Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria

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The Lower Cretaceous Koonwarra Fossil Bed, encountered in a road cutting south of Leongatha on the South Gippsland Highway, yielded more than 80 species of invertebrates. More than 70 are insects, associated with an ostracode, a syncarid (*Koonaspides indistinctus* gen. et sp. nov.), an anostracan and a cladoceran among the Crustacea, two spiders and a harvestman among the arachnids, possible earthworms, bryozoan statoblasts and a bivalved mollusc. The insects represent 12 orders dominated by the Hemiptera, Coleoptera and Diptera in terms of diversity but dominated numerically by aquatic immature Ephemeroptera and Diptera; Odonata, Blattodea, Plecoptera, Orthoptera, Psocoptera, Mecoptera, Trichoptera, Hymenoptera and probably Siphonaptera are lesser components.

Insects, identified specifically and described taxonomically, are *Promirara cephalota* gen. et sp. nov., *Australurus plexus* gen. et sp. nov., *Dulcimanna sculptor* gen. et sp. nov., *Peraphlebia tetrastichia* gen. et sp. nov., *Eodinotoperla duncanae* gen. et sp. nov., *Edgariekia una* gen. et sp. nov., *Duncanovelia extensa* gen. et sp. nov., *Choristopanorpa drinnani* sp. nov., *Neoparachorista clarkae* sp. nov., *Prochoristella leongatha* sp. nov., *Cretacochorista parva* gen. et sp. nov., *Tarwinia australis* gen. et sp. nov., *Niwratla elongata* gen. et sp. nov., *Chironomaptera collessi* sp. nov., *Pseudalysiinia fragmenta* sp. nov., *Atherimorpha festuca* sp. nov., *Eoichneumon duncanae* gen. et sp. nov., *Westratia nana* gen. et sp. nov., and *Cretacoformica explicata* gen. et sp. nov. However, the majority of the fauna is left in open nomenclature because features of generic or specific importance among living relatives are not clearly preserved on the fossils.

The emphasis is on immature stages of the insects; some of the fossils are more or less in life position; in several instances larval and adult stages may be referred to the same species. Most significantly, many of the insects are referred to living families; closer relationship to the living insects may be anticipated when more features used in modern taxonomy become available on the fossils. This fauna provides the first real insight into the antiquity of the living insect fauna of Australia.

The palaeoenvironment indicated by the invertebrate fauna is a shallow, semi-isolated body of water marginal to a shallow freshwater lake with periodic, probably seasonal, replenishing of the fauna from the lake and periodic mass-mortality of the isolated fauna; the mechanism for this mortality remains uncertain. A present-day environment in Lake Muirhead just east of the Grampians in western Victoria is suggested as possibly comparable to the fossil setting.

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FOSSIL INSECTS have been known from the Australian continent since 1870 but it was not until this century that extensive studies by Tillyard, Riek, Evans, Dunstan and others made known the diverse Permian and Triassic insect faunas of southern Queensland and New South Wales. Virtually all of the living orders of insects are represented among these Permian and Triassic faunas but because no representatives of living families are present, they provide minimal information on the antiquity of the living Australian fauna. Discovery of post-Triassic faunas is necessary to shed any light on this question. A brief review of Australian fossil insect faunas (Riek, 1970b) indicated a relatively poor record, with those from the Tertiary of southern Queensland the best known. The only Cretaceous form described to date is a dragonfly wing from the marine Lower Cretaceous of north Queensland (Woodward, 1884). Riek (1970b) and Willmann (*in* Hennig, 1981, p.83, note 98) briefly alluded to the Koonwarra fauna described below.

The Lower Cretaceous Koonwarra Fossil Bed was discovered in 1961 by Country Roads Board of Victoria workmen straightening and widening a section of the South Gippsland Highway 3km east of Koonwarra and 142km from Melbourne; the site appears as NMVPL425 on the Museum of Victoria Palaeontological Locality Register and all material described below comes from this one locality, although from several different levels within the 8m bed. The sediments have been dated

as late Aptian in age using macro and micro plant fossils (Dettmann, 1963, this memoir; Douglas, 1969, 1973; Douglas *in* Douglas *et al.*, 1976). Accounts of the fish fauna, the geological setting, the age, and the palaeoecology as well as a measured section and detailed locality maps of the site were provided by Waldman (1971) who referred to the fossiliferous horizon as the 'Koonwarra fish-bed'. We prefer the more general 'Koonwarra Fossil Bed' in so far as the fish are not dominant either in numbers of species or in numbers of individuals; they may have provided the greatest amount of biomass but even in that regard vegetable matter may have been more significant.

