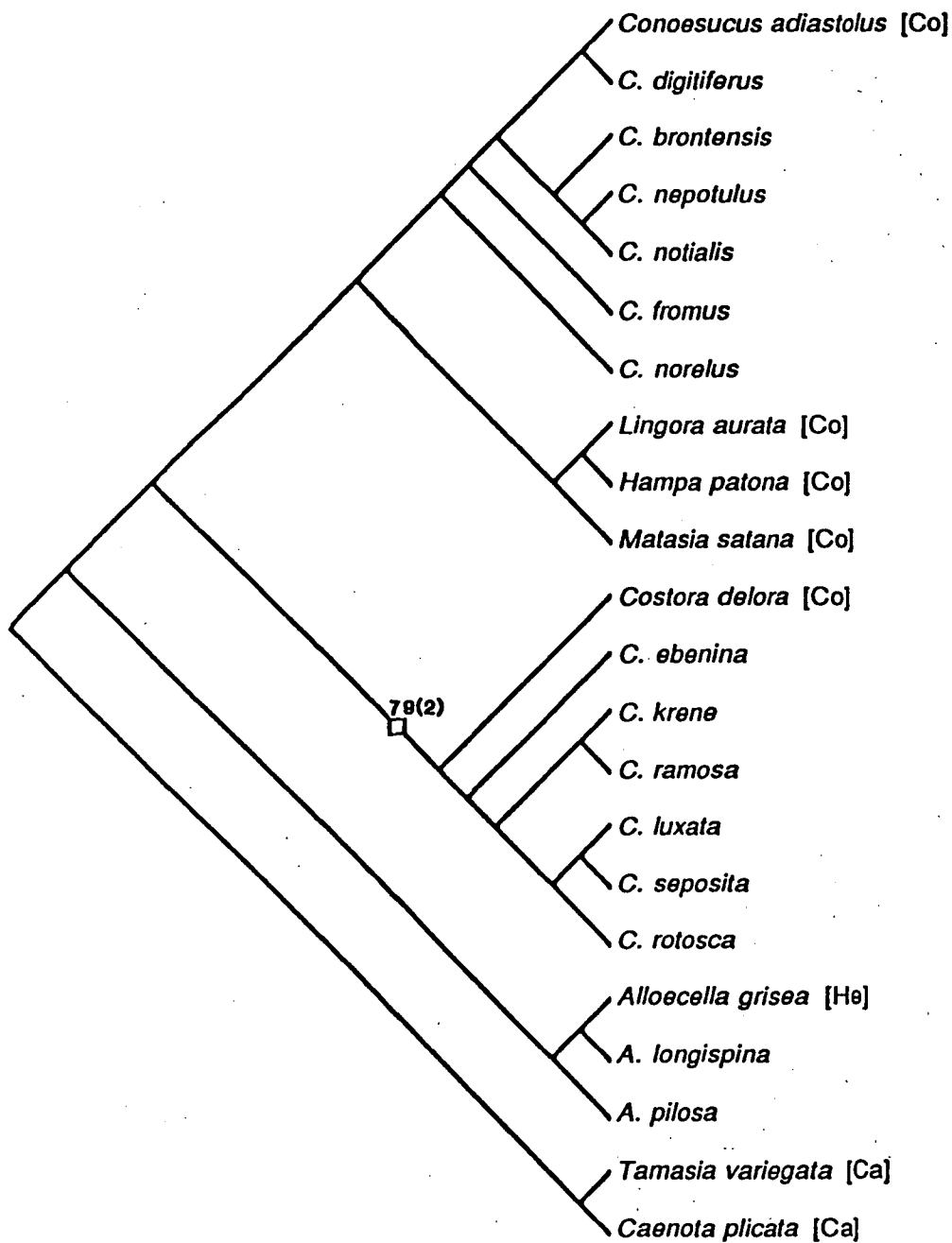
Figure 6.7. Rearrangement of the shortest tree including Tasmanian taxa and based on all characters, to unite *Costora*. This tree is two steps longer than the shortest tree.
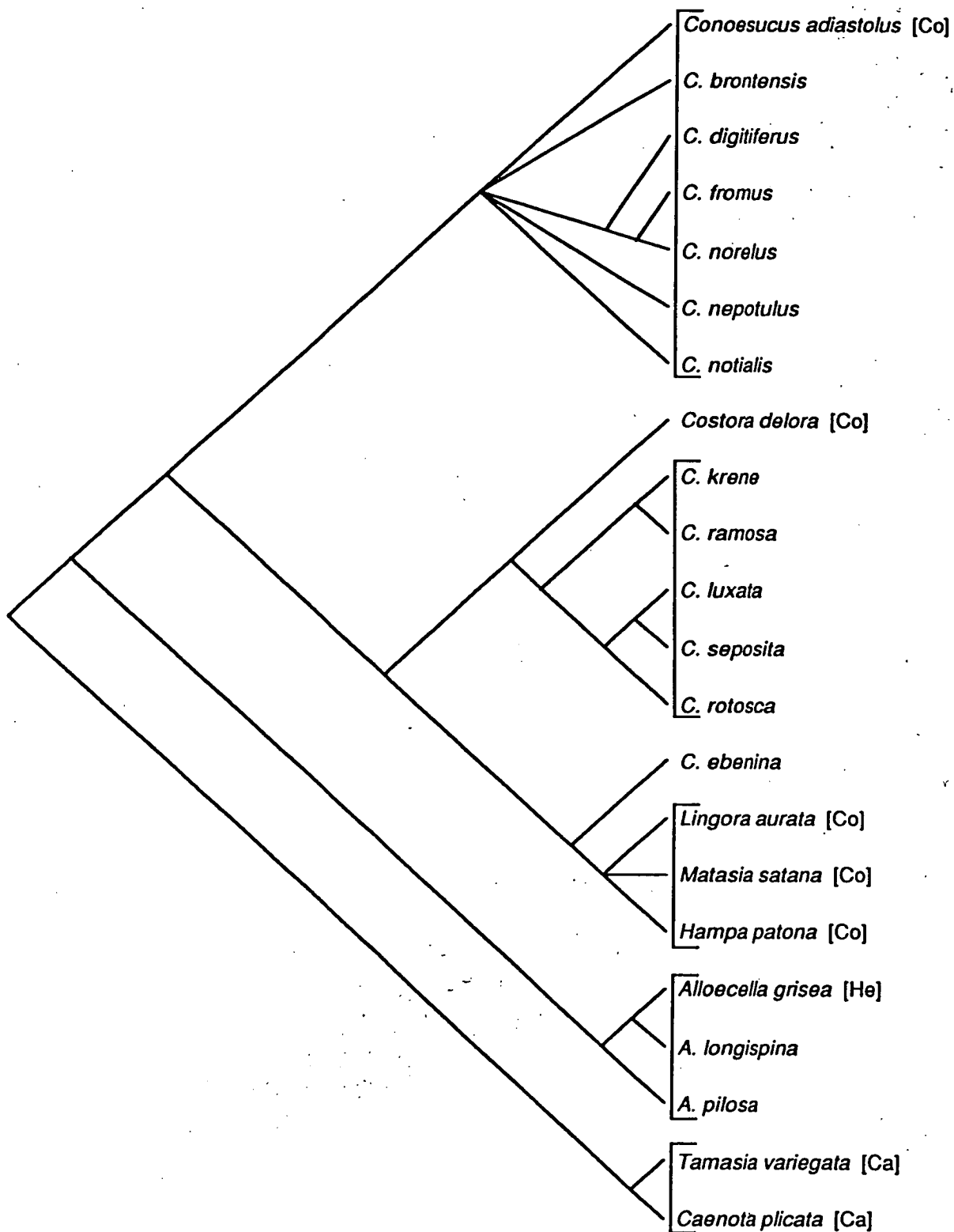
Figure 6.8. Consensus tree based on larval characters only, including the Tasmanian taxa studied in detail. Clades congruent with the tree based on all characters (Fig. 6.6) are bracketed.
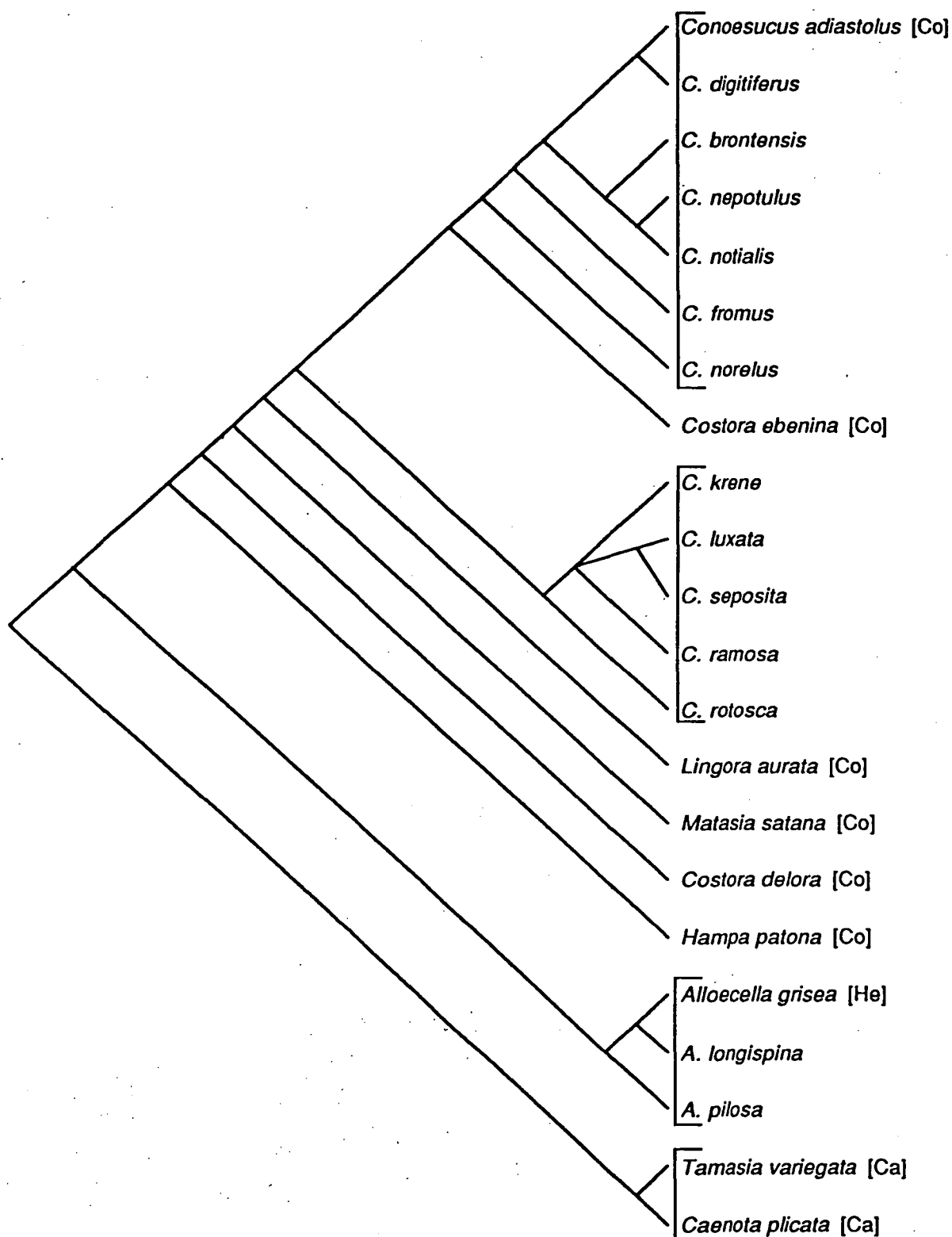
Figure 6.9. Consensus tree including the Tasmanian taxa, based on pupal characters only. Clades congruent with the tree based on all characters (Fig. 6.6) are bracketed.

merging of the conoesucid genera *Hampa*, *Matasia* and *Lingora* (although this conflicts with adult data-see Taxonomy Introduction, 5.1).

However, analysis including additional taxa shows that not all existing taxa are monophyletic. Monophyly of the Conoesucidae is demonstrated conclusively, but failure to demonstrate monophyly for the families Helicophidae and Calocidae on the basis of larval and pupal characters means that their status remains uncertain. Future analysis of a more complete larval data set (such as that for Tasmanian taxa) and adult characters may clarify their status. Additional karyological data is likely to be particularly informative, as chromosome number is characteristic at the family level for Tasmanian taxa (ch. 2). In the absence of evidence to support an alternative classification of these family groups, the current classification should remain unchanged.

The grouping of New Zealand taxa with Australian confamilials suggests that some species are congeneric, e.g. *Pycnocentria* and *Costora*. However, any synonymies must await more complete studies of all the New Zealand species - few were available for inclusion in this analysis. In other groups, southern hemisphere taxa have been designated differently in different places due to insufficient comparative study of related taxa (e.g. plant genera *Leptospermum* and *Kunzea* in Australia and New Zealand (G. Jordan, pers. comm.)), and this may be the situation with some Trichoptera.

Antipodoecia and *Anomalopsyche* are closely related, providing evidence for a Gondwanic origin of the families studied. Additional data are required to determine whether it would be appropriate to transfer these species to the Helicophidae, with which they group in this analysis. This grouping supports the conclusion of Flint (1981), based on adult, larval and pupal characters, that the closest relatives to Anomalopsychidae are the Beraeidae and the Helicophidae, and possibly the Antipodoeciidae.

Trees based on pupal characters show some congruence with trees based on larval characters, although groupings are weaker and less well resolved by pupal characters. This may be due to the relative paucity of pupal characters, and possibly to a lesser degree of specific differentiation in pupal morphology than in larvae.

The derived phylogenies do not differ greatly from that reflected in the existing classification, although there are some disparities. Species of Conoesucidae are more closely related to each other than to other taxa, but not all species of Calocidae and Helicophidae are most closely related to confamilials. Thus, although these analyses have further resolved relationships within families, the phylogeny remains unresolved at the family level.

In these analyses all characters were weighted equally; however, examination of the disparities between the cladograms and current classification may lead to subjective reinterpretation of the reliability with which particular characters reflect phylogenetic relationships. For example, an internal character such as testis structure, which groups *Costora delora* with other *Costora*, seems likely to be more conservative and therefore a more reliable indicator of phylogeny than a character such as tergite 9

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pigmentation (uniting *C. delora* with *Lingora+ Hampa + Matasia*), which may be influenced by stage of development, and is less well defined and therefore scored more subjectively.

Nothing is known about the function of most characters and therefore the selective pressures influencing them, or the genetic control of their expression. Therefore, it is difficult to assess the likelihood of convergence in character states. Subsequent analysis could include *a priori* weighting of characters according to their complexity and possible selective pressures (hypothetical or empirically demonstrated). In this study, some characters that might be considered *a priori* to be of value in showing relationships, e.g. the separation or fusion of the protrochantin from the pleuron, were found to be convergent and therefore uninformative.

Clearly, results of such phylogenetic analyses are dependent on the characters chosen and the way states are designated. Perceived differences in complex shapes may be difficult to define as discrete states, e.g. the shape of the pronotum anterolateral corner or the pupal terminal processes. There is no well defined scientific procedure by which characters are generated, and problems of character definition and character state delineation have recently been analysed by Pogue & Mickevich (1990), who conclude that the "synthetic" method normally used is deficient, mainly due to its attempt to force highly variable features into a few states.

Although the shortest (i.e. optimal) trees found by parsimony analysis may not be in complete agreement with the current classification (e.g. Fig. 6.6), trees agreeing with current groups (e.g. Fig. 6.7) may not be so far from optimal that the existing classification should be changed. As Baverstock (1987) has pointed out, the "nearly as good" tree can be very different from the "best" tree; a single character may account for large differences between trees.

The phylogeny proposed should be regarded as a hypothesis, which can be tested and modified as new comparative data become available. Analysis including additional taxa from these families will test the monophyly of groups found in this analysis. Character states predicted on the basis of this phylogeny can be tested with new character information, e.g. where there are much missing data for some characters (such as chromosome numbers), or taxa, e.g. *Hampa patona*. Discovery of *Hampa* larvae will enable testing of part of the phylogeny through confirmation or refutation of the character states predicted (Table 6.4).

Deficiencies of data in this study result mainly from the inadequacy of species descriptions as sources of character state information. Published descriptions generally emphasize characters which are of use for species identification, and these may be only a small proportion of those valuable for phylogenetic analyses. Detailed descriptions and drawings such as those of Lepneva (1966) are required, rather than mere diagnoses. Even so, interpretation of descriptions in terms of character states equivalent to those scored from specimens can be difficult.

Many possibilities for further exploration of character evolution arise from the results of this study. Case characters are particularly interesting, as they represent a

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Table 6.4. Predicted character states for undetermined larval characters of *Hampa patona.*

Char. no.	state	Char. no.	state
1	0	29	0/1
2	2	30	0/1
3	0	41	1
4	0	42	1
5	1	43	0/1
6	1	60	1
7	0	61	0/1
8	1	62	0/1
9	0	63	0
10	0	64	0
11	0	65	1
12	2	66	1
13	0	67	0
14	1/0	68	1
15	1	69	2
16	0	70	1
17	0	71	1
18	0/1	74	1
19	0/1	75	0/1
20	1	77	1
21	0/1	78	1
22	1	79	0
23	0	80	1
24	0		
25	0		
26	1		
27	1/2		
28	0/1		

structural record of behaviour.

Sound phylogenies (derived from cladistic analysis) are prerequisite for zoogeographical analyses (Ross 1974); however, before this phylogeny could form the basis of such analysis, more taxa must be included to give accurate representation from all the relevant zoogeographical regions. In particular, taxa from the Australian mainland must be included. Zoogeographical analysis may not be informative, though, since the phylogeny represented in Fig. 6.2 fails to reveal any clear correlation between phylogenetic relationship and geography. Taxa as disjunct as those from Australia and New Zealand did not form clearly separate groups.

This close relationship of the Australian and New Zealand taxa suggests that these taxa may represent an old and conservative group that has changed little since the separation of New Zealand and Australia (see ch. 5.4).

In conclusion, despite the problems discussed, a phylogenetic tree based on cladistic analysis of characters of several types will better represent the true phylogeny than a phylogeny based on an "evolutionary scenario" of evolution of a few characters. The phylogeny of Trichoptera based on pupation, proposed by Wiggins & Wichard (1989), has been strongly criticised by Weaver (1991) on these grounds.

Trees resulting from even a preliminary analysis such as this have considerable heuristic value and provide a basis for further investigation of phylogenetic relationships and character evolution. This cladistic analysis of the southern hemisphere sericostomatoid families establishes for the first time the monophyly of some of the existing family and generic taxa (Conoesucidae, *Conoesucus*, *Alloecella*), and provides evidence for a change in status of some taxa (*Lingora*, *Hampa* and *Matasia*). The status of other taxa (Helicophidae, Calocidae, Antipodoeciidae, Anomalopsychidae, *Costora*) requires further investigation.

CHAPTER 7. GENERAL DISCUSSION

7.1 Status of Conoesucidae, Calocidae, Helicophidae and Antipodoeciidae.

The findings of this study have resolved some of the systematic problems of the group outlined in the General Introduction, but other problems remain. The Conoesucidae have been conclusively shown to be monophyletic (ch. 6), but the status of the Calocidae, Helicophidae and Antipodoeciidae remains unclear. Monophyly has not been demonstrated for these families and reliable diagnostic characters are difficult to find, at least in immatures. However, in the absence of evidence to support alternative classification, the current family classification should remain unchanged.

Clarification of the problems with these families was made more difficult by the small number of species for which larvae were found and associated with adults. The species not associated are apparently uncommon (pers. obs., Neboiss 1977), and occupy unusual habitats such as bogs or waterfalls (pers. obs.). Also, larvae of Antipodoeciidae are small and cryptic.

The framework developed here enables classification of mainland species of Conoesucidae. The status of the monospecific genus *Coenoria*, the only conoesucid genus not occurring in Tasmania, requires further investigation. It has a tibial spur formula of 2:2:2, unlike other Conoesucidae with 2:2:4. It also occurs in the far north of Australia, whereas other species are found in cool waters south of southern Queensland (Neboiss 1988). The larva is not known.

This study has gone some way towards elucidating relationships within the Sericostomatoidea, but monophyly of remaining taxa needs to be established before their relationships can be resolved.

7.2 Applicability of Methods.

The methods applied to Trichopteran systematics for the first time in this study (karyology, allozyme electrophoresis and morphometric analysis) have all contributed data valuable for elucidation of problems not resolved on the basis of descriptive morphology alone. Additional important morphological characters are likely to be revealed by the use of scanning electron microscopy.

The karyological study showed that chromosome number varies at the family level in the group studied, and therefore karyological data will be particularly valuable for further resolution of family divisions and relationships.

The electrophoretic data was, as expected, useful for the delimitation of species, as there was greater genetic divergence between species than between conspecific populations. Although allozyme data is generally considered useful only within genera (Berlocher 1984, Richardson *et al.* 1986), the degree of variation at different taxonomic levels will depend on the group (J. Benzie pers. comm.). The low genetic variation found in the species examined indicates that the method may be applicable to problems of generic status, in the Conoesucidae at least, such as the validity of *Lingora, Hampa* and *Matasia*. Examination of generic relationships would require an

electrophoretic survey of the entire family.

Continuing development of new biochemical techniques for use in insect systematics (e.g. mtDNA analysis) promises new insights, although such methods seem likely to remain impractical for most taxonomists.

Morphometric analysis, although limited to univariate analysis in this study, enabled quantification of the range of variation in previously diagnostic characters and assignment of probability levels to their usefulness. New methods of shape analysis (Rohlf 1990) offer solutions to problems of defining and describing complex character states. In this study, problems of shape description were encountered with male genitalia (the differences in *Conoesucus brontensis*, *C. adiastolus* and *C. nepotulus* were difficult to define) and pronotal shape (definition of slight differences observed e.g. between *Costora seposita* and *C. luxata*).

Cladistic analysis, applied to the families studied here for the first time, proved valuable in establishing monophyly of some taxa, and in examination of the character distributions resulting in other groupings. Although the outcome of analysis will depend on the characters used and the designation of states (e.g. Pogue & Mickevich 1990), such analysis was particularly valuable for examining character state distribution and highlighting the characters which are important in various groups, enabling development of hypotheses for further analysis.

Cladistic analysis of adults of the group studied would be very informative, to allow valid comparison between classifications based on different life stages. Such comparison cannot be made at present, since the existing classification was developed on the basis of intuitive, not cladistic, analysis of adults. The frequent incongruence of phenetic classifications of larvae and adults of holometabolous insects (e.g. Rohlf 1963) was taken by Hennig (1943, cited in Dupuis 1984) as demonstration that there is no absolute coincidence between similarity and genealogy (Dupuis 1984), i.e. cladistic relationships are not the same as the phenetic relationships, since the cladistic relationships of adults and larvae of the same species must be the same (Sokal & Sneath 1963). Therefore, phenetic analysis is inadequate for establishing classification which reflects genealogical relationships. However, this interpretation of incongruence is valid only if the set of organisms being studied is monophyletic, which is just what is to be demonstrated (Dupuis 1984).

The close relationships of some Australian and New Zealand taxa shown in this study mean that New Zealand taxa should be included in any further analysis of the group.

7.3 Use of Data from Immatures.

As expected, information from larvae and pupae enabled refinement of the existing classification based on adults. The existing classification based on adults was largely supported by data from immatures, although evidence from immatures supports some generic changes, and more information is needed on the calocid, helicophid and antipodoeciid family groups. For other Trichoptera (e.g. Wiggins & Wisseman 1990), shared derived larval characters have indicated close common ancestry (and congeneric status) not previously recognised on the basis of adults. Cowley (1978) reinterpreted

several relationships in the light of new larval data, although without phylogenetic analysis.

The importance of knowledge of larvae for delimiting species was demonstrated in this study, by showing the presence of more species than were recognised on the basis of adult morphology (*Conoesucus adiastolus* sp. n., *C. brontensis*, *C. nepotulus*). Correct identification of morphologically similar adults by rearing from distinct larvae enabled a search for diagnostic characters of adults.

In Lepidoptera also, characters of immatures (eggs, larvae and pupae) have been used in systematic studies, for diagnosis of species (Mutuura 1980) and elucidation of higher classification (Common 1975, Nielsen 1989). In some cases larval characters have strongly disagreed with relationships proposed on the basis of adults, such as the placement of *Heterobathmia* in Micropterigidae, which subsequent study of immatures clearly refuted (Kristensen & Nielsen 1983). After doubts about the subordinal classification had been raised earlier by larval characters, Common (1975, p.199) suggested that "[f]urther detailed study of the larvae of primitive families....may help to resolve the question." The example of *Heterobathmia* shows that although larvae may provide a rich source of new characters, they may raise further problems of classification!

There are also many examples in the Lepidoptera of species for which differences in larval morphology and/or ecology permit diagnosis of morphologically similar adults (e.g. Matsuoka *et al.* 1983). Different types of data are likely to have different systematic value in different taxa; for example, electrophoretic characters are more useful than chromosome number or immature morphology in delimitation of some species of Lepidoptera (Sims 1979).

The strong emphasis of systematic work on the adult stage in most groups of aquatic insects is somewhat surprising, considering the value of systematic data from immatures, and the relative life spans of the different stages. In Trichoptera, Plecoptera (Hynes & Hynes 1975, Yule 1985), most Ephemeroptera (Brittain 1982, Marchant 1982, Marchant *et al.* 1984) and other aquatic groups including Psephenidae (Williams 1980), the larval stage lasts a year or more, whereas the adult lives only a few days or weeks. The common name for Trichoptera ("caddis-fly") refers to the larva, although its origin is uncertain and there are several alternative derivations (Hickin 1967).

This general emphasis on adults has a historical basis, and probably reflects the viewpoint of entomologists rather than freshwater biologists. Initial workers on the groups have often been entomologists, and indeed most of the early development of insect classification was based on the adult stage (Wiggins 1981). In Trichoptera, the first Australian species was described from adults (*Plectrotarsus gravenhorsti* Kolenati) in 1848. The first larva described, in 1879, was mistakenly identified as a mollusc (Helicopsychidae from Tasmania) (Neboiss 1988). For many years, all major new studies were based entirely on adults (e.g. Mosely & Kimmins 1953). However, more recent studies have usually been more balanced and deal with both immatures and

adults (e.g. Wells 1985, St Clair 1991), and much systematic work has also been done on immatures of other aquatic groups (e.g. Hynes 1978, 1989, Suter 1978, Allbrook 1979).

The use of data from different life stages raises questions about the selective pressures acting on the different stages and their influence on character variation, and hence the reliability with which characters reflect genealogical relationships. Most discussion of such influences is of course speculative. Hynes (1984) proposes that for aquatic insects, most of the selective pressure exerted on the species has been on the immature stages, as the adult life is brief and primarily reproductive. Brittain (1982) suggests that mayfly adults show general uniformity in structure because their main functions are mating and oviposition (they are non-feeding), but in contrast the nymphs show considerable diversity in habitat and appearance. Therefore the nymphs of mayflies are likely to be more useful systematically, and new species have been described mainly on the basis of nymphs (e.g. Bae *et al.* 1990). In relation to Trichoptera, Schmid (1979) has asserted that adults are a richer source of morphological characters than larvae, and claimed that therefore knowledge of larvae is not necessary for sound classification, a claim which Wiggins (1981) has presented much evidence to refute.

On the basis of Hynes' (1984) proposal, it might be predicted that larvae of Trichoptera will be more morphologically diverse than adults, due to their longer life and subjection to perhaps a greater variety of selective pressures. However, sexual selection may lead to greater diversity among adults, particularly in genitalic features, to ensure reproductive isolation.

The "lock and key" hypothesis (that genitalic incompatibility provides mechanical reproductive isolation between species), proposed to explain the species specificity of insect genitalia, has been critically examined by Shapiro & Porter (1989). This hypothesis has generally not been supported by evidence (Scudder 1971, Shapiro & Porter 1989), and it seems instead that genitalic morphology may often be a by-product of other processes, rather than a direct target of selection (Shapiro & Porter 1989). That is, differences arise as a result of isolation, and rarely function to cause it. It remains unclear how specific differences in genitalia arise and what they are for (Scudder 1971).

No functional analysis of genitalia structure has been done in Trichoptera, but in Lepidoptera interspecific matings are known to occur (e.g. Oliver 1979, Grula & Taylor 1980), and some can mate without parts of their genitalia (Sengun 1944, cited in Shapiro & Porter 1989). Therefore, premating isolating (or recognition *sensu* Paterson 1980, 1982) mechanisms are likely to be more important than genitalic incompatibility. For example, Petersson & Solem (1987) have shown that premating mate recognition by male Leptoceridae (Trichoptera) is mainly visual, and they suggest that mating swarms of males are a species-specific mating aggregation which prevents interspecific mating.

Pheromones have been shown to be important in premating isolation in many Lepidoptera (Roelofs & Comeau 1969, Roelofs & Brown 1982) and other insects, and

sex pheromones have been found in Trichoptera although few species have been studied (Wood & Resh 1984, Resh *et al.* 1987). Pheromone studies in Trichoptera are likely to be useful in revealing systematic relationships at the species and family level, and interordinal relationships between Trichoptera and Lepidoptera (Resh & Wood1985). In the group studied, the modified structure of male maxillary palps and the presence of probable scent organs on the male head in some species indicate the likely importance of pheromones in interaction between the sexes. In many groups of Trichoptera, adults have paired exocrine glands on abdominal sternite 5 (Wood & Resh 1984), which have been shown to be the most likely site of female sex pheromone production in three species studied by Resh & Wood (1985).

7.4 Further Studies.

Systematic study arising from the present study should concentrate on the family status of the Calocidae, Helicophidae and Antipodoeciidae, and should use several types of data from all life stages. Resolution of these family relationships and others in the Sericostomatoidea is important systematically, and because of the distribution of the group is also of biogeographic importance. The South American fauna should be studied more closely to determine which families occur there, and their relationship with other southern hemisphere faunas. Although Flint (pers. comm.) suggests that Chilean South America is now fairly well collected so that novelties are rather rare, immatures are not known for many species, although they are needed to sort out uncertain relationships.

Females are another potential source of valuable systematic data. Most species of Trichoptera are defined mainly on the basis of male genitalia, and characters of females have been little used. Females are morphologically conservative compared to males, lacking specialised wing venation or maxillary palps, and therefore may shed light on interspecific and higher levels of classification. Weaver (1984, pers. comm.) considers that the egg extrusion and deposition behaviour of the female is phylogenetically important in the order.

A further avenue for exploration is the systematic value of the larval case, which is the most conspicuous character of the larva. Case type is genetically determined (Cummins 1964), and is considered to be generally characteristic at the generic level (Wiggins 1977). Previous systematic use of case characters (e.g. Cowley 1975), and observation in this study that case characteristics are systematically useful at the generic level (shape) and specific level (shape and material), leads to questions about the degree of flexibility in case materials and shape (i.e. the reliability of these characters), and the selective pressures acting on the evolution of cases. Do different case types function differently? There is evidence that case type affects predation (Otto & Svensson 1980, Jackson 1984) and respiration (Jackson 1984). What is the significance of different materials? Is their use influenced by availability, behavioural limitations, or functional properties such as buoyancy, respiration, durability, rigidity? Do changes in material with age of the larva (as in *Conoesucus norelus*) result in concommitant changes in its biology? Unfortunately, past discussion of case function

has often suffered from "the inference of function from morphology" (Lauder 1990) (e.g. Tomaszewski 1973, Mackay & Wiggins 1979), with few studies using direct experimental measurement of function.

Functional analysis of structure can help in understanding the causal basis of character distributions on cladograms, and general patterns and principles in the evolution of form and function (Lauder 1990). Other unusual larval structures found in this study, which raise questions about function, include the posterior-facing lateral sclerites on the anal proleg of *Lingora* and *Matasia*, and the abdominal humps (reduced dorsal hump and ventral bulge) of the Conoesucidae.