Although discovered more than 20 years ago, the extensive Koonwarra insect fauna has received only passing comment to date (Carroll, 1962; Talent, 1965; Talent *et al.*, 1966; Riek, 1970a, 1970b; Waldman, 1971). Insect specimens from Koonwarra in the collections of the Museum of Victoria numbering several thousand, thanks to the painstaking preparation by P.M.D. over many years, have been considered the most interesting part of the fauna from 'one of the great fossil localities of the Mesozoic Era' (Dettmann & Douglas, 1976). None of the accounts mentioned has done justice to either the diversity or the fine preservation. Moreover, a further collecting effort in 1981, although principally seeking plants, yielded a considerable number of invertebrate taxa not previously available from the site.

The Koonwarra fauna is the oldest in which the emphasis is on immature stages of insects and the oldest in Australia in which the majority of individuals are preserved more or less in life position. Most fossil insect remains from older horizons consist of wings or wing fragments. The comments of Hennig (1981) and Schlee (*in* Hennig, 1981) with regard to the dangers of assigning insect fossil compressions to living taxa are noted but the Koonwarra species are, in general, more fully known than most fossil insect specimens. Moreover, we make no assignments to living species and the concept, espoused by Hennig (1981), that all the close matches with living taxa could be arrived at by convergence, whereas all features still to be elucidated on the same individuals will prove to be distinctly different, is not accepted. It is outside the scope of this paper to argue the philosophy of palaeoentomological classification and we have employed the traditional methods of palaeoentomology. Perhaps the most significant feature of the Koonwarra fauna is that the majority of its constituents may be referred to insect families with living representatives, and a number of these fossil species may belong to or be closely related to living genera. Indeed this

relationship may be even closer than that which has been suggested by their tentative classification if more of the diagnostic characters used in the accepted classification of living species had been available from the fossils. In this respect indicates that the modern Australian insect fauna is at least 120 million years old and that the transition from or demise of the distinctive Triassic fauna probably occurred in the Jurassic; discovery of Jurassic insect faunas in Australia will be necessary to further define the event. In a number of the fossil species it is possible to associate the adult insect with immature aquatic stages (e.g., in some of the midges there are pupae and adults and in the beetles larvae and adults) which is almost without precedent in the fossil history of the insects. This relatively complete fauna of the insects of a shallow lake enables comparison of rates of evolution, of a number of different insect orders, over a considerable time span; 120 million years is approximately one-third of the total time span of insect life and half the duration of stabilized insect evolution.

The fauna contains several invertebrates other than insects that are of considerable significance with regard to the evolution of their respective groups. The conchostracan *Cyzicus(?) banchocarus* Talent 1965 and the xiphosuran *Victalimulus macqueeni* Riek & Gill 1971 have already been described and fully discussed, with the latter receiving further attention from Pickett (1984). *Koonaspides indistinctus* gen. et sp. nov. provides the first Cretaceous record of the Syncarida. Its occurrence towards the middle of the enormous time span between the Triassic *Anaspidites* Brooks 1962 from New South Wales and the several genera of the group living in Tasmania suggests that this small primitive group has had a continuous evolutionary history in the lakes of southeastern Australia for 200 million years. The cladoceran and anostracan provide records of their respective groups that are close to their origins.

Invertebrate palaeoecology

Interpretations pertaining to the invertebrates are based on known ecological settings of related living species. On this basis the Koonwarra fauna has three main components (Table 1):–
1, the resident lake fauna with preservation of whole larvae as well as moulted cuticles; 2, a transported stream fauna of moulted cuticles of larvae that dwelt in the inflow stream; and 3, a terrestrial component floundering onto the lake surface and dying there outspread under the stress of surface tension. All three components were concentrated at the point of preservation probably

under the action of directional winds. The lake inhabitants should be most numerous under these conditions with the stream and terrestrial components much rarer; this is found to be the case (Table 1).

The resident lake fauna

The fauna of the lake was apparently very similar to that of present-day, shallow, cold, freshwater lakes of southeastern Australia including Tasmania. This component includes both benthos and plankton and both may be represented by dead bodies or moulted cuticles. For example the complete pupae of chironomids are preserved in lateral aspect with the abdomen curved (Fig. 57E-L) whereas cast pupal cuticles from which the adult emerged on the surface of the lake are preserved in dorsoventral aspect with the abdomen stretched out straight and all intersegmental membranes fully extended (Fig. 57A-D). It would be easy to interpret these two forms as separate species.

The plankton included chaoborid larvae and pupae, pupae of chironomid midges, the anostracan, the conchostracan, the cladoceran and the statoblasts.

The bottom fauna in the shallows would have included the immature stages of the mayfly *Australurus plexus* gen. et sp. nov., the dragonfly, the scorpionfly *Nannochorista* sp., the stonefly, the caddisfly and the dytiscid and hydrophilid beetles. In the weeds, probably in slightly deeper water, would have been the coenagrionid damselfly larvae, some hydrophilid beetles, ostracodes and possibly some *Australurus*. The chironomid larvae, which are rare in the collection although the free-swimming pupae are common, would have burrowed in the mud, especially in the less consolidated zone some distance from shore. This may also have been the home of the syncarid and of the xiphosuran if indeed the latter was a permanent inhabitant of the lake.

The transported stream fauna

Species from the inflow stream were represented only by moulted cuticles which were carried either in the body of the stream or on the surface, depending on the method of ecdysis and the amount of agitation through the course of the stream. Those cuticles that floated were more likely to be preserved, and to be preserved intact than those that travelled submerged and tended to settle to the lake floor as the flow rate dropped, settling into situations not conducive to good fossilization. The fauna from the inflow stream is represented by moulted cuticles of the immature stages of the mayflies *Promirara cephalota* gen. et sp. nov., *Dulcimanna sculptor* gen. et sp. nov. and Siphlonuridae? gen. nov. (the former having affinity with *Mirawara* Harker 1954 that lives

along stream margins and in slow-flowing pools, while the other two have been compared with *Coloburiscoides* Lestage 1935 that clings to rocks in fast riffles), and of the simuliid larvae. The simuliid was probably a sand-dwelling form similar to living ones that occur in the sandy sections of some streams just before they enter a lake, or during drier periods, where the flow disappears into the sand.

The terrestrial fauna

Only a small part of what must have been an extensive terrestrial insect fauna is preserved. The semiaquatic gerroid waterbugs probably lived in marginal aquatic sites or on plant-covered water surfaces around the margins of the lake in habitats similar to those of their modern relatives (Andersen, 1982, p.264). The rhagionid dipteran, the dragonfly, and the adult scorpionflies all lived on the wing above the lake or its feeder stream, or in the surrounding vegetation. The carabid and staphylinid beetles probably scavenged in the litter along the water's edge. Among the parasitic wasp fossils are some whose living relatives attack wood-boring beetle larvae; they are active fliers or small enough to be carried by the wind. The pulicid fleas tend to indicate the presence of marsupials and/or some other terrestrial vertebrates; to date the site has yielded only a few bird feathers (Talent et al., 1966; Waldman, 1970) to represent that group but a substantial contemporary reptilean fauna is being discovered in Victoria (Molnar et al., 1981).

Site palaeoecology

Waldman (1971) discussed the palaeoecology of this site at great length, stating in his abstract that it was 'lacustrine or paludal, and mass mortality occurred periodically due to anoxic winter conditions beneath an ice-cover; the phenomenon known as 'winterkill'.'

We agree with Waldman's conclusions that:-
1. The palaeo-environment formed a shallow part of, or was periodically linked with, a larger body of water (e.g. a lake) from which it received a periodic repopulation of its aquatic fauna. 2. Conditions within this environment were of the still-water type, or nearly so, for most of the period of sedimentary deposition. 3. Mass-mortality of fish fauna occurred periodically. His further conclusion that a surface film caused the death of the fauna and caused the environment to become anaerobic, as well as his preferred option of snow covered ice forming the surface film, is quite plausible. Indeed the siphlonurid mayflies live today in cool mountain streams and lakes in central Tasmania and the cantharid beetle being similar to a species that swarms, at times, in the

	A	B	C
EPHEMEROPTERA			
Promirara cephalota	c	n	i
Australurus plexus	c	n	s
Dulcimanna sculptor	r	n	i
Siphlonuridae? gen. nov.	r	n	i
ODONATA			
Peraphlebia tetrastichia	r	a,n	s
Coenagrionid indet.	c	n	w
BLATTODEA			
Methana sp.	c	a,n	t
PLECOPTERA			
Eodinotoperla duncanae	c	a,n	s
ORTHOPTERA			
Gryllacridoid? indet.	u	a	t
Tridactylid indet.	u	n	t
PSOCOPTERA			
Edgariekia una	u	a	t
HEMIPTERA			
Cixiid indet.	u	a	t
Cicadelloid indet. 1	c	a	t
Cicadelloid indet. 2	u	a	t
Psyllid indet.	u	a	t
Anthocorid indet.	u	a	t
Veliid indet.	r	a	t
Duncanovelia extensa	r	a	t
Gelastocorid indet.	r	n	t
Homopteran indet.	u	a	t
COLEOPTERA			
Dytiscid indet. 1	r	a,l	s
Dytiscid indet. 2	c	a,l	s
Dytiscid indet. 3	u	a	s
Gyrinid? indet.	r	a	b
Hydraenid indet.	u	a	t
Hydrophilid indet.	c	a	w
Hydrophilid larva indet.	r	l	w
Staphylinid indet. 1	r	a	t
Staphylinid indet. 2	u	a	t
Pselaphid indet.	u	a	t
Helodid indet.	c	l	w
Cantharid indet.	u	a	t
Mordellid indet.	u	a	t
Coleoptera indet.	c	a,l	t
MECOPTERA			
Choristopanorpa drinnani	u	a	t
Neoparachorista clarkae	u	a	t
Prochoristella leongatha	u	a	t
Cretacochorista parva	u	a	t
Nannochorista sp.	c	l	s