Collection records are an unutilised source of information on life history, and possibly community structure (e.g. are there patterns of co-occurrence in species or case type?). Obviously, the reliability of such data is limited by the accuracy of identification.

In conclusion, the foregoing discussion demonstrates the potential for further studies of Trichoptera to contribute to general concepts in many areas of biology. The present study has contributed to systematic knowledge of the families studied, and Trichoptera in general, by investigation of the immatures and application of methods not previously used in systematic studies of the order. Knowledge of the immatures, particulary in an aquatic insect group, makes possible a whole range of studies including biology and ecology, life history, and functional analysis of morphology, all of which contribute to understanding of the evolution of the group.

"And that....is the ultimate fascination in our work- the opportunity to discover some of the marvellous diversity of the planet Earth and to comprehend the natural processes through which it came to be."

(G.B. Wiggins 1984, p. 10; address to the 4th International Symposium on Trichoptera.)

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APPENDIX 1

Figures 1-19. Gel diagrams for scorable enzymes. Enzyme abbreviations are given in Table 3.2. Numbers representing species:

      1 *Conoesucus brontensis*

      2 *Conoesucus adiastolus* sp. n.

      3 *Costora ramosa*

      4 *Costora krene*

      5 *Costora seposita*

      6 *Costora luxata*

M = male adult; **F** = female adult; **L** = larva

* = repeated sample

Figs 1-8. *C. brontensis* and *C. adiastolus*

Figs 9-13. *C. ramosa* and *C. krene*

Figs 14-19. *C. seposita* and *C. luxata*

1

ACON

2

1

O

| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 |
| M | M | M | M | M | F | M | M | F | M | M | M | F | M | M | L | L | L | L | L | L | M |

2

GPD

O

| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 |
| M | M | M | M | M | F | M | M | F | M | M | M | F | M | M | M | M | L | L | M | F | F | L | L | L | M |

3

GPI

O

| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 |
| M | M | M | M | M | F | M | M | F | M | M | M | F | M | M | M | M | L | L | M | F | F | L | L | L | F |

4

PGM

O

| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 |
| M | M | M | M | M | F | M | M | F | M | M | M | F | M | M | M | M | L | L | M | F | F | L | L | L | M |

5

IDH

2 — — — — — — — — — — — — — — — — «‹‹‹« »»»» — — — — — — ▬
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  M M M M M F M M F M M M F M M M M L L M F F L L L M

6

HK

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  M M M M M F M M F M M M F M M M M L L M F F L L L M

7

MDH

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  M M M M M F M M F M M M F M M M M L L M F F L L L F

8

ME

— — — — — — — — — — — — — — — —

O —
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  M M M M M F M M M M F M M M M L L M F F L L M

9

GPI

O

| 3 M | 3 M | 3 M | 3 M | 3 L | 3 L | 3 M | 3 M | 3 M | 3 M | 3 M | 4 M | 4 M | 3/4 L | 3/4 L | 3 M |

10

PGM

O

| 3 M | 3 M | 3 M | 3 M | 3 L | 3 L | 3 M | 3 M | 3 M | 3 M | 3 M | 3 M | 3 M | 4 M | 4 M | 4 M | 3/4 L | 3/4 L |

11

HK

2

1

O

| 3 M | 3 M | 3 M | 3 M | 3 L | 3 M | 3 M | 3 M | 3 M | 3 M | 4 M | 4 M | 4 M | 3/4 L | 3/4 L | 3/4 L | 3/4 L | 3 M |

12

IDH

2

1

O

| 3 M | 3 M | 3 L | 3 L | 3 M | 3 M | 3 M | 3 M | 3 M | 3 M | 4 M | 4 M | 4 M | 4 M | 4 M | 3/4 L | 3/4 L | 3/4 L | 3 M |

13

MDH

3	3	3	3	3	3	3	3	3	4	4	4	4	4	3/4	3/4	3	3
M	M	M	M	M	M	M	M	M	M	M	M	M	M	L	L	M	M

14

GPD

O ————————————————————————————————————

| 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 |
| M | M | F | F | L | L | L | L | L | L | L | M | L | M | L | L | M | M | M | L | L | M | F | M | M |

15

GPI

O ————————————————————————————————————

| 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 5 |
| M | M | F | F | L | L | L | L | L | L | M | L | M | L | L | M | M | M | L | L | M | M | M | M |

16

IDH

2

1

O ————————————————————————————————————

| 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 5 |
| M | F | L | L | L | L | L | L | M | M | M | L | M | M | M | L | M | M | M | M | L | L | M |

17

MDH

O ————————————————————————————————————

| 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 5 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 5 |
| L | L | L | M | L | L | L | L | L | L | M | L | L | L | M | M | F | M | M | L |
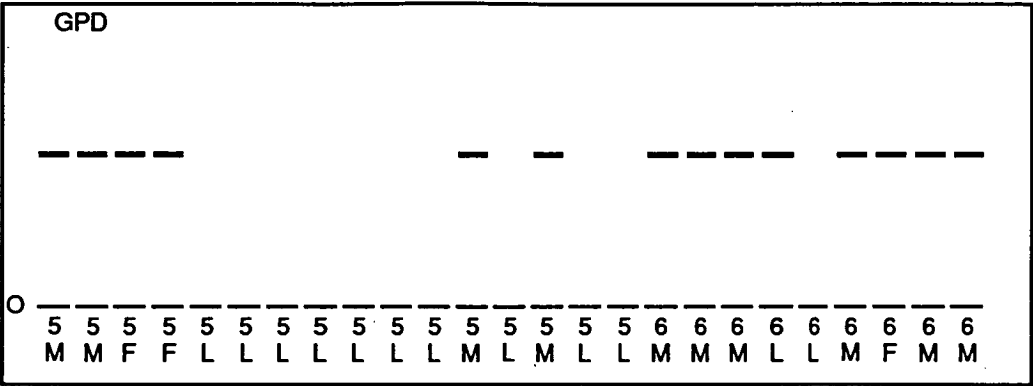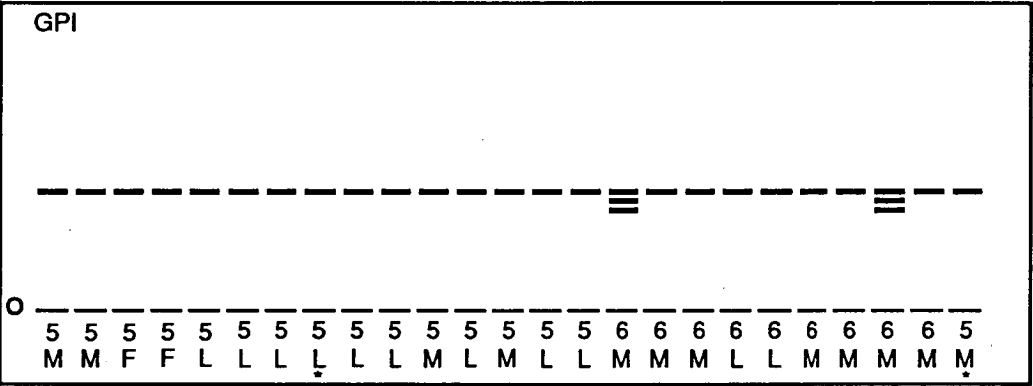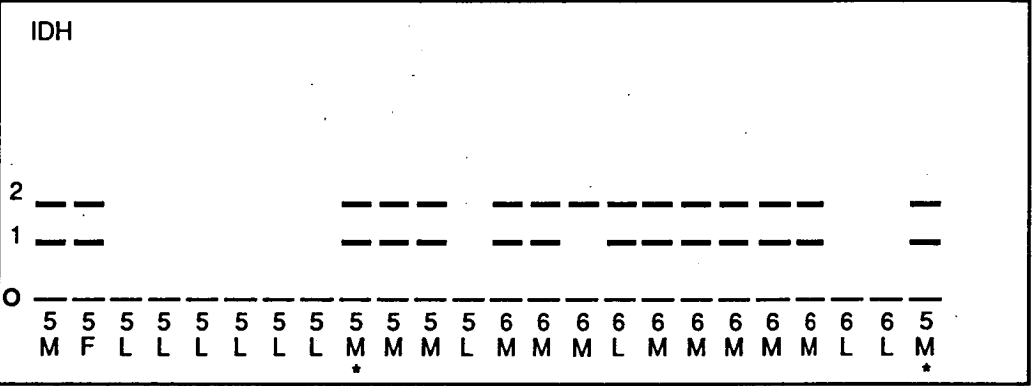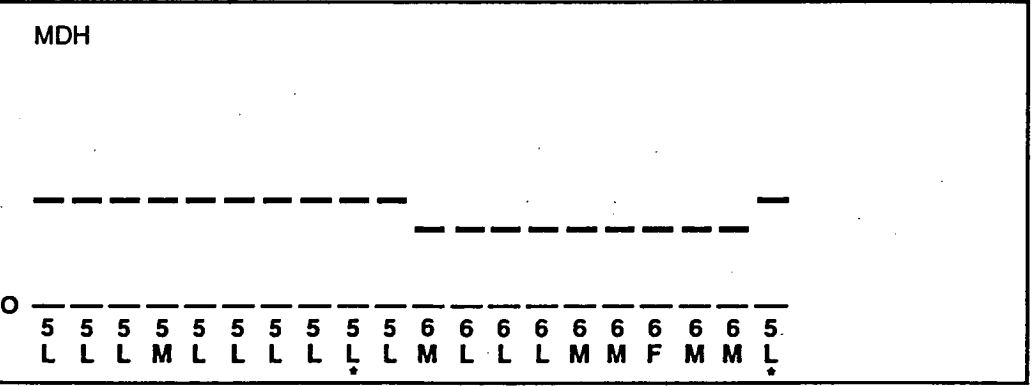
18

ME

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O  — — — — — — — — — — — — — — — — — — —
   5  5  5  5  5  5  5  5  5  5  5  5  6  6  6  6  6  5
   F  L  L  L  L  M  L  L  L  L  L  L  M  L  L  M  M  L
                            *                          *
```

19

SOD

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O  — — — — — — — — — — — — — — — — — — — — — — —
   5  5  5  5  5  5  5  5  5  5  5  5  5  5  6  6  6  6  6  6  6  5
   M  M  F  L  L  M  M  L  L  L  L  L  L  L  M  L  L  L  M  M  M  L
                              *                                    *
```

Appendix 2. Male specimens of *Conoesucus nepotulus* and *C. brontensis* examined from the Victorian Museum (refer to ch. 4.2).
+ Specimens have now been identified as *C. brontensis*
* "   "   "   "   "   *C. adiastolus* sp. n.

Conoesucus nepotulus:

    2, (paratypes) Dip River Falls 1 Dec. 1974 A. Neboiss

    +2   "

    2   " "   "   "   "   "

    1, Iris River trib 15km N Cradle Mt 13 Dec. 1974 A. Neboiss

    5, Mersey River trib 4km E of Liena 15 Dec. 1974 & 17 Nov. 1974 A. Neboiss

    14, Guide River Falls nr Ridgely 18 Nov. 1972 A. Neboiss

    +1, Flowerdale River Meunna 4 Nov. 1972 A. Neboiss

    +1, Leven River nr Heka 17 Nov. 1972 A. Neboiss

    1, Arrowsmith Ck 18km SW Derwent Bridge 9 Dec. 1974 A. Neboiss

    1, Bull Ck Cradle Mt Rd 13 Dec. 1974 A. Neboiss

    2, Creekton Rt nr Dover 14 Nov. 1972 A. Neboiss

    1, Cradle Mts Black Boy 19 Jan. 1976 A. Wells

    1, Wedge River SW Tas 17 Feb. 1971 A. Neboiss

    *3, Sir John Falls Cataract Ck Gordon River trib. 9 Jan. 1977 Neboiss, Coleman, Allbrook.

    2, "   "   "   "

    3, Pencil Pine River Cradle Mt Rd 19 Jan. 1976 A. Wells

    *3, Ropeway Ck 400m below Smith & Gordon River junction 2 Feb. 1977 Coleman, Richardson, Edgar

    *4, small creek Gordon River 0.5km upstream Olga River 23 Feb. 1977 Coleman & Allbrook

    1, Cradle Valley Rd 15 mls N of Waldheim 18 Jan. 1976 A. Wells

    9, Waldhiem Cradle Mt N.P. 7 Feb.1971 A. Neboiss

    12, Gordon River 0.5km below 2nd Split 12 Jan. 1977 Coleman, Allbrook, Neboiss, Swain

    1, Farm Ck Murchison Hwy 21 Jan. 1976 A. Wells

    1, Condominium Ck nr Mt Eliza 9 Feb. 1965 A. Neboiss

    1, Russell Falls 20 Feb. 1971 A. Neboiss

    *1, Franklin River-Roaring Ck junction 1km above Gordon River 8 Jan. 1977 Coleman, Neboiss, Allbrook.

Conoesucus brontensis:

    4 (paratypes) 5km W of Bronte small creek 8 Nov. 1972 A. Neboiss

    1, Mersey River Liena 16 Nov. 1972 A. Neboiss

    13, Collingwood River Bridge Lyell Hwy 9 Dec. 1974 A. Neboiss

    2, 5km W of Bronte small creek 8 Nov. 1972 A. Neboiss

    3, Fisher River Pencil Pine Grove below Lake Mackenzie dam 15 Dec. 1974 A. Neboiss

APPENDIX 3.

Map and list of collection sites.

0   50   100km
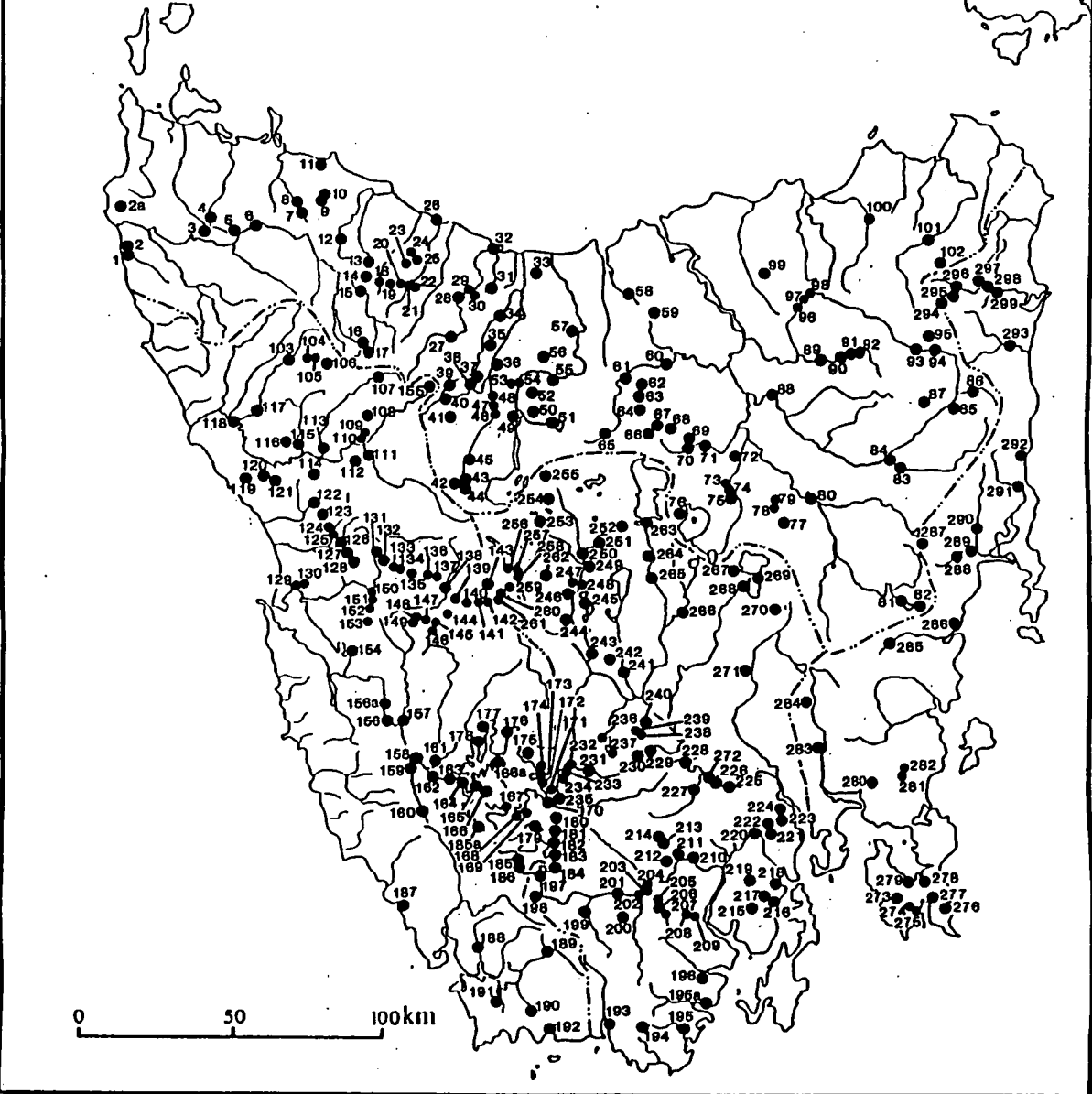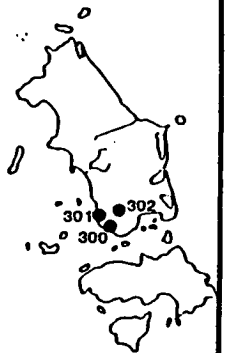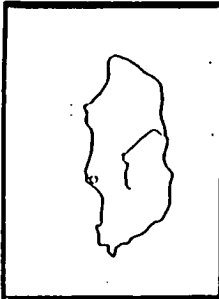
Site no.	Locality	Tasmap ref.
1	Nelson Bay River Temma Rd NW	7815 058 441
2	Bluff Hill Creek 12km S of Marrawah	7815 038 575
2	Sundown Creek Temma Rd NW	7815 057 454
3	Eckberg Creek 12km S of Roger River	7815 313 499
4	Duck River 6km SW of Roger River	7915 338 557
5	Trowutta Arch	7915 415 520
6	Arthur River Tayatea Bridge	7915 484 526
7	Dip River Falls	7915 634 558
8	Dip River trib. S of Mawbanna	7915 609 596
9	Newhaven Creek NW	7916 694 602
10	Alarm River NW	7916 700 618
11	Wilson Creek near Hellyer	7916 695 732
12	Flowerdale River Meunna	7915 717 507
13	Inglis River NW	8015 854 397
14	Cam River Oonah	8015 840 350
15	Hellyer Gorge Murchison Hwy	8015 838 298
16	Gully Creek Murchison Hwy	8015 826 125
17	Fossey River Murchison Hwy	8015 846 102
18	East Cam River Nw	8015 895 328
19	St Josephs River	8015 926 314
20	Guide River near Hampshire	8015 966 311
21	Emu River Upper Natone Rd	8015 988 304
22	Wollastonite Creek E of Hampshire	8015 995 301
23	Guide River near Highclere	8015 979 383
24	Guide River Falls near Ridgley	8015 995 428
25	Pet River Highclere Rd	8015 009 401
26	Burnie	8015
27	Leven River Loongana	8015 144 144
28	Leven River near Heka	8015 157 279
29	Leven River Gunns Plains	8115 187 307
30	Preston Creek above Falls	8115 216 288
31	Crawfords Creek 1km N of Central Castra	8115 258 288
32	Ulverstone, 4km NW	8115
33	Don River Eugenana caravan park	8115 418 356
34	Wilmott River Spellman Bridge	8115 299 217
35	15 mls S of Wilmott	
36	Tin Spur Creek near Lake Cethana	8115 288 900
37	Lehmans Creek Cradle Valley Rd	8114 221 018
38	Bull Creek Cradle Valley Rd	8114 220 013
38	Weaning Paddock Creek Cradle Valley Rd	8114 189 000
39	Iris River Cradle Valley Rd	8014 134 994
39	Iris River trib. 15km N of Cradle Mtn	
40	Black Bog Creek Cradle Valley Rd	8014 115 969
41	Cradle Mt	
41	Dove River near Dove Lake	8014 135 882
41	Dove River near Mt Kate hut Cradle Valley	8014 124 902
41	Dove River-Ronny Creek Cradle Valley	8014 124 899
41	Lake Dove Cradle Valley	
41	Lake Lilla outflow Cradle Valley	8014 129 883
41	Lilla Creek at road Cradle Valley	8014 124 899
41	Ronny Creek at road Cradle Valley	8014 124 899
41	Ronny Creek, Overland Track Cradle Valley	8014 121 893
41	Waldheim Cradle Valley	8014 119 897
42	Forth River Frog Flats Overland Track	8114 173 673
42	unnamed creek 0.25km E of Frog Flats Overland Track, Cradle Mt NP	8114 179 678
43	Douglas Ck High Bridge, near Old Pelion Hut Cradle Mt NP	8114 198 690
43	Douglas Creek Pelion Rangers Hut Cradle Mt-L. St Clair NP	8114 208 685
43	Douglas Creek upstream confluence with Lake Ayr outlet stream	8114
43	Lake Ayr outlet stream about 100m d/stream of lake	8114 211 696
43	Lake Ayr outlet stream upstream confluence with Douglas Creek Cradle Mt NP	8114

Site no.	Locality	Tasmap ref.
43	small trickle flowing into Lake Ayr Cradle Mt-L. St clair NP	8114
44	Douglas Creek about 2.5km N of Pelion Gap Cradle Mt-L. St Clair NP	8114
44	headwater stream beside Overland Track 100m N of Pelion Gap Cradle Mt NP	8114 217 649
44	unnamed creek, Overland Track about 1.5km N of Pelion Gap Cradle Mt NP	8114
44	unnamed creek, Overland Track about 2.5km N of Pelion Gap Cradle Mt NP	8114 208 661
45	Oakleigh Creek Forth Valley	8114 200 705
46	Borradaile Creek Forth Valley	8114 282 900
47	Lemonthyme Creek Forth Valley	8114 282 934
48	Addison Creek Lorinna Rd	8114 283 946
49	Gads Creek near L. Parangana	8114 353 887
50	Snake Creek Fisher River Rd	8114 402 904
51	Fisher River, Pencil Pine Grove below L. MacKenzie Dam	8114 480 855
52	creek nr Marakoopa Cave W of Mole Creek	8114 406 968
53	Lynds Creek near Liena	8114 332 989
54	Mersey River Liena	8114 357 997
55	Sassafras Creek 4km W Mole Creek	8114 466 996
56	Minnow River S of Paradise	8115 446 088
57	Dasher River Bryan's Bridge S of Sheffield	8115 523 132
58	Saxon Creek 10km NW Frankford	8215 720 310
59	Franklin Rt Frankford	8215 812 230
60	Meander River 3km N Westbury	8215 847 061
61	Deloraine	8214
62	Quamby Brook near Osmaston	8214 770 993
63	Quamby Brook, Quamby Brook	8214 757 950
64	Quamby Brook Golden Valley	8214 766 917
65	Meander River 7km SW of Deloraine	8214 640 832
66	Liffey River above falls	8214 797 834
67	Bluff Creek near Liffey	8214 819 858
68	Liffey River Liffey	8214 868 853
69	Brumby's Creek nr Forest farm N of Blackwood Ck	8214 922 808
70	Garcias Creek near Blackwood Creek	8214 922 776
71	Brumby's Creek near Canara	8214 972 783
72	Lake River 1.5km W of Pisa	8314 080 742
72	Lake River 200m W of Pisa	8314 089 738
72	Lake River 5km S of Delmont	8314
73	Dabool Rt Lake River Rd	8314 053 652
74	Sugarloaf Creek Lake River Rd	8314 064 622
75	Shoobridge Creek Lake River Rd	8314 067 603
76	Hydro Creek near Arthurs Lake	8214 553 888
77	Isis river near Auburn	8314 235 522
78	U51 small creek S of Taylors Creek Auburn Rd	8314 203 583
79	Isis River near Single Hill	8314 204 597
80	Macquarie River 8km W of Campbelltown	8314 323 602
81	Tooms River Just Below Tooms Lake	8413 645 263
82	Tower Rd near Tooms Lake	8413
82	Tower Rd, 20m from Anglers Creek E of Tooms Lake	8413
83	St Pauls River 5km SE of Avoca	8414 625 701
84	St Pauls River Avoca	8414 596 738
85	Fingal Rt	8414 816 900
86	Break O'Day River Killymoon Bridge	8514 880 946
87	Tower Rt near Mangana	8414 723 921
88	Evandale	8314
88	South Esk River Evandale	8314 199 979
89	North Esk River Musselboro Rd	8315 359 063
90	North Esk River Burns Creek Rd	8415 418 076
91	North Esk River nr Ben Lomond Rd	8415 478 081
92	Ford River Upper Blessington	8415 478 089
93	Tyne River Upper Esk Rd	8415 648 085
94	South Esk River near Mathinna	8415 743 091
95	Dan's Rt N of Mathinna	8415 726 132

Site no.	Locality	Tasmap ref.
96	St Patricks River Pecks Hill Rd	8315 287 243
97	St Patricks River Targa	8315 307 266
98	Seven Time Creek near Targa	8315 314 266
99	creek 2km N of Lilydale	8315 178 355
99	Lilydale Falls	8315 178 355
100	Great Forester River 5km NW of Forester	8415 524 543
101	Ringarooma River Moorina	8415 728 467
102	Weld River near Weldborough	8415 774 372
103	Heazlewood River	7915 585 073
104	Luina Creek Luina	7915 648 080
105	Whyte River Luina	7915 657 080
106	Magnet Creek	7915 700 068
107	Hatfield River Murchison Hwy	8014 882 018
108	Animal Creek Murchison Hwy	8014 844 898
109	Farm Creek Murchison Hwy	8014 839 818
110	Farm Creek Lower Pieman Dam Rd	8014 826 803
111	Murchison R S of Tullah, now Lake Rosebery	8014
111	Sterling River Murchison Hwy	8014 843 747
112	Mountain Creek near Rosebery	8014 800 735
113	Huskisson River Lower Pieman Dam Rd	7914 702 784
114	Argent Creek Murchison Hwy	7914 683 703
115	Salmon Creek	7914 592 808
116	Stanley River	7914 576 810
117	Eight Mile Creek Corinna Rd	7914 478 923
118	Corinna	7914 399 870
119	Tasman River W of Zeehan	7914 448 683
120	Heemskirk River W of Zeehan	7914 518 692
121	Piney Creek W of Zeehan	7914 551 672
122	Dundas River Murchison Hwy	7914 674 599
123	Farrell Rt Murchison Hwy	7914 707 554
124	Ewart Creek Murchison Hwy	7914 725 518
125	Henty River 10km NW of Queenstown Murchison Hwy	7914 766 472
126	Yolande River Murchison Hwy	8013 766 472
127	Pearl Creek Murchison Hwy	8013 792 427
128	Conglomerate Creek Queenstown	8013 808 405
129	Hogarth Falls Strahan	7913 641 319
130	10mls E of Strahan	7913
131	King River site 3	8013 892 432
132	Princess River N of Lyell Hwy	8013 909 409
133	Nelson Creek Lyell Hwy	8013 942 379
133	Nelson Valley Creek Lyell Hwy	8013 933 385
134	Nelson River Lyell Hwy	8013 954 378
135	Snake Creek Lyell Hwy	8013 989 368
136	Cardigan River Lyell Hwy	8013 034 352
137	U50 small unnamed creek 7km NW of Collingwood River Lyell Hwy	8013 073 357
138	Collingwood River Lyell Hwy	8013 113 314
138	Cool Creek Lyell Hwy	8013 096 324
139	Double Barrel Creek Lyell Hwy	8013 138 275
140	Franklin River Lyell Hwy 20km SW of Derwent Bridge	8113 190 257
141	Taffys Creek Lyell Hwy	8113 223 256
142	Arrowsmith Creek 18km SW Derwent Br	8113 251 262
142	Griffiths Creek Lyell Hwy=Arrowsmith Creek	8113 251 262
143	Franklin River above Lake Dixon	8113 261 321
144	Loddon River, campsite on Frenchmans Cap track	8013 125 226
145	Lake Vera outflow creek Frenchmans Cap NP	8013 079 194
145	Vera Creek above Lake Vera	8013 079 194
146	Lake Whitham near Frenchmans Cap	8013 071 163
147	Lake Tahune, Frenchmans Cap NP	8013 038 198
148	Lake Nancy near Frenchmans Cap	8013 033 207
149	Lake Gwendolen near Frenchmans Cap	8013 028 203

Site no.	Locality	Tasmap ref.
150	Governor River Crotty Rd	8013 882 304
151	Baxter River Crotty Rd	8013 875 290
152	Andrew River Crotty Rd	8013 857 248
153	Crotty River Crotty Rd	8013 860 213
154	Kelly Basin Macquarie Harbour	8013
155	Vale River Cradle Mountain Link Rd	8014 066 994
156	Lower Gordon River	8012
156	Sir John Falls, Cataract Creek trib. of Gordon River	8012 925 858
157	Franklin River-Roaring Creek junction 1km above Gordon River	8012 965 845
158	Gordon River-Smith River junction area	8012 017 735
159	Olga River 4km above Gordon River junction	8012 001 692
160	Olga River 19km above Gordon River junction	8012 040 547
161	Maxwell- Denison River junction	8013 073 727
162	Gordon River 0.5km above 1st split	8012 064 669
162	Gordon River 0.5km below 2nd split	8012 073 667
163	Gordon River 2km below Serpentine junction	8012 134 667
164	U13 small unnamed creek Serpentine Dam Rd	8012 168 644
165	U12 small unnamed creek just W of Strathgordon	8112 213 637
166	Lake Gordon Site 5 Pleiades Basin nr Junction Ra	8112 289 701
166	U11 small unnamed creek 100m E of Teds Beach Gordon Rd	8112 233 618
166	U15 & 16 near Teds Beach Gordon Rd	8112 231 625
167	Hermit Valley Gordon Rd	8112 305 571
167	U8 W of McPartlan Pass Gordon Rd	8112 315 562
167	U8A about 100m E of U8 Gordon Rd	8112
168	U7 small creek N of Sentinal Ra. Gordon Rd	8112 341 541
169	Wedge River Gordon Rd	8112 370 544
170	Boyd River Gordon Rd	8112 445 579
171	Charlies Creek Clear Hill Rd	8112 455 618
172	Clear Hill Rd site 5	8112 424 654
173	Clear Hill Rd site 4	8112 424 677
174	Adams River Clear Hill Rd	8112 424 698
175	Clear Hill Rd sites 1 & 3	8112 378 740
176	Lake Gordon site 7 Pokana Bay	8112 320 818
177	Lake Gordon Holley Basin	8112 248 833
178	Lake Gordon site 2 Pearce Basin	8112 219 801
179	Maria Creek Lake Pedder impoundment	8112 420 503
180	Huon River Crossing Port Davey Track	8112
180	Huon River Scott's Peak Dam Rd	8112 483 548
180	Huon River-Serpentinite Creek junction Scott's Pk Dam Rd	8112 485 533
181	Sandfly Creek Scott's Peak Dam Rd	8112 484 493
182	"Channelled Creek" Scott's Pk Dam Rd	8112 479 434
182	Condominium Creek Scott's Pk Dam Rd	8112 479 434
183	Twin Creeks Scott's Peak Dam Rd	8112 483 413
184	Red Tape Creek Scott's Peak Dam Rd	8111 482 367
185	Forest Creek Lake Pedder impoundment	8112 493 222
185	Pebbly Creek Lake Pedder impoundment	8112 352 395
186	Giblin Bay creek Lake Pedder impoundment	8111 358 364
187	Mulcahy Bay Alec Rt	8011 971 253
188	Spring River Port Davey track	8111 233 102
189	Old River-Collins River junction S of Arthur Ra.	8111 460 092
190	Ray River	8111 405 895
191	Melaleuca Creek near Melaleuca	8111 311 919
192	Louisa Creek South Coast track	8111 473 854
193	Damper Creek New River Lagoon	8211 658 850
193	Limestone Creek New River Lagoon	8211 655 837
193	Urquhart Creek New River Lagoon	8210 655 830
194	D'Entrecasteaux River source	8211 782 844
194	Maxwell Ridge, Reservoir Lakes, Picton River source	8211 781 853
194	Picton River trib. above Reservoir Lakes	
194	Pigsty Ponds area, D'Entrecasteaux River source	8211 782 844