	A	B	C
SIPHONAPTERA			
Tarwinia australis	u	a	
Niwratia elongata	u	a	
Pulicid indet. 1	u	a	
Pulicid indet. 2	u	a	
DIPTERA			
Tipulid larva indet.	u	l	
Tipulid pupa indet. 1	u	p	
Tipulid pupa indet. 2	u	p	
Tipulid? indet.	u	a	
Limoniinid indet. 1	r	a	
Limoniinid indet. 2	u	a	
Dixid indet.	u	a	
Chironomaptera collessi	c	l,p	
Tanypodine indet.	c	a	
Tanypodine pupa indet. 1	c	p	
Tanypodine pupa indet. 2	c	p	
Simuliid indet. 1	c	a,l	
Simuliid indet. 2	u	a	
Pseudalysiinia fragmenta	u	a	
Mycetophilidae gen. nov.	u	a	
Atherimorpha festuca	u	a	
Acalyptrate wings indet.	r	a	
Brachyceran larvae indet.	r	l	
TRICHOPTERA			
Calamoceratid pupa indet.	u	p	
Oecetis? sp.	u	l	
HYMENOPTERA			
Eoichneumon duncanae	u	a	
Aulacid indet.	u	a	
Westratia nana	r	a	
Proctotrupid indet.	u	a	
Bethyloid? indet.	u	a	
Pemphredonine? indet.	r	a	
Cretacoformica explicata	u	a	
CONCHOSTRACA			
Cyzicus ? banchocarus Talent 1965	c	a	p
CLADOCERA			
Daphniid indet.	c	e,a	p
ANOSTRACA			
Anostracan indet.	c	a	p
OSTRACODA			
Cypridoid indet.	u	a	b
SYNCARIDA			
Koonaspides indistinctus	u	a	b

...NIDA
...indet.
...indet. 1
...indet. 2
...*dus macquee...*
...Gill 1971

...OCHAETA
...aete indet. 1

...Faunal list for
...2-5; c = comm
...; l = larva; p
...s and preserv
...f = infauna; t

ARACHNIDA	A	B	C		Oligochaete indet. 2	c	a	f
Opilione indet.	u	a	t		Oligochaete indet. 3	u	a	f
Araneae indet. 1	u	a	t		BRYOZOA			
Araneae indet. 2	u	a	t		Phylactolaematid			
Victalimulus macqueeni					statoblasts	c	c	p
Riek & Gill 1971	u	a	b					
OLIGOCHAETA					BIVALVIA			
Oligochaete indet. 1	r	a	f		Unionoid indet.	u	a	f

Table 1. Faunal list for Koonwarra Fossil Bed showing in Column A specimen numbers (u = unique specimen; r = rare i.e. 2-5; c = common i.e. more than 5); in Column B growth stages represented (a = adult; e = ephippium; n = nymph; l = larva; p = pupa); in Column C ecological setting (i = inflow; p = plankton; s = resident benthos in shallows and preserved in place; w = resident benthos in weed bed or further offshore; b = undifferentiated benthos; f = infauna; t = terrestrial).

snow gum country tend to support Waldman's theory of an ice cover on the lake during winter.

However, the occurrence of well-preserved, complete, adult insects (e.g. the cockroaches, the gerroid waterbugs, the large beetles, the mecopterans *Neoparachorista clarkae* sp. nov. and *Prochoristella leongatha* sp. nov., the fleas, the rhagionid, some of the parasitic wasps and the flying ant) in the same beds as the aquatic fauna begs the question of how they came to be there if the fine clay laminae were deposited under ice. It seems inconceivable that they floated on the surface of the water before it froze, were not incorporated in the frozen layer and then gradually sank into the fine sediments on the floor of the shallow backwater of the lake. Moreover, the more even and uncrowded distribution of invertebrate fossils, particularly the aquatic nymphs preserved as dead animals either on or through the fine clay layers, tends to suggest that the mass mortality event that affected the fish fauna (Waldman, 1971) may not have been as catastrophic for the invertebrates. In this regard it should be noted that the insects and fish are largely separated within the fossil bed with the insects and plants dominant in the finer laminae near the base and the fish in coarser laminae higher in the Bed (Drinnan & Chambers, this memoir). In the same way that Waldman (1971) dismissed alternative interpretations on the basis of apparently contrary evidence we might now ignore his ice film theory. However, we are not prepared to dismiss it as a possibility provided an explanation can be found for the mixing of the terrestrial and aquatic insects; that explanation is not apparent to us now.

Waldman (1984) indicated that occurrence of varves implied traditional seasonal control (i.e. for deepwater varves) on sedimentation with coarser laminae in spring-summer due to run-off from melting ice and the finer laminae laid down in autumn-winter. However, if they are shallow water varves (Waldman, 1971, 1984), as seems most likely, then the coarser laminae will have been deposited during and immediately after the greatest rainfall period. This means that the fine fosil-bearing layers may not have been deposited during autumn-winter as suggested by Waldman (1984, fig. 1) if the same rainfall pattern existed then as now. Predominantly winter rains would mean fossil laminae deposition in summer-autumn and make a surface ice cover less likely. Until the Early Cretaceous rainfall regime is better understood the seasonality of the varves remains in doubt.