Site no.	Locality	Tasmap ref.
195	D'Entrecasteaux River at South Cape Rd bridge	8210 898 827
195	Hythe S of Dover	
196	Creekton Rt nr Dover	8211 966 003
197	Huon River below Scott's Peak Dam	8111 427 351
198	Junction Creek Arthur Plains	8111 408 271
199	Cracroft River Crossing	8111 574 221
200	Lake Riveaux outflow	8211 704 205
201	Huon River near Blakes Opening, Huon Track	8211 690 279
202	Huon-Picton River junction	8211 768 281
202	Trugarra Creek	8211 756 287
203	Huon River Tahune Bridge	8211 778 285
204	Warra Creek South Weld Rd	8211 783 303
205	West Creek Arve Rd	8211 823 257
206	Keoghs Creek Arve Rd	8211 832 223
207	Arve River Arve Rd	8211 842 214
207	Haymans Creek Arve Rd	8211 845 210
208	Crookes Rt Geeveston	8211 913 213
209	Geeveston	
210	Judds Creek Judbury	8212 937 397
211	Russell River Denison Rd	8212 884 408
212	Little Denison River Denison Rd	8211 860 390
213	Russell River Lonnavale	8212 855 433
214	Russell River upper	8212 825 455
215	Nicholls Rt Channel Peninsula	8311 123 233
216	Little Oyster Cove Creek	8311 199 254
217	Oyster Cove Rt	8311 182 275
218	Snug River	8311 206 318
218	Snug River upper	8311 192 311
219	Pelverata Falls	8311 113 319
220	North West Bay River above Wellington Falls	8312 152 478
221	Ferntree Bower	8312 210 478
222	Mt Wellington	
223	Guy Fawkes Rt Hobart	8312 230 507
223	Hobart Rt Strickland Falls	8312 213 492
223	Lambert Rt Churchill Ave Sandy Bay	
223	Sandy Bay Rt above Waterworks Reserve Hobart	8312 232 490
224	Newtown Rt Lenah Valley	8312 208 528
225	New Norfolk	8312
226	Derwent River 3km W of New Norfolk	8312 022 647
227	Plenty River 6km E Moogara	8212 953 623
228	Styx river near Bushy Park	8212 919 713
229	Tyenna River W of Westerway	8212 778 743
230	Russell Falls Creek	8212 765 744
230	Russell Falls Mt Field NP	8212 763 749
230	Tyenna River Mt Field NP	8212 765 739
231	"log creek" Gordon Rd	8212
231	Kallister Creek upstream Gordon Rd	8212 598 665
232	Churchill Creek nr Tim Shea Gordon Rd	8112 545 698
233	Little Florentine River Gordon Rd	8112 527 680
233	U17 small unnamed creek NE of Little Florentine River Gordon Rd	8112 533 691
234	Needles picnic area Gordon Rd	8112 513 657
235	Florentine River Gordon Rd	8112 488 593
236	Valhalla Creek near Twilight Tarn Mt Field NP	8212 648 778
237	Broad River, Lake Dobson outflow	8212 666 739
238	Jones River Ellendale	8212 765 817
239	Montos Creek N of Ellendale	8212 758 834
240	Jones River NE of Ellendale	8212 783 859
241	Dee River 8km W of Ouse	8213 731 024
243	Nive River Lyell Hwy near Wayatinah	8213 599 084
244	creek S of Wentworth Canal C601	8113 513 212

Site no.	Locality	Tasmap ref.
245	Brady's Lake	8113
246	Brown Marsh Creek C601	8113 523 298
246	Clarence River C601	8113 523 297
247	small creek 5km W of Bronte	8113 535 335
248	Nive River 2km W of Bronte	8113 559 324
249	Penelope Creek near Pine Tier Lagoon	8113 582 385
250	Pine River above Pine Tier Lagoon	8113 568 422
251	Little Pine River	8213 623 458
252	Black Bobs Rt Lyell Hwy	8213 662 070
252	Ouse River 8km W of Miena Marlborough Hwy	8214 705 512
253	Nive River above Lake Tidler Central Plateau	8114 437 519
254	NE Lake Rotuli Central Plateau	8114 458 619
255	Powena Creek Central Plateau	8114 463 682
256	Cynthia Bay bottom drag	8113 315 372
257	Derwent River 2km N of Derwent Bridge	8113 350 357
257	Derwent River trib. N of Derwent Bridge	8113 347 356
258	Derwent Bridge Lyell Hwy	8113 363 349
259	Coates Creek Lyell Hwy	8113 324 307
260	Navarre River Lyell Hwy	8113 302 293
261	King William Creek Lyell Hwy	8113 289 268
262	Clarence River Lyell Hwy	8113 449 350
263	Great Lake	8214
263	Great Lake, River Shannon	8214
263	Miena	8214 770 520
264	Penstock Lagoon Trib. Waddamana Rd	8213 806 415
265	Rocky Gully Waddamana Rd	8213 842 324
265	Waddamana Creek	8213 791 355
266	Shannon River 0.5km E of Hermitage	8213 902 216
267	small creek Alma Tier	8313 063 369
268	Clyde River nr Lake Sorell	8313 116 312
269	Interlaken	8313 142 339
270	Blackman River 15km NW Oatlands	8313 209 240
271	Little Den Creek Bothwell Rd	8313 113 028
272	Derwent River nr Plenty railway bridge	8212 989 659
273	Parsons Bay Creek near Nubeena	8411 616 255
273	Plummers Creek near Nubeena	8411 618 257
274	Kennedys Creek Tasman Peninsula	8411 669 231
275	Radcliffe Creek near Port Arthur	8411 687 219
276	Agnes Creek nr Fortescue Bay	8411 773 223
277	Simmonds Creek Fortescue Bay Rd	8411 736 260
278	Allens Creek Tasman Peninsula	8411 703 318
279	Cascades Rt nr Koonya	8411 660 318
280	Iron Creek near Wattle Hill past Sorell	8412 534 656
281	Carlton River Copping Rd	8412 620 683
282	Carlton River trib 1 nr Brooklyn	8412 633 696
283	Native Hut Rt Campania	8312 348 768
284	Wallaby Rt Colebrook	8312 300 912
285	Little Swanport River	8413 584 106
286	Lisdillon Rt Tasman Hwy	8413 820 180
287	Lost Falls Creek near Lake Leake	8413 700 451
288	O'Connors Rt near Doctors Hills W of Swansea	8413 811 396
289	Wye River Tasman Hwy	8513 879 419
290	Swan River Tasman Hwy	8514 893 498
291	Apsley River 5km NW of Bicheno	8514 028 648
292	Douglas River Tasman Hwy	8514 043 736
293	Scamander River Upper Scamander	8515 997 112
294	St Columba Falls Pyengana	8415 770 250
295	South George River	8415 802 274
296	North George River NE	8415 812 306
297	Groom River NW of St Helens	8515 906 322

Site no.	Locality	Tasmap ref.
298	George River Goshen	8515 918 303
299	Powers Rt NE	8515 947 291
300	Cronley Creek SW Flinders Island	8517 906 441
301	Fotheringate Creek SW Flinders Island	8517 878 471
302	Bob Smith Gully Flinders Island	8517 948 497

character	state char name	0	1	2	3	4	5
CASE:							
Case material	1	sand	plant bands	silk	plant panels		
	2	spiral	panels/plates	irregular			
	2a	no projections	projecting bits				
Case shape	3	cylinder	d-v flattened				
	4&5	strongly tapered & curved	slight taper & curve	straight			
Case size cf. larva	6	just longer	same/smaller	much longer			
Case anterior margin	7	straight/slight obl.	strongly oblique				
Posterior closure membr.	8	flat	cone	dome	oblique flat	absent	dors overhang
Post. closure opening	9	round	oval	slit	other		
	10	central	ventral	dors	terminal		
ABDOMEN:							
Shape	11	cylindrical	d-v flattened				
Gills	12	absent	simple	branched			
	12a	few sgts	all sgts				
Lateral fringe	14	absent	present				
Segment 8 spicules	15	bifid	single	absent	both		
	16	row	band				
" 3-7	17	bifid & single	single only	bifid only	absent		
" 2	18	absent	present				
Tergite 9 sclerite	19	single	double				
	20	pigm. mostly	unpigmented	pigm. slightly			
" " post. setae	21	4 -7 pairs	many				
	21a	post. margin	all over				
	22	1-2 pairs long	even sized				
" other setae	23						
Segment 1 ventral bulge	24	absent	present				
" humps	25	prominent	low				
Lat. hump spiny sclerite	26	small oval	large cresent	lacks spines			
longitudinal scler.	27	absent	present				
additional scler.	28	absent	present				
Elongate spicule areas	29	dorsal & ventr.	ventral	absent			
ANAL PROLEGS:							
Lat. scler. pigmentation	30	pale	even brown/irreg.	median v. dark			
" setae	31	even long	stout bristles	few much longer	sparse		
" orientation	32	dorsal	posterior				
Ventral sclerite	33	brown oval	bar (brown/pale)	oval pale			
Accessory hook	34	large	small	medium			
	35	prominent	low				
	36	notched	simple				
Claw convex face setae	37	long black	pale	short?			
Fleshy proc. mes. to claw	38	absent	present				
Anal claw sole plate	39	smooth	toothed				
	40	slopes ventral	perpendicular				
HEAD:							
Shape from dorsal	41	round	tapered/oval				
Dorsal surface	42	flat	posterolateral bumps				
Eyes	43	bulge	smooth				
Texture	44	spiny	honeycomb	smooth			
Colour	45	almost black	dark brown	golden			
Scar colour	46	paler	darker	same			
Scar shape	47	w=2-4l	w much > l				
	48	large	small				
Carina shape	49	around capsule	posteriad of eye	ant/1/2 to eye	absent		
	50	strong	weak				
Antennae position	51	anterior	1/2 way	near eye			
" size	52	l=2w	l>2w				
Minute dorsal setae	53	absent	present				
other setae							
lateral anterior setae	54	2	>2				
Frontoclypeus shape	55	ant w>>post w	ant w just > post w				
	56	ant. strong bulge	slight curve/straight				
	57	constriction strong	cons weak				
" ant.lat. setae	58	2 long+clear curved	many				
" other setae	59	3 lat pairs	2 lat pairs				
	60	no lateral group	lat gp				
	61	all lat prs long dk	post.&mid fine pale	post.&ant pale	all pale		
Ventral pigmentation	62	median only lacking	mostly lacking				
ventral dark scars	63	absent	present				

character	char name	0	1	2	3	4
Ventral setae	64	ns + spine	2 small	other?		
Lateral minute setae	65	absent	2	9 to 18		
Ventral apotome shape	66	triangular	quadrate tapering	long tri/oblong		
anterior margin	67	straight/curved forw	triang projn			
Genae separate	68	wide	abut			
Ventr. mandib. articn	69	prominent	not prom.			
Mandibles shape	70	l=w	l>w			
no. basal setae	71	2	many			
apical teeth	72	absent	present			
mesal brush	73	absent	present			
other mesal structures	74	absent	present			
dorsal margin L/R	75	blade/square tooth	smooth			
Labrum shape	76	oval w>l	rounded quadrate			
ant. margin undertumed	77	yes	no			
median brush	78	short	long			
setae colour	79	pale	dark			
dorsal round brush	80	absent	present			
PRONOTUM:						
texture	81	ant 2/3 spiny	spiny ant band	reticulate	shiny retic.	
no. median elong. scars	82	one	two			
scar colour		same	paler	darker		
Shape in dorsal view	83	square	tapers laterally	tapers ant		
Carina	84	absent	fold	pinched ridge, weak post.curve	ridge,strong post.curve	ridge, straight
Carina shape	85	from comer	from behind comer	1/2-1/3 to ant		
	86	straight	curve dorsad mid			
Carina setae	88	wide space	medium	close		
	89	long	med	short		
Ant-lat comer shape	90	obtuse	square	acute		
	90a	comer not fold under	folded under			
Ant-lat comer shape	91	round	square	pointed		
	92	not projected	proj.	projects strongly		
Anterior margin	93	straight	concave	partly convex		
Fine dorsal setae	94	absent	present			
large dorsal setae	94a	absent	present			
Ant. fine setae	95	present	absent			
ant. large setae	96	absent	3 to 7	many		
	97	rel. fine	very stout			
	97a	v. stout setae absent	present			
Lateral face setae	98	sparse	dense			
Lateral face shape						
MESONOTUM shape	99	square	triang.	w>l		
pigmentation	100	entire	ant 2/3	other		
ant. setae no. rows	101	one	two-four			
	102	long	med-short	mixture		
	103	fine	stout	both		
setae shape	104	tips taper	tips spatulate			
Post setae	105	pair	row or band			
dorsal setae	106	absent	scattered all over	few median		
pale ant. setae	107	absent	present			
METANOTUM scler. all SA	108	absent	SA 1 only	SA 1& 2	all SAs	SA 1&3
	108a	scler. spots	entire area scler.			
Metanotum setae SA1	109	0	1	1-2 lng+1-3smll	>3 long	v. many
SA2	110	0	1	0-3lng+1-3smll	>3long	many
SA3	111	0	1	1-3lng+smll	>3long	many
Metanotum fold	112	absent	present			
LEGS:						
Protrochantin shape	113	slender taper pointed	broad hom/rect/tri			
	113a	small	large			
Fused to propleuron	114	suture	fused			
ant. margin setae		present	absent			
Pleural humps	115	small	large			
	116	pigmented	not			
	117	long setae	minute setae+long			
Hind tibia	118	cylindrical	bent and flattened			
Troch. brush of hairs	119	absent	fore	fore+mid	all	
Fore femur shape	120	l=w	l>w			
OTHER:						
Feeding	121	wood	algae	detritus	moss/liverw	
habitat						

character	state	char name	0	1	2	3	4	
Testes no. lobes		122	4	2				
shape		123	round	long				
colour		124	white	clear	green			
Chromosome number		125	22	25	32-40			
Eggmass colour			green	white				
shape								

APPENDIX 4. B: pupal characters initially scored for phylogenetic analysis; not all were used in final analyses (see Table 6.3).

character / states	char. name	0	1	2	3	4
CASE						
Anterior membrane	P1	flat	domed	opening raised	oblique	absent
	P1a	inset	flush			
	P2	single	double			
Anterior margin	P2a	straight	flared	constricted		
Anterior opening	P3	curved slit	straight slit	oval	seive	
	P4	central	ventrad	dorsad		
	P5	wide	narrow			
Posterior membrane	P6	flat	domed	opening projected	oblique	
Post. end of case	P6a	retained	removed	partly removed		
" opening	P7	circular	oval	slit	seive	
	P8	vertical	transverse			
	P9	central	dorsad	ventrad		
Adhesive discs	P10	anterior	posterior	both	absent	
	P11	ventral	all round			
	P12	one	several	many		
	P13	small	large	medium		
	P14	stalked	not stalked			
ABDOMEN						
Hair fringe: foreleg	P15	absent	dense 1 side	dense 2 sides	sparse 1 side	sparse 2 sides
midleg	P16	absent	dense 1 side	dense 2 sides	sparse 1 side	sparse 2 sides
	P17	tarsus	tibia			
Lat. abdominal fringe	P20	sgts 6-8	sgts 7-8	absent		
Hookplates post. shape	P21	w+l	W>>l			
no. hooks	P22	two-four	eight-15	3 to 7		
	P23	row	scattered			
Ant. hookpl. shape	P24	irreg drop	rectangular	oval		
no. hooks	P25	two-five	many			
Colour	P26	even	pale bands			
Post. on sgt 4	P27	present	absent			
additnal scler. ant. rows	P28	all sgts	sgts 7 & 8	other	absent	
lat. longit. scler.	P29	all sgts	sgts 7&8	absent		
Segt 2 toothed hump	P30	absent	present			
MOUTHPARTS						
Mandibles shape	P31	l > 3w	l < 2w			
curve	P32	strong	slight			
	P33	1/2 curved	1/3 curved			
serrations	P34	large	small	absent		
	P35	square	round			
R more strongly hooked	P36	yes	no			
No. outer basal setae	P37	2	many			
Labrum shape	P38	subquadr	hemisph/cone			
ant. setae	P39	2 pairs	3 pairs	> 3 prs		
post-lat setae	P40	2 prs	3-4 prs	many		
Facial setae	P41	2 prs	other			
TERMINALIA						
Male ventral humps	P42	lat. & central	lat. only	smooth		
Tergite 9 setae	P43	1 row	several rows			
	P44	4-6 prs	many	absent		
processes basal width	P45	wide	narrow			
shape	P46	apex str	turned up	turned up & out	in & up	
	P46a	pointed	round			
	P47	taper evenly	dorsal hump			
Distal overhang	P48	none	short	longer		
Clear terminal setae	P49	present	absent			
Other setae	P50	dors	dors+lat	&ventral		
	P51	basal	entire	distal		
	P52	long	med			
Texture dors	P53	smooth	toothed	scales	papillate	
apical	P54	smooth	toothed	scales	papillate	
Pupation	P55	single	several	lrge aggregates		
	P56	under rocks	plant bases	moss/liverw.	etc.	

APPENDIX 5.

Material examined from New Zealand and South America.

L = larvae; P = pupae

SOUTH AMERICA:

Eosericostoma inaequispina
   3 L, 7 P
                             Chile: Prov. Malleco, Rio Manzanares
                              2 Jan. 1966. Flint & Cekalovic.

Austrocentrus griseus
   6 L, 1 P
                             Argentina: Neuq. Ao. Culebra, 20km S.,
                             San Martin de los Andes
                             2 Feb. 1974. O.S. Flint, Jr.

Notidobiella sp.
   7 L, P cases
                             Chile: Osorno P.N. Puy. Brooklets,
                             2km S. Aguas Calientes
                             2 Feb. 1978. C.M. & O.S. Flint, Jr.

Parasericostoma laterale
   11 L, 1 P
                             Chile: as above. 9 Feb 1978

P. cristatum
   1 L +sclerites, P cases
                             Chile: Palena 22km S. Villa Sta. Lucia
                             24 Jan. 1987. C.M. & O.S. Flint, Jr.

Anomalopsyche minuta
   5 L, 3 P
                             Argentina: Neuquen cascades, 6km N
                             Lago Alumine, 1100m
                             3 Feb. 1987. C.M. & O.S. Flint, Jr.

NEW ZEALAND:

Olinga feredayi
   2 L, 3 P
                             MC, Oxford State Forest
                             18 Dec. 1976. J. McMillan.

Periwinklia childi
   2 L, 1 P
                             CO Rock & Pillar Range 4400'
                             No date. A.G. McFarlane.

Zelolessica cheira
   6 L
                             NN Waikoropupa Springs
                             A.G. McFarlane.

Pycnocentrella eruensis
   4 L, 4 P
                             BP, Mahuia
                             28 Oct. 1964. A.G. McFarlane.

Pycnocentria evecta
   3 L, 2 P
                             no data

Beraeoptera roria
   3 L
                             spring at roadside 1 mile W of
                             L. Lyndon. 26 Oct. 1964.

B. roria pupae
   2 P
                             Whaeo River
                             14 Jan. 1958. A.G. McFarlane.

Confluens sp.
   2 L
                             BP Tauranga Water Supply
                             10 Dec. A.G. McFarlane.

Pycnocentrodes aeris
   2 L
                             Bay of Plenty
                             10 Dec. 1957. A.G. McFarlane.

P. "kehua" & P. aureola
   6 L
                             Kaituna stream
                             13 Oct. 1964.

Pycnocentrodes sp.
   2P
                             FD Te Anau
                             2 Feb. 1961. A.G. McFarlane.

APPENDIX 6. Data matrix used in final phylogenetic analysis.

Species: char.name	2	2a	3	4&5	6	7	8	9	10	11	12	12a
Conoesucus adiastolus	0	0	0	1	0	0	0	0	0	0	0	0
C. brontensis	0	0	0	1	0	0	1	0	0	0	0	0
C. digitiferus	0	0	0	1	0	0	1	0	0	0	0	0
C. fromus	0	0	0	1	0	0	1	0	0	0	2	0
C. nepotulus	2	0	0	1	0	0	0	1	0	0	0	0
C. norelus	2	0	0	1	0	0	0	0	0	0	2	0
C. notialis	0	0	0	1	0	0	1	0	2	0	1	0
Costora delora	0	0	0	0	2	0	2	0	0	0	2	0
C. ebenina	0	0	0	1	0	0	1	0	0	0	2	0
C. krene	0	0	0	0	2	0	1	0	0	0	2	0
C. luxata	0	0	0	0	2	0	4	0	0	0	2	0
C. ramosa	0	0	0	0	2	0	1	0	0	0	2	0
C. rotosca	0	0	0	0	2	0	4	0	0	0	2	0
C. seposita	0	0	0	0	2	0	0	0	0	0	2	0
Lingora aurata	0	0	0	1	1	0	0	0	0	0	2	0
Matasia satana	0	0	0	1	1	0	1	0	2	0	2	0
Hampa patona	2	0	0	1	?	?	?	?	?	?	?	?
Pycnocentrodes aureola	2	0	0	1	0	1	0	0	0	0	2	1
P. aeris	2	0	0	1	0	1	0	0	2	0	2	?
Confluens hamiltoni	0	0	0	1	0	0	0	0	0	0	2	1
Beraeoptera roria	0	0	1	1	0	1	1	0	2	0	2	1
Pycnocentria evecta	0	0	0	0	2	0	0	0	0	0	2	0
P. sylvestris	2	0	0	1	0	0	5	1	4	0	0	0
P. funerea	?	0	0	1	0	0	1	0	0	0	0	0
Conuxia gunni	0	0	0	1	0	0	1	0	0	0	0	0
Periwinklia childi	0	0	0	1	0	0	1	0	0	0	2	0
Olinga feredayi	0	0	0	1	0	0	1	0	0	0	2	0
O. jeanae	0	0	0	1	0	0	2	0	0	0	2	0
Alloecella grisea	2	0	1	1	0	0	3	?	3	1	0	0
A. pilosa	2	0	0	1	0	0	5	3	4	0	0	0
A. longispina	2	1	1	1	0	1	3	1	4	1	0	0
Zelolessica cheira	0	0	0	1	0	0	3	1	4	0	0	0
A'centrella magnicornis	0	1	0	1	0	0	3	?	3	0	0	0
Austrocentrus griseus	2	0	0	1	0	0	5	1	4	0	0	0
Eoser'stoma inaequispina	2	0	1	1	0	1	3	0	2	1	0	0
Parasericostoma laterale	0	0	0	1	0	0	0	0	0	0	1	1
P. cristatum	2	0	0	1	0	0	0	0	0	0	1	1
Notidobiella sp.	2	0	0	1	0	0	1	1	0	0	1	1
Caloca saneva	2	0	0	1	0	0	4	0	0	0	0	0
Tamasia variegata	2	0	0	1	0	0	0	3	0	0	0	0
Caenota plicata	1	0	1	1	0	1	4	?	0	1	1	1
Pycnocentrella eruensis	2	0	0	1	0	0	0	0	0	0	0	0
Anomalopsyche minuta	2	0	0	1	0	0	5	1	2	0	0	?
Antipodoecia turneri	2	0	0	1	1	0	5	1	2	0	0	?

Species: char.name	16	17	18	19	20	21	21a	22	24	26	27	28
Conoesucus adiastolus	0	0	0	1	0	0	0	0	1	0	0	0
C. brontensis	0	0	1	1	0	0	0	0	1	0	0	0
C. digitiferus	0	0	1	1	0	0	0	0	1	0	0	0
C. fromus	0	0	0	1	0	0	0	0	1	0	0	0
C. nepotulus	0	0	1	1	0	0	0	0	1	0	0	0
C. norelus	0	0	0	1	0	0	0	0	1	0	0	0
C. notialis	0	0	1	1	0	0	0	0	1	0	0	0
Costora delora	0	1	0	0	2	0	0	0	1	0	0	0
C. ebenina	0	1	1	0	0	0	1	0	1	0	0	0
C. krene	0	1	0	0	0	0	0	0	1	0	0	0
C. luxata	0	1	0	0	0	0	0	0	1	0	0	0
C. ramosa	0	1	0	0	0	0	0	0	1	0	0	0
C. rotosca	0	1	0	0	0	0	0	0	1	0	0	0
C. seposita	0	1	0	0	0	0	0	0	1	0	0	0
Lingora aurata	1	1	0	0	2	1	1	1	1	0	0	0
Matasia satana	?	3	0	0	2	1	1	1	1	0	0	0
Hampa patona	?	?	?	?	?	?	?	?	?	?	?	?
Pycnocentrodes aureola	0	?	?	0	0	0	0	0	1	0	0	0
P. aeris	0	?	?	0	2	0	0	0	1	0	0	0
Confluens hamiltoni	?	?	?	0	0	0	0	0	1	0	0	0
Beraeoptera roria	0	?	0	0	0	0	0	0	1	0	0	0
Pycnocentria evecta	0	3	0	0	2	0	0	0	1	0	0	0
P. sylvestris	0	?	?	0	2	0	0	0	?	0	0	0
P. funerea	0	?	?	0	2	0	0	0	?	0	0	0
Conuxia gunni	0	?	?	?	2	0	0	0	?	0	0	0
Periwinklia childi	1	?	?	0	0	0	0	0	1	0	0	0
Olinga feredayi	0	?	?	0	2	0	0	0	1	2	0	0
O. jeanae	0	?	?	?	2	0	0	0	?	?	0	0
Alloecella grisea	1	1	0	0	1	0	0	0	0	0	1	0
A. pilosa	0	1	0	0	1	0	0	0	0	0	1	0
A. longispina	0	1	0	0	2	0	0	0	0	0	1	0
Zelolessica cheira	0	?	?	0	1	0	0	0	0	1	1	1
A'centrella magnicornis	?	?	?	0	1	1	0	?	0	?	?	?
Austrocentrus griseus	0	?	?	0	2	0	0	0	0	0	1	1
Eoser'stoma inaequispina	0	?	?	0	1	0	0	1	0	1	1	0
Parasericostoma laterale	0	?	?	0	2	0	0	0	0	1	0	1
P. cristatum	0	?	?	0	2	0	0	1	0	1	0	1
Notidobiella sp.	0	2	0	0	0	1	1	1	0	1	0	0
Caloca saneva	0	?	0	0	1	1	1	0	0	1	0	0
Tamasia variegata	0	1	0	0	1	0	0	0	0	0	0	0
Caenota plicata	0	1	0	0	2	0	0	0	0	1	0	0
Pycnocentrella eruensis	0	?	?	0	1	0	0	0	0	?	0	0
Anomalopsyche minuta	0	?	?	0	1	0	0	0	1	1	?	1
Antipodoecia turneri	0	?	?	?	?	?	?	?	?	1	1	?

Species: char.name	29	30	32	33	38	41	44	46	47	49	51	53
Conoesucus adiastolus	0	1	0	0	0	1	1	0	0	1	0	0
C. brontensis	0	1	0	0	0	1	1	0	0	1	0	0
C. digitiferus	0	1	0	0	0	1	1	1	0	1	0	0
C. fromus	0	1	0	0	0	1	1	0	0	1	0	0
C. nepotulus	0	1	0	0	0	1	1	2	0	1	0	0
C. norelus	0	1	0	0	0	1	1	2	0	1	0	0
C. notialis	0	0	0	0	0	1	1	0	0	1	0	0
Costora delora	1	0	0	0	0	1	1	1	0	1	0	0
C. ebenina	1	1	0	0	0	0	0	0	1	1	0	1
C. krene	1	1	0	0	0	0	1	1	0	2	0	0
C. luxata	1	1	0	0	0	0	1	0	0	2	0	0
C. ramosa	1	1	0	0	0	0	1	0	0	2	0	0
C. rotosca	1	1	0	0	0	0	1	0	0	2	0	0
C. seposita	1	1	0	0	0	0	1	2	0	2	0	1
Lingora aurata	1	2	1	1	1	0	0	0	1	1	0	1
Matasia satana	1	2	1	1	0	0	0	0	1	1	0	1
Hampa patona	?	?	?	?	?	0	0	0	0	1	0	1
Pycnocentrodes aureola	?	1	0	0	0	1	1	1	0	0	0	?
P. aeris	?	1	0	0	0	1	1	1	0	0	0	?
Confluens hamiltoni	?	1	0	0	0	0	2	1	0	0	0	?
Beraeoptera roria	?	1	0	0	0	1	1	1	1	1	0	?
Pycnocentria evecta	?	1	0	0	0	0	1	0	0	2	1	?
P. sylvestris	?	1	0	?	0	?	3	?	0	1	?	?
P. funerea	?	1	0	?	0	1	3	0	0	2	?	?
Conuxia gunni	?	1	0	0	0	0	1	0	1	2	0	?
Periwinklia childi	?	1	0	0	0	1	1	0	1	1	0	?
Olinga feredayi	?	1	0	0	0	1	2	0	0	2	0	?
O. jeanae	?	1	0	?	?	1	?	2	?	1	?	?
Alloecella grisea	?	0	0	2	0	1	1	1	0	1	1	?
A. pilosa	1	0	0	2	0	0	1	1	0	0	1	0
A. longispina	?	0	0	2	0	1	1	1	0	3	1	0
Zelolessica cheira	?	0	0	1	0	1	3	0	0	0	1	?
A'centrella magnicornis	?	0	0	1	0	1	?	0	0	1	2	?
Austrocentrus griseus	?	0	0	1	0	1	1	0	0	1	1	?
Eoser'stoma inaequispina	?	0	0	1	0	1	2	0	0	3	0	?
Parasericostoma laterale	?	0	0	1	0	1	2	0	0	1	1	?
P. cristatum	?	0	0	1	0	1	1	0	0	1	1	?
Notidobiella sp.	?	1	0	1	0	1	0	0	1	1	0	?
Caloca saneva	?	0	0	1	0	1	0	0	0	3	2	?
Tamasia variegata	1	1	0	1	0	1	0	0	1	2	2	1
Caenota plicata	1	1	0	1	0	1	1	0	0	2	2	0
Pycnocentrella eruensis	?	0	0	1	0	0	1	1	0	1	2	?
Anomalopsyche minuta	?	1	0	1	?	1	?	1	0	2	?	?
Antipodoecia turneri	?	0	0	?	?	0	?	1	0	?	1	?