Another ecological observation worth noting is the extreme rarity (1 valve only) of ostracodes. In present-day lakes of southeastern Australia where flourish invertebrate faunas comparable to that from Koonwarra, ostracodes are invariably a common element of the fauna. All indicators suggest that the lake at Koonwarra should have had a similarly rich ostracode fauna. The virtual absence of ostracodes in the Fossil Bed suggests that the body of water in which those sediments were laid down was isolated from the main lake by dry land. This suggests possibly a levee along the mouth of an inflow stream isolating a pool that received surface waters from the lake only when strong winds blew across the lake to form waves that carried the flotsam, plankton and some benthos over into the shallow isolated backwater. As ostracode shells sink after death they would have remained on the floor of the main lake.

Clearly there is more work to be done on the interpretation of paleoecology of the site; it is not within the scope of this paper to begin that work as a considerable amount of detailed sedimentological study is necessary.

Modern analogy

Lake Muirhead, a clay-pan just east of the Grampians in western Victoria, has been suggested as having an ecological setting today that closely resembles that of the Lower Cretaceous Koonwarra Fossil Bed (E.F. Riek, pers. comm.). The Grampians area is an isolated mountain region reaching elevations of around 1000m with steep eastern slopes descending abruptly to a badly drained peneplain at an elevation of 200-300m. The few small short streams have beds on the slopes of boulders and pebbles of metamorphosed sandstone and siltstone but on the plain they have open shallow beds of sand size and smaller particles entering large claypan regions within 3–5km.

Lake Muirhead is one such shallow claypan that is fed by a single small broad shallow sandy stream, that is almost dry in summer and that has no outlet stream. During the wet season sheet flooding is general on the peneplain and the inflow stream brings a component of fine sand and silt. Most of the sand is deposited close to the inlet. The lake is of such size and depth that wind action can produce obvious waves and cause water to back up on the lee shore, with periodic overflow into shallow marginal basins, which then retain some water when the winds abate and lake levels return to normal. These marginal basins develop slight bars on their lakeward side.

The sediment in at least one of these marginal basins has a varve-like character with a number of microlamellae distinguishable within the darker bands. These bands in the sediment are undoubtedly due to changes in water level, but it is not known whether these are due mainly to inflow into the basin or to changes produced through wind action. Sedimentation rates in the lake are not known but it appears that wider bands of coarser material represent wet-season inflow; the microlamellae within the narrower fine zones are correlated with smaller changes in level due to combination of overbank flooding and wind action. Prevailing winds would be uniform close to mountains so development of marginal basins in which microlamellae could develop would be restricted to a small part of the lake margin.

The fauna of Lake Muirhead is similar to that found in the Koonwarra Fossil Bed but it has not been possible to determine whether the microlamellae at Lake Muirhead enclose any animals or not. Moreover, no data are available on the chemical environment of this marginal basin to determine whether it has all the necessary features to qualify as a direct analogy for the Koonwarra situation. Assembling such data may require considerable study over a number of years

and is outside the scope of the present study. However, possible analogy is mentioned to promote study of that modern environment in the hope that it will shed further light on the Koonwarra Fossil Bed. In particular it seems that 'The Clay-Settling Hypothesis' mentioned by Waldman (1971, p.107) might well apply in this marginal basin at Lake Muirhead, but faunal content of the sediments in that basin needs study.

Systematic palaeontology

Throughout this paper we have, as far as possible, applied morphological terminology and classification used in 'The Insects of Australia' (CSIRO, 1970).

Specimens described below all come from NMVPL425 in the Koonwarra Fossil Bed and are housed in the following collections indicated by the prefixes (in brackets) attached to the registration numbers:- (NMVP) Palaeontological Collection, Museum of Victoria, Melbourne; (MUGD) Palaeontological Collection of the Department of Geology, University of Melbourne; (AMF) Palaeontological Collection, Australian Museum, Sydney. The bulk of the material described was collected by P.M.D. between 1962 and 1967. Over 300 specimens from the total collection of several thousand formed a numbered (PD1-338) set containing most of the illustrated material. With the donation of the Duncan Collection to the Museum of Victoria those numbered specimens have been registered in the range NMVP103001-103338 so that original numbers are retained as the last three digits. Other specimens previously registered in collections of the Geological Survey of Victoria and of the Zoology Department at Monash University are now in the Museum of Victoria collections and re-registered accordingly. Suffixes 'A' and 'B' with a registration number indicate part and counterpart of the same specimen.

Phylum ARTHROPODA

Class INSECTA

Order EPHEMEROPTERA (Mayflies)

Superfamily BAETOIDEA Klapalek 1909

Family SIPHLONURIDAE Banks 1900

PROMIRARA gen. nov.

Etymology. From Latin prefix *pro* — before and slight variation on generic name *Mirawara*.

Type species. Promirara cephalota sp. nov.

Diagnosis. Based on nymph only. Similar to living *Mirawara* but with mouthparts less highly adapted

Fig. 1. *Promirara* [...]
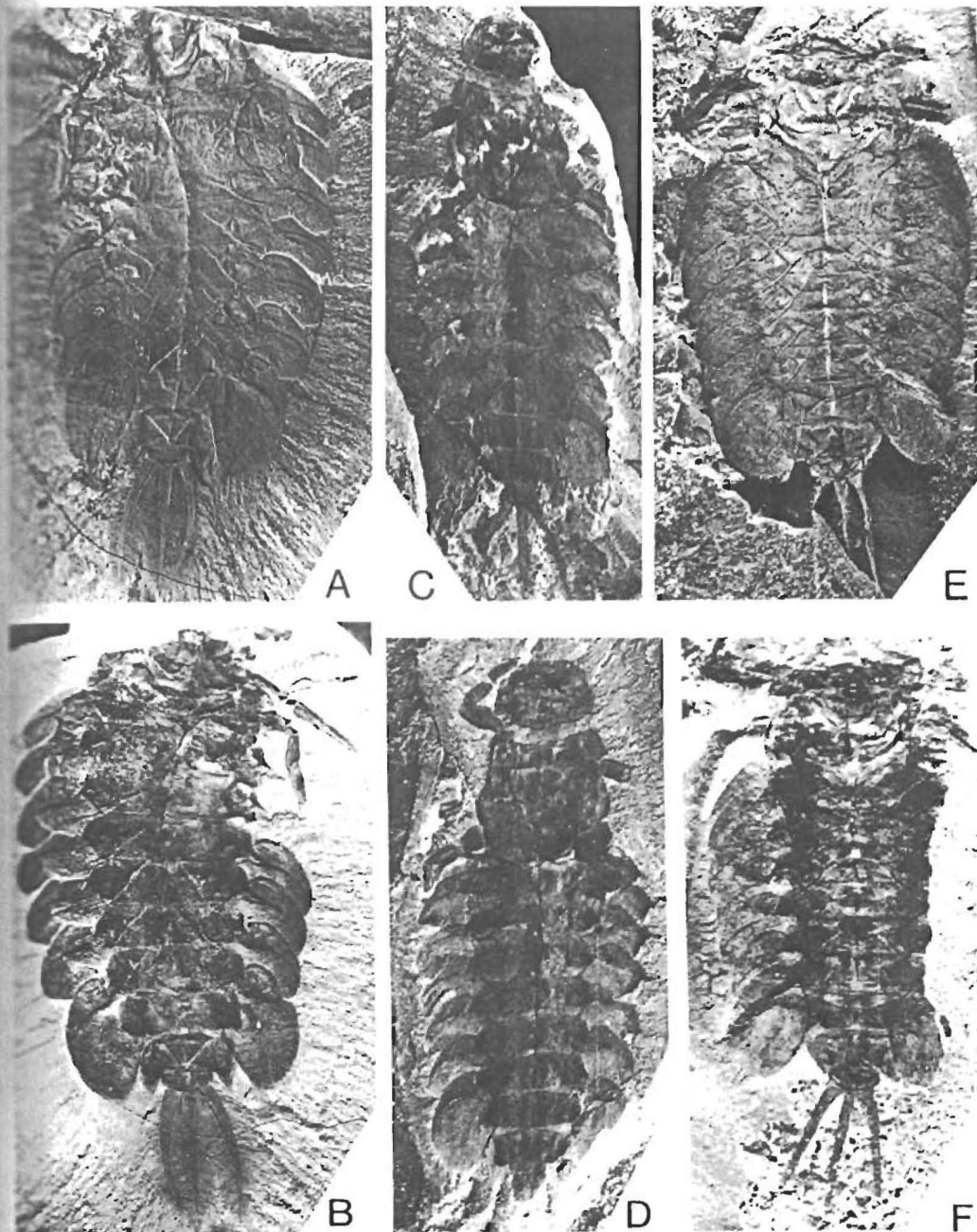chloride NM[...]
×4. C,D, dor[...]
E, dorsal view [...]
of incomplet[...]

Fig. 1. *Promirara cephalota* gen. et sp. nov. A, dorsal view of almost complete holotype whitened with ammonium chloride NMVP102472B, ×3.5. B, dorsal view of almost complete holotype in natural state NMVP102472A, ×4. C,D, dorsal views of counterparts of incomplete paratype NMVP102468B and A, ×6 and ×7, respectively. E, dorsal view of incomplete paratype whitened with ammonium chloride NMVP102473A, ×5. F, dorsal view of imcomplete paratype counterpart in natural state NMVP102473B, ×5.