Species: char.name	54	55	58	62	63	65	66	68	69	71	80	81
Conoesucus adiastolus	0	1	0	1	1	2	1	0	1	0	1	2
C. brontensis	0	1	0	1	1	2	1	0	1	0	1	2
C. digitiferus	0	1	0	1	1	2	1	0	1	0	1	2
C. fromus	0	1	0	1	1	2	1	0	1	0	1	2
C. nepotulus	0	1	0	1	1	2	1	0	1	0	1	2
C. norelus	0	1	0	1	1	1	1	0	1	0	1	2
C. notialis	1	1	0	1	1	2	1	0	1	0	1	2
Costora delora	0	1	0	1	1	1	1	0	0	0	1	2
C. ebenina	0	1	0	1	1	1	1	0	1	1	1	2
C. krene	0	1	0	1	1	1	1	0	1	0	1	2
C. luxata	0	1	0	1	1	1	1	0	1	0	1	2
C. ramosa	0	1	0	1	1	1	1	0	1	0	1	2
C. rotosca	0	1	0	1	1	1	1	0	1	0	1	2
C. seposita	0	1	0	1	1	1	1	0	0	0	1	2
Lingora aurata	1	1	1	1	1	0	1	0	0	1	1	0
Matasia satana	1	1	1	1	1	0	1	0	0	1	1	0
Hampa patona	1	1	1	?	?	?	1	0	0	1	1	1
Pycnocentrodes aureola	0	1	0	1	1	?	1	0	1	0	1	4
P. aeris	0	1	0	1	1	?	1	0	1	0	1	2
Confluens hamiltoni	0	1	0	1	1	?	1	0	1	0	1	3
Beraeoptera roria	0	1	0	1	1	?	1	0	1	0	1	2
Pycnocentria evecta	0	1	0	1	1	?	1	0	1	0	1	2
P. sylvestris	?	1	0	1	?	?	1	0	?	0	?	4
P. funerea	?	1	0	1	?	?	1	0	?	0	?	2
Conuxia gunni	?	1	0	1	?	?	1	0	?	0	?	2
Periwinklia childi	0	1	0	1	1	?	1	0	?	0	1	2
Olinga feredayi	0	0	0	1	1	?	1	0	0	0	1	3
O. jeanae	?	?	0	1	?	?	1	0	?	0	?	?
Alloecella grisea	0	1	0	1	1	1	0	1	1	0	0	2
A. pilosa	0	0	0	1	1	1	0	1	1	0	0	2
A. longispina	0	1	0	1	1	1	0	1	1	0	0	2
Zelolessica cheira	0	0	0	1	1	?	0	?	?	0	?	3
A'centrella magnicornis	?	1	0	?	?	?	?	?	?	0	?	?
Austrocentrus griseus	0	0	0	0	0	?	2	1	1	0	?	2
Eoser'stoma inaequispina	0	1	0	1	0	?	2	1	1	0	?	3
Parasericostoma laterale	0	1	0	0	1	?	2	1	0	0	0	3
P. cristatum	0	1	0	1	1	?	2	1	1	0	0	2
Notidobiella sp.	0	1	0	1	0	?	0	1	1	0	0	3
Caloca saneva	0	1	0	0	0	?	0	1	1	0	0	0
Tamasia variegata	0	1	0	0	1	1	0	1	1	0	0	2
Caenota plicata	0	0	0	0	1	0	0	1	1	0	0	2
Pycnocentrella eruensis	0	0	0	0	0	?	0	1	1	0	0	2
Anomalopsyche minuta	?	1	1	1	2	?	0	1	1	0	0	2
Antipodoecia turneri	?	0	1	1	2	?	0	1	?	0	?	?

Species: char.name	84	90	90a	91	92	94	94a	96	97a	99	100	101
Conoesucus adiastolus	2	0	0	0	0	1	0	0	0	0	1	1
C. brontensis	2	0	0	0	0	1	0	0	0	0	1	1
C. digitiferus	2	0	0	0	0	1	0	1	0	0	1	1
C. fromus	2	0	0	2	1	1	0	1	0	0	0	1
C. nepotulus	2	0	0	1	0	1	0	0	0	0	1	1
C. norelus	2	0	0	2	0	1	0	1	0	0	1	1
C. notialis	2	0	0	2	1	1	0	0	0	0	1	0
Costora delora	2	2	0	2	1	1	0	1	0	0	1	0
C. ebenina	0	0	0	0	0	1	0	0	0	0	0	0
C. krene	0	0	0	0	0	1	0	0	0	0	1	0
C. luxata	0	1	0	1	0	1	0	0	0	0	1	0
C. ramosa	0	0	0	0	0	1	0	0	0	0	1	0
C. rotosca	0	0	0	0	0	1	0	0	0	0	1	0
C. seposita	0	1	0	1	1	1	0	0	0	0	1	0
Lingora aurata	2	0	0	2	0	1	0	0	0	2	1	1
Matasia satana	3	0	0	2	2	1	0	1	0	2	1	?
Hampa patona	2	0	0	2	1	1	0	0	0	2	?	?
Pycnocentrodes aureola	2	2	0	1	1	0	1	1	0	0	1	1
P. aeris	2	0	0	1	0	0	1	2	?	0	1	0
Confluens hamiltoni	0	0	0	0	0	0	1	2	1	0	1	1
Beraeoptera roria	0	0	0	0	1	0	0	1	0	0	1	1
Pycnocentria evecta	2	1	0	1	0	1	0	0	0	0	1	1
P. sylvestris	2	2	?	2	1	?	0	1	0	0	1	1
P. funerea	2	?	?	?	1	?	0	1	0	0	1	?
Conuxia gunni	2	?	?	?	1	?	0	?	0	0	1	?
Periwinklia childi	2	0	0	0	0	?	0	1	0	0	1	1
Olinga feredayi	0	1	0	0	0	1	0	1	0	0	1	0
O. jeanae	0	0	?	0	0	?	?	1	0	0	1	?
Alloecella grisea	1	0	1	1	1	0	0	2	1	1	2	0
A. pilosa	4	0	1	1	0	1	0	0	0	2	2	1
A. longispina	4	0	1	1	0	0	0	0	0	1	2	0
Zelolessica cheira	0	0	?	0	0	0	1	2	?	0	1	0
A'centrella magnicornis	?	0	?	0	0	?	?	?	0	0	1	?
Austrocentrus griseus	0	0	0	0	1	1	0	0	0	1	2	1
Eoser'stoma inaequispina	0	0	0	0	0	?	1	1	?	0	2	0
Parasericostoma laterale	0	0	0	0	1	1	1	1	0	0	0	1
P. cristatum	0	0	0	1	1	1	0	1	0	0	0	1
Notidobiella sp.	0	0	0	0	0	0	1	2	0	0	2	1
Caloca saneva	1	0	0	0	0	?	0	2	1	0	1	1
Tamasia variegata	2	1	0	0	1	1	0	0	1	0	1	0
Caenota plicata	0	1	1	0	0	0	1	2	1	0	0	0
Pycnocentrella eruensis	2	1	1	0	0	?	0	0	1	0	0	0
Anomalopsyche minuta	3	2	0	0	2	?	0	0	0	0	0	0
Antipodoecia turneri	3	2	0	2	2	?	0	1	0	1	2	1

Species: char.name	103	104	105	106	108	108a	109	110	111	113	113a	114
Conoesucus adiastolus	0	0	0	0	1	0	2	2	2	1	0	0
C. brontensis	0	0	0	0	1	0	1	2	2	1	0	0
C. digitiferus	0	0	0	0	2	0	2	2	2	1	0	0
C. fromus	0	0	0	2	3	0	2	2	2	1	0	0
C. nepotulus	0	0	0	0	1	0	1	2	2	1	0	0
C. norelus	0	0	0	1	1	0	4	4	4	1	0	0
C. notialis	0	0	0	0	0	0	1	2	2	1	0	0
Costora delora	1	0	0	1	2	0	2	2	1	1	0	1
C. ebenina	1	0	0	1	2	0	1	2	2	1	0	1
C. krene	1	0	1	1	1	0	3	1	2	1	0	1
C. luxata	1	1	1	1	3	0	3	2	2	1	0	1
C. ramosa	1	0	1	1	1	0	3	1	2	1	0	1
C. rotosca	0	0	1	1	3	0	3	2	2	1	0	1
C. seposita	1	1	1	1	0	0	3	2	2	1	0	1
Lingora aurata	0	0	1	1	1	0	2	2	2	0	0	1
Matasia satana	0	0	0	1	1	0	1	2	2	1	0	1
Hampa patona	?	?	?	?	?	?	?	?	?	1	0	1
Pycnocentrodes aureola	0	0	0	2	1	0	1	2	2	1	0	0
P. aeris	0	0	0	2	1	0	1	2	2	1	0	0
Confluens hamiltoni	0	0	0	0	1	0	1	2	2	1	0	0
Beraeoptera roria	0	0	0	0	1	0	1	1	2	1	1	0
Pycnocentria evecta	0	0	1	0	1	0	2	1	2	1	0	1
P. sylvestris	?	0	?	1	1	?	1	1	1	1	0	?
P. funerea	?	0	0	1	1	?	1	1	1	1	?	?
Conuxia gunni	?	0	0	1	2	?	1	1	1	1	?	?
Periwinklia childi	0	0	0	0	1	0	1	2	2	1	0	0
Olinga feredayi	0	0	0	0	2	0	1	1	2	1	0	0
O. jeanae	?	0	?	?	1	?	2	1	2	1	0	0
Alloecella grisea	0	0	0	0	4	0	2	1	3	1	1	0
A. pilosa	1	0	0	0	0	0	1	2	3	1	1	0
A. longispina	1	0	0	0	4	0	1	2	3	1	1	0
Zelolessica cheira	1	0	0	1	1	0	3	1	3	0	0	0
A'centrella magnicornis	1	0	?	1	4	?	3	1	3	0	0	1
Austrocentrus griseus	0	0	0	2	1	0	3	1	3	1	0	0
Eoser'stoma inaequispina	0	0	0	0	2	0	1	2	3	1	1	0
Parasericostoma laterale	1	0	0	0	3	1	2	1	3	1	0	0
P. cristatum	1	0	0	0	1	1	2	1	3	1	0	0
Notidobiella sp.	0	0	?	1	1	1	4	2	4	1	0	0
Caloca saneva	1	0	1	0	1	1	3	2	3	0	0	1
Tamasia variegata	0	0	1	1	1	1	3	1	3	0	1	1
Caenota plicata	0	0	0	0	1	1	3	2	3	0	0	1
Pycnocentrella eruensis	0	0	1	1	1	0	3	1	3	0	1	1
Anomalopsyche minuta	0	0	?	1	3	1	3	?	2	1	0	1
Antipodoecia turneri	0	0	1	1	4	1	3	1	2	?	?	?

Species: char.name	115	117	118	122	123	124	125	P1	P1a	P2	P3	P4
Conoesucus adiastolus	1	1	0	0	0	0	1	2	0	0	0	0
C. brontensis	1	1	0	0	0	0	1	1	1	0	0	1
C. digitiferus	1	1	0	0	0	0	1	0	0	0	0	0
C. fromus	1	1	0	0	0	0	1	0	1	0	0	1
C. nepotulus	1	1	0	0	0	0	1	1	1	0	0	1
C. norelus	1	1	0	0	0	0	1	0	0	0	0	1
C. notialis	1	?	0	0	0	0	1	1	1	0	0	1
Costora delora	1	?	0	0	1	2	1	2	1	0	0	1
C. ebenina	1	0	0	0	?	2	1	0	1	0	0	1
C. krene	1	1	0	0	1	2	1	0	1	0	0	1
C. luxata	1	1	0	0	1	2	1	0	0	0	1	1
C. ramosa	1	1	0	0	1	2	1	0	1	0	0	1
C. rotosca	1	1	0	0	1	2	1	0	1	0	0	1
C. seposita	1	1	0	0	1	2	1	0	1	0	0	1
Lingora aurata	1	1	0	1	1	0	1	1	1	0	0	1
Matasia satana	1	0	0	1	1	0	1	1	1	0	1	1
Hampa patona	?	?	0	?	?	?	?	1	1	0	0	1
Pycnocentrodes aureola	?	?	0	?	?	?	?	1	1	0	0	1
P. aeris	1	0	0	?	?	?	?	0	1	0	0	1
Confluens hamiltoni	1	0	0	?	?	?	?	1	1	0	0	1
Beraeoptera roria	1	?	0	?	?	?	?	1	1	0	0	1
Pycnocentria evecta	1	0	0	?	?	?	?	0	0	0	0	1
P. sylvestris	?	?	0	?	?	?	?	0	1	0	0	1
P. funerea	?	?	0	?	?	?	?	?	?	0	0	1
Conuxia gunni	?	?	0	?	?	?	?	1	1	0	0	?
Periwinklia childi	1	0	0	?	?	?	?	1	1	0	0	1
Olinga feredayi	1	0	0	?	?	?	?	1	1	0	0	1
O. jeanae	?	?	0	?	?	?	?	1	1	0	0	?
Alloecella grisea	0	0	1	0	0	1	2	3	1	1	2	2
A. pilosa	0	0	1	0	0	1	2	1	1	1	0	0
A. longispina	0	0	1	0	0	1	2	3	1	1	2	2
Zelolessica cheira	0	0	1	?	?	?	?	?	1	?	0	?
A'centrella magnicornis	?	?	?	?	?	?	?	?	?	?	?	?
Austrocentrus griseus	0	0	0	?	?	?	?	0	1	0	3	0
Eoser'stoma inaequispina	0	0	0	?	?	?	?	3	1	0	1	2
Parasericostoma laterale	0	0	0	?	?	?	?	2	1	0	0	1
P. cristatum	0	0	0	?	?	?	?	0	1	0	0	1
Notidobiella sp.	0	0	0	?	?	?	?	?	?	?	?	?
Caloca saneva	0	0	0	?	?	?	?	?	?	?	1	1
Tamasia variegata	0	0	0	0	?	0	0	0	0	0	1	2
Caenota plicata	0	?	0	0	?	0	0	0	0	0	1	0
Pycnocentrella eruensis	0	0	0	?	?	?	?	0	0	0	0	0
Anomalopsyche minuta	?	0	0	?	?	?	?	0	1	0	1	1
Antipodoecia turneri	?	?	0	?	?	?	?	?	?	?	?	?

Species: char.name	P6	P6a	P7	P8	P9	P10	P11	P12	P14	P15	P16	P21
Conoesucus adiastolus	2	1	2	0	0	2	0	1	0	0	3	1
C. brontensis	1	1	2	0	0	2	1	1	0	0	3	1
C. digitiferus	0	1	2	0	0	2	0	1	0	0	3	1
C. fromus	0	1	2	0	0	2	1	2	0	0	3	0
C. nepotulus	3	1	1	0	0	2	1	1	0	0	3	1
C. norelus	0	1	2	0	0	2	1	1	0	0	3	0
C. notialis	1	1	1	1	0	2	0	1	1	0	0	1
Costora delora	2	1	0	?	0	2	0	0	0	0	2	0
C. ebenina	2	1	2	0	0	2	1	2	0	0	2	0
C. krene	2	1	2	0	0	2	1	2	0	0	2	0
C. luxata	0	1	2	0	0	2	1	2	0	0	2	0
C. ramosa	2	1	2	0	0	2	1	2	0	0	2	?
C. rotosca	2	1	2	0	0	2	1	1	0	0	2	0
C. seposita	2	1	2	0	0	2	1	0	0	0	2	0
Lingora aurata	2	1	1	0	0	2	1	1	0	0	2	0
Matasia satana	2	1	2	0	0	2	0	1	1	0	2	0
Hampa patona	0	?	1	0	0	1	0	0	0	0	2	0
Pycnocentrodes aureola	0	0	2	0	0	0	0	0	1	0	2	0
P. aeris	?	?	2	0	0	2	0	?	?	?	?	?
Confluens hamiltoni	1	?	2	1	0	2	0	1	?	?	?	?
Beraeoptera roria	0	1	2	0	0	2	0	0	1	0	0	0
Pycnocentria evecta	0	?	2	0	0	1	1	1	0	0	?	?
P. sylvestris	1	?	2	0	0	2	?	1	?	?	?	?
P. funerea	?	?	2	0	0	2	0	?	?	?	?	?
Conuxia gunni	1	?	2	0	0	2	?	1	?	?	?	?
Periwinklia childi	0	1	2	0	0	2	0	1	0	0	3	0
Olinga feredayi	1	1	2	0	0	2	0	0	0	3	2	0
O. jeanae	1	?	2	0	0	2	0	0	?	?	?	?
Alloecella grisea	3	2	1	1	1	0	0	0	1	4	2	0
A. pilosa	3	1	1	1	1	0	0	0	1	4	2	0
A. longispina	3	1	0	?	1	0	0	0	1	2	2	0
Zelolessica cheira	?	2	2	1	?	2	0	1	?	?	?	?
A'centrella magnicornis	?	?	?	?	?	?	?	?	?	?	?	?
Austrocentrus griseus	1	1	3	?	0	?	?	?	?	4	2	0
Eoser'stoma inaequispina	3	1	0	?	1	2	0	0	1	2	2	0
Parasericostoma laterale	0	1	2	0	0	0	0	0	1	?	?	?
P. cristatum	0	?	2	0	0	?	?	?	?	?	?	?
Notidobiella sp.	0	1	2	0	0	?	?	?	?	?	?	?
Caloca saneva	?	?	2	1	0	3	?	?	?	?	?	?
Tamasia variegata	0	1	2	1	2	2	0	1	0	0	1	0
Caenota plicata	0	1	2	1	0	1	0	1	0	0	1	0
Pycnocentrella eruensis	0	0	2	1	0	0	0	0	1	0	2	0
Anomalopsyche minuta	3	1	1	1	1	0	0	1	1	0	0	0
Antipodoecia turneri	?	?	?	?	?	?	?	?	?	?	?	?