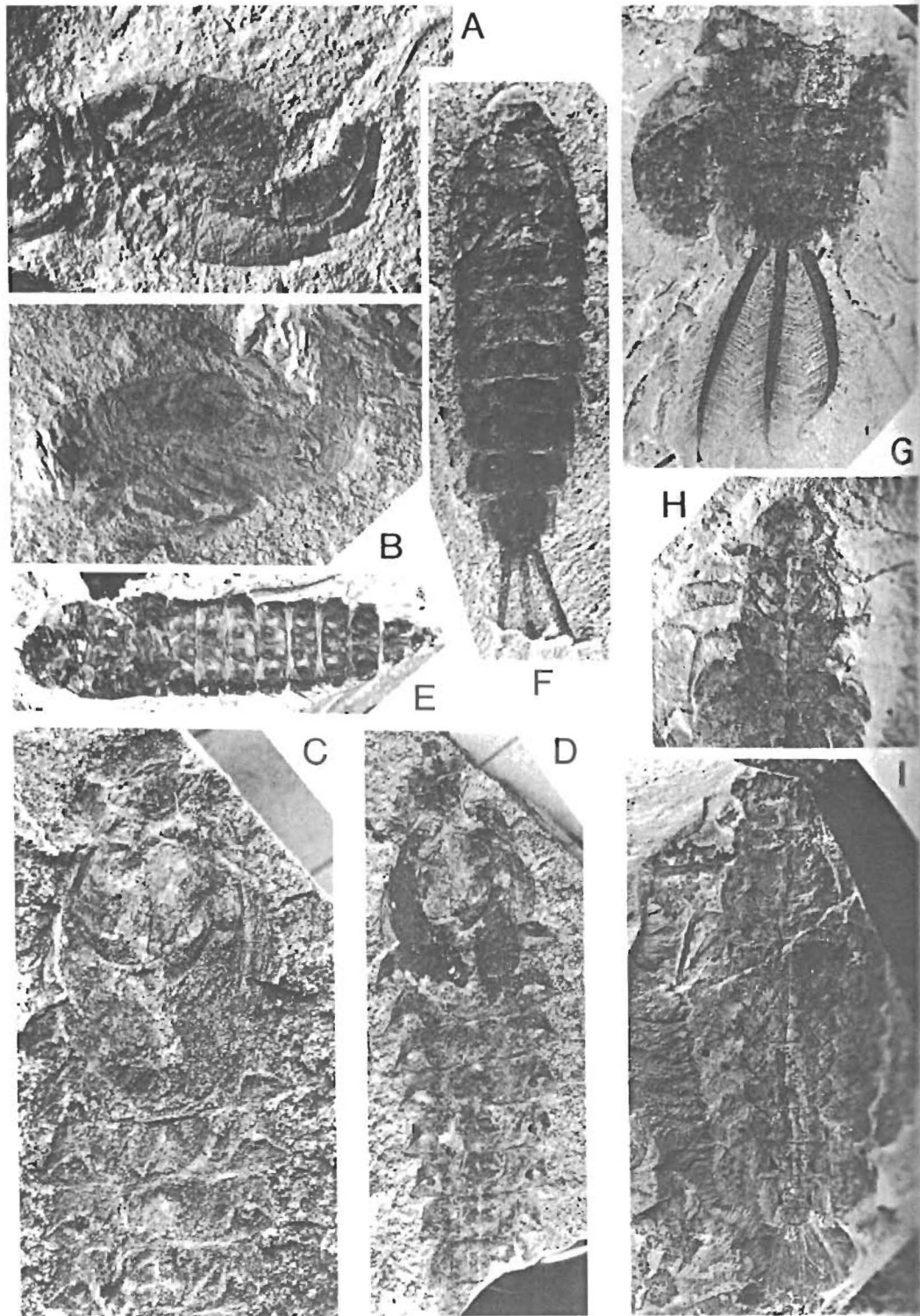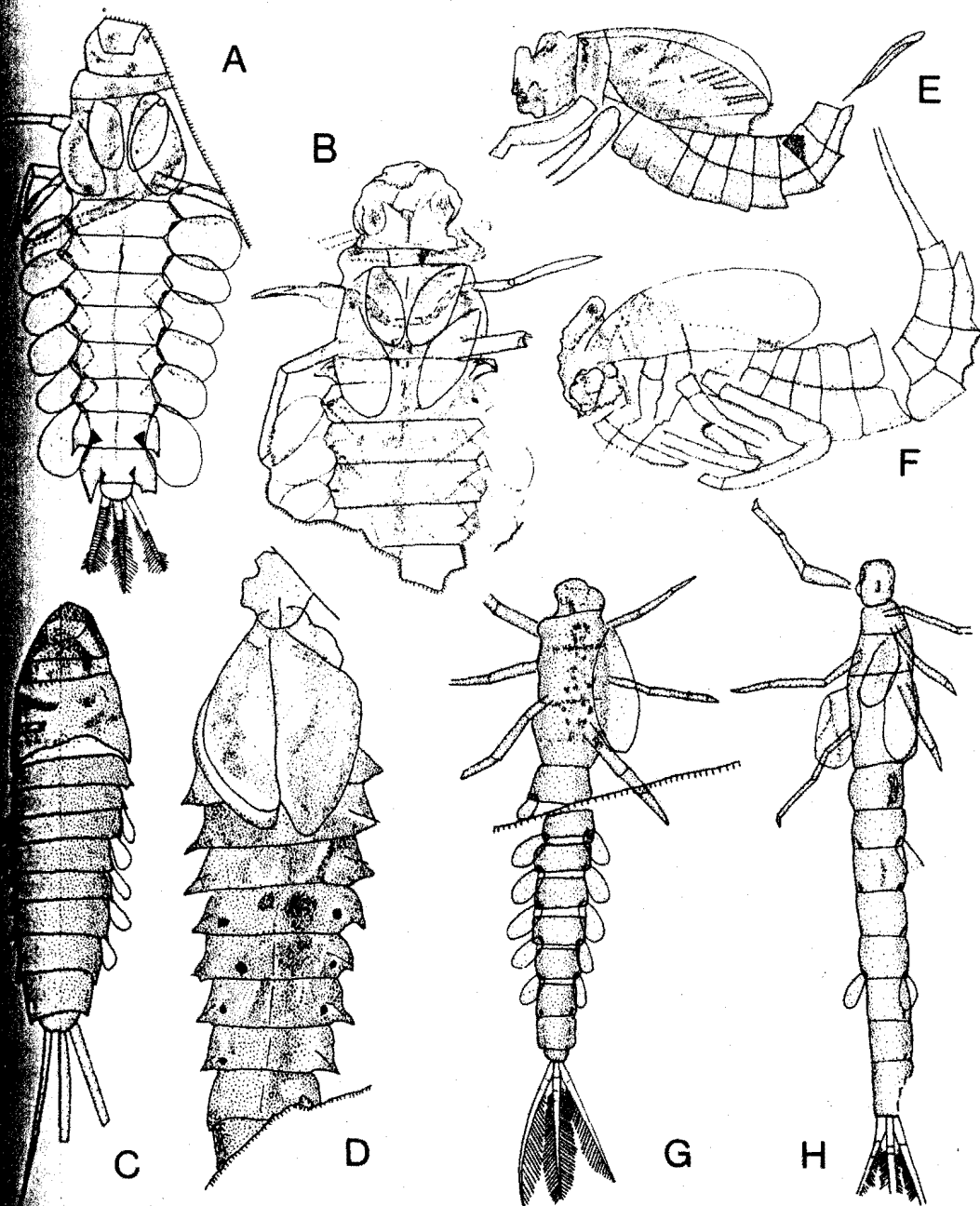**Fig. 3.** A–D, *Promirara cephalota* gen. et sp. nov. A,B, camera lucida sketches from Fig. 2I and 2H, respectively. C,D, camera lucida sketches of very immature and mature nymphs from Fig. 2F and 2D, respectively. E,F, Siphlonuridae? gen. nov., camera lucida sketches of nymphs from Fig. 2A and 2B, respectively. G,H, *Dulcimanna sculptor* gen. et sp. nov., camera lucida sketches of nymphs from Fig. 7E and 7D, respectively.

Fig. 2. A,B, Siphlonuridae? gen. nov. A, lateral view of mature nymph NMVP103210, ×9. B, lateral view of nymph NMVP103209, ×7. C–I, *Promirara cephalota* gen. et sp. nov. C,D, dorsal view of mature paratype nymph NMVP103208, ×5 and ×3.5, respectively. E, paratype nymph NMVP27038, ×4. F, very immature paratype nymph MUGD3757A, ×10. G, dorsal view of paratype posterior abdominal segment NMVP102467B, ×7. H, dorsal view of anterior half of paratype adult NMVP22400B, ×4. I, dorsal view of paratype adult NMVP22500A, ×3.

for predation. Abdomen with seven pairs of subequal gills, first pair not reduced. Cerci with hairs on the lateral as well as median margin but hairs on lateral margin shorter and not extending to the base of the cercus.

Remarks. Promirara is so similar to *Mirawara* that it may be considered ancestral to the recent genus. *Promirara* was probably a less active swimmer with less developed predatory habits than *Mirawara*, if one may judge from structure of the abdominal gills and of the mouth-parts. *Mirawara*, which has a wide but discontinuous distribution over much of the higher regions of eastern Australia, is cold-adapted and needs well aerated water for survival. As there is no reason to consider that these are recently acquired characters, it is reasonable to assume that *Promirara* was also cold-adapted.

PROMIRARA CEPHALOTA sp. nov. (Figs 1, 2C-I, 3A-D)

Etymology. Greek *Kephalotos* — with a head.

Material. Holotype NMVP102472 an almost mature nymph 30mm long. Paratypes NMVP-22400, 22500, 27038, 102467, 102468, 102473, 102480, 102599, 102683, 103208, MUGD3753, 