Species: char.name	P22	P25	P30	P30a	P31	P32	P36	P38	P39	P40	P42	P44
Conoesucus adiastolus	1	1	1	1	0	0	0	1	0	0	0	0
C. brontensis	2	0	1	1	0	0	1	1	0	0	0	0
C. digitiferus	2	1	1	1	0	0	0	1	0	0	0	0
C. fromus	2	0	1	1	0	0	0	1	0	0	0	0
C. nepotulus	2	0	1	1	0	0	1	1	0	0	0	0
C. norelus	0	0	1	1	0	0	0	1	0	0	0	0
C. notialis	2	0	1	1	0	0	1	1	0	0	0	0
Costora delora	2	0	1	1	0	0	1	1	0	0	0	0
C. ebenina	0	0	1	1	0	0	0	1	0	0	0	1
C. krene	0	0	1	1	0	0	0	1	0	0	0	0
C. luxata	0	0	1	1	0	1	0	1	0	0	0	0
C. ramosa	0	0	1	1	0	0	0	1	0	0	0	0
C. rotosca	0	0	1	1	0	0	0	1	0	0	0	0
C. seposita	0	0	1	1	0	1	1	1	0	0	0	0
Lingora aurata	0	0	1	1	0	0	1	1	0	1	0	1
Matasia satana	0	0	1	1	0	0	1	1	0	2	0	0
Hampa patona	0	0	1	1	0	0	0	1	?	0	0	1
Pycnocentrodes aureola	0	0	1	1	0	0	1	1	0	0	?	0
P. aeris	?	?	?	?	?	?	?	?	?	?	?	?
Confluens hamiltoni	?	?	?	?	?	?	?	?	?	?	?	?
Beraeoptera roria	0	0	1	1	0	0	1	1	0	0	?	0
Pycnocentria evecta	2	0	1	1	0	0	0	1	0	0	?	0
P. sylvestris	?	?	?	?	?	?	?	?	?	?	?	?
P. funerea	?	?	?	?	?	?	?	?	?	?	?	?
Conuxia gunni	?	?	?	?	?	?	?	?	?	?	?	?
Periwinklia childi	0	0	1	1	?	?	?	?	?	?	?	?
Olinga feredayi	2	1	1	1	0	0	1	1	0	0	?	0
O. jeanae	?	?	?	?	?	?	?	?	?	?	?	?
Alloecella grisea	0	0	1	0	0	1	1	1	1	0	1	0
A. pilosa	0	0	1	1	1	1	1	1	1	0	1	0
A. longispina	0	0	1	1	1	1	1	1	0	0	1	0
Zelolessica cheira	?	?	?	?	?	?	?	?	?	?	?	?
A'centrella magnicornis	?	?	?	?	?	?	?	?	?	?	?	?
Austrocentrus griseus	0	0	1	0	1	1	1	1	0	0	?	?
Eoser'stoma inaequispina	0	0	1	0	0	1	1	1	0	0	2	0
Parasericostoma laterale	?	?	?	?	0	?	1	1	?	0	?	?
P. cristatum	?	?	?	?	?	?	?	?	?	?	?	?
Notidobiella sp.	?	?	?	?	?	?	?	?	?	?	?	?
Caloca saneva	0	0	0	?	0	1	1	0	0	0	?	?
Tamasia variegata	0	0	0	1	1	0	1	0	1	0	0	0
Caenota plicata	0	0	0	1	1	1	1	0	1	0	0	0
Pycnocentrella eruensis	0	0	0	?	0	1	1	0	1	0	0	0
Anomalopsyche minuta	2	0	0	0	1	1	1	1	1	2	?	0
Antipodoecia turneri	?	?	?	?	?	?	?	?	?	?	?	?

Species: char.name	P46	P46a	P48	P49	P52	P53	P54
Conoesucus adiastolus	0	0	1	0	1	0	0
C. brontensis	0	1	0	0	1	0	0
C. digitiferus	0	1	0	0	1	0	0
C. fromus	0	1	0	0	0	0	0
C. nepotulus	1	0	1	0	0	3	3
C. norelus	0	0	1	0	1	0	0
C. notialis	0	1	1	0	1	1	1
Costora delora	1	0	2	0	1	3	0
C. ebenina	0	?	1	0	1	3	0
C. krene	0	1	2	0	1	?	3
C. luxata	0	1	2	0	1	0	3
C. ramosa	?	?	?	0	1	?	3
C. rotosca	0	1	2	0	1	0	3
C. seposita	0	1	2	0	1	0	3
Lingora aurata	0	1	2	0	1	1	1
Matasia satana	0	0	2	0	1	0	0
Hampa patona	1	0	2	0	1	1	1
Pycnocentrodes aureola	0	0	1	0	1	0	0
P. aeris	?	?	?	?	?	?	?
Confluens hamiltoni	?	?	?	?	?	?	?
Beraeoptera roria	0	0	2	0	1	?	?
Pycnocentria evecta	?	0	?	0	0	?	3
P. sylvestris	?	?	?	?	?	?	?
P. funerea	?	?	?	?	?	?	?
Conuxia gunni	?	?	?	?	?	?	?
Periwinklia childi	?	?	?	?	?	?	?
Olinga feredayi	?	0	2	0	0	0	0
O. jeanae	?	?	?	?	?	?	?
Alloecella grisea	3	0	2	0	1	0	1
A. pilosa	0	0	2	0	1	3	3
A. longispina	1	0	2	0	0	3	3
Zelolessica cheira	?	?	?	?	?	?	?
A'centrella magnicornis	?	?	?	?	?	?	?
Austrocentrus griseus	3	0	2	?	?	1	1
Eoser'stoma inaequispina	3	0	2	0	1	0	0
Parasericostoma laterale	?	?	?	?	?	?	?
P. cristatum	?	?	?	?	?	?	?
Notidobiella sp.	?	?	?	?	?	?	?
Caloca saneva	?	?	?	?	2	?	?
Tamasia variegata	2	0	2	1	0	0	0
Caenota plicata	2	0	2	1	0	0	0
Pycnocentrella eruensis	2	0	1	1	0	0	0
Anomalopsyche minuta	1	0	?	1	?	3	3
Antipodoecia turneri	?	?	?	?	?	?	?

(output from MacClade). Character numbers refer to characters listed in Tables 6.2 and
6.3. u=unordered; r=reversable; C.I= Consistency Index.pp. 1-2=all taxa; pp. 3-4 =
Tasmanian taxa only.

Character	type	weight	states	steps	C.I.
1.	u	0	4	8	0.38
2.	u	1	3	5	0.40
3.	r	1	2	1	1.00
4.	r	1	2	2	0.50
5.	r	1	2	2	0.50
6.	u	1	3	3	0.67
7.	r	1	2	2	0.50
8.	u	1	6	11	0.45
9.	u	1	3	3	0.67
10.	u	1	4	4	0.75
11.	r	1	2	2	0.50
12.	u	1	3	4	0.50
13.	r	1	2	1	1.00
14.	r	1	2	2	0.50
15.	u	1	3	2	1.00
16.	r	1	2	3	0.33
17.	r	1	2	1	1.00
18.	u	1	3	4	0.50
19.	r	1	2	1	1.00
20.	r	1	2	2	0.50
21.	r	1	2	1	1.00
22.	r	1	2	1	1.00
23.	r	1	2	1	1.00
24.	r	1	2	1	1.00
25.	r	1	1	0	
26.	r	1	2	1	1.00
27.	u	1	3	4	0.50
28.	r	1	2	1	1.00
29.	u	1	3	3	0.67
30.	r	1	2	1	1.00
31.	r	1	2	3	0.33
32.	r	1	2	3	0.33
33.	u	1	3	7	0.29
34.	r	1	2	4	0.25
35.	u	1	4	4	0.75
36.	u	1	3	2	1.00
37.	r	1	2	4	0.25
38.	r	1	2	2	0.50
39.	r	1	2	2	0.50
40.	r	1	2	1	1.00
41.	r	1	2	1	1.00
42.	r	1	1	0	
43.	u	1	3	3	0.67
44.	r	1	2	1	1.00
45.	r	1	2	1	1.00
46.	r	1	2	2	0.50
47.	r	1	2	2	0.50
48.	r	1	2	1	1.00
49.	u	1	3	2	1.00
50.	u	1	5	5	0.80
51.	u	1	3	3	0.67
52.	r	1	2	2	0.50
53.	u	1	3	6	0.33
54.	u	1	3	8	0.25
55.	r	1	2	2	0.50
56.	r	1	2	1	1.00
57.	u	1	3	6	0.33
58.	r	1	2	2	0.50
59.	u	1	3	3	0.67
60.	u	1	3	4	0.50
61.	r	1	2	4	0.25
62.	r	1	2	5	0.20

Character	type	weight	states	steps	C.I.
63.	r	1	2	1	1.00
64.	r	1	2	3	0.33
65.	u	1	3	4	0.50
66.	u	1	5	9	0.44
67.	r	1	2	1	1.00
68.	u	1	4	7	0.43
69.	u	1	3	4	0.50
70.	u	1	4	3	1.00
71.	r	1	2	2	0.50
72.	r	1	2	2	0.50
73.	r	1	2	2	0.50
74.	r	1	2	1	1.00
75.	r	1	2	3	0.33
76.	r	1	2	1	1.00
77.	r	1	2	1	1.00
78.	r	1	2	2	0.50
79.	u	1	3	3	0.67
80.	u	1	3	2	1.00
81.	u	1	4	6	0.50
82.	r	1	2	4	0.25
83.	r	1	2	1	1.00
84.	u	0	3	4	0.50
85.	u	1	3	4	0.50
86.	u	1	3	4	0.50
87.	u	1	4	8	0.38
88.	u	1	2	1	1.00
89.	u	1	3	5	0.40
90.	r	1	2	2	0.50
91.	u	1	3	2	1.00
92.	u	1	3	3	0.67
93.	r	1	2	5	0.20
94.	u	1	3	7	0.29
95.	r	1	2	3	0.33
96.	u	1	3	2	1.00
97.	u	1	4	3	1.00
98.	r	1	2	1	1.00
99.	u	1	3	3	0.67
100.	r	1	2	1	1.00
101.	r	0	2	3	0.33
102.	r	1	2	1	1.00
103.	r	1	2	1	1.00
104.	r	1	2	2	0.50
105.	r	1	2	3	0.33
106.	r	1	2	5	0.20
107.	r	1	2	1	1.00
108.	r	1	2	2	0.50
109.	u	1	3	2	1.00
110.	r	1	2	1	1.00
111.	r	1	2	2	0.50
112.	u	1	4	6	0.50
113.	r	1	2	5	0.20
114.	u	1	3	5	0.40
115.	r	1	2	1	1.00
116.	r	1	2	4	0.25
117.	u	1	3	7	0.29
118.	u	1	3	6	0.33

Character	type	weight	states	steps	C.I.
1.	u	0	4	15	0.20
2.	u	1	3	9	0.22
3.	r	1	2	2	0.50
4.	r	1	2	4	0.25
5.	r	1	2	2	0.50
6.	u	1	3	4	0.50
7.	r	1	2	5	0.20
8.	u	1	6	19	0.26
9.	u	1	3	7	0.29
10.	u	1	4	11	0.27
11.	r	1	2	3	0.33
12.	u	1	3	7	0.29
13.	r	1	2	4	0.25
14.	r	1	2	3	0.33
15.	u	1	4	4	0.75
16.	r	1	2	3	0.33
17.	r	1	2	1	1.00
18.	u	1	3	10	0.20
19.	r	1	2	4	0.25
20.	r	1	2	3	0.33
21.	r	1	2	3	0.33
22.	r	1	2	2	0.50
23.	u	1	3	5	0.40
24.	r	1	2	3	0.33
25.	r	1	2	3	0.33
26.	r	1	2	1	1.00
27.	u	1	3	7	0.29
28.	r	1	2	1	1.00
29.	u	1	3	3	0.67
30.	r	1	2	1	1.00
31.	r	1	2	6	0.17
32.	u	1	4	10	0.30
33.	u	1	3	10	0.20
34.	r	1	2	7	0.14
35.	u	1	4	12	0.25
36.	u	1	3	4	0.50
37.	r	1	2	3	0.33
38.	r	1	2	2	0.50
39.	r	1	2	7	0.14
40.	r	1	2	2	0.50
41.	r	1	2	3	0.33
42.	u	1	3	5	0.40
43.	u	1	3	3	0.67
44.	u	1	3	4	0.50
45.	r	1	2	1	1.00
46.	r	1	2	4	0.25
47.	r	1	2	1	1.00
48.	r	1	2	1	1.00
49.	u	1	5	10	0.40
50.	u	1	5	12	0.33
51.	u	1	3	7	0.29
52.	r	1	2	3	0.33
53.	u	1	3	12	0.17
54.	u	1	3	13	0.15
55.	r	1	2	4	0.25
56.	r	1	2	5	0.20
57.	u	1	3	13	0.15
58.	r	1	2	3	0.33
59.	u	1	3	4	0.50
60.	u	1	3	7	0.29
61.	r	1	2	11	0.09
62.	r	1	2	9	0.11

Character	type	weight	states	steps	C.I.
63.	r	1	2	1	1.00
64.	r	1	2	5	0.20
65.	u	1	3	12	0.17
66.	u	1	5	14	0.29
67.	r	1	2	5	0.20
68.	u	1	4	14	0.21
69.	u	1	3	11	0.18
70.	u	1	4	5	0.60
71.	r	1	2	2	0.50
72.	r	1	2	5	0.20
73.	r	1	2	4	0.25
74.	r	1	2	1	1.00
75.	r	1	2	3	0.33
76.	r	1	2	2	0.50
77.	r	1	2	1	1.00
78.	r	1	2	2	0.50
79.	u	1	3	4	0.50
80.	u	1	3	2	1.00
81.	u	1	4	12	0.25
82.	r	1	2	5	0.20
83.	r	1	2	1	1.00
84.	u	0	3	6	0.33
85.	u	1	4	8	0.38
86.	u	1	3	7	0.29
87.	u	1	4	13	0.23
88.	u	1	3	4	0.50
89.	u	1	4	7	0.43
90.	r	1	2	4	0.25
91.	u	1	3	3	0.67
92.	u	1	4	7	0.43
93.	r	1	2	5	0.20
94.	u	1	3	12	0.17
95.	r	1	2	4	0.25
96.	u	1	4	5	0.60
97.	u	1	4	6	0.50
98.	r	1	2	1	1.00
99.	u	1	3	5	0.40
100.	r	1	2	2	0.50
101.	r	0	2	3	0.33
102.	r	1	2	2	0.50
103.	r	1	2	3	0.33
104.	r	1	2	3	0.33
105.	r	1	2	3	0.33
106.	r	1	2	5	0.20
107.	r	1	2	1	1.00
108.	r	1	2	3	0.33
109.	u	1	3	3	0.67
110.	u	1	3	2	1.00
111.	r	1	2	2	0.50
112.	u	1	4	8	0.38
113.	r	1	2	5	0.20
114.	u	1	3	7	0.29
115.	r	1	2	2	0.50
116.	u	1	3	7	0.29
117.	u	1	3	8	0.25
118.	u	1	3	7	0.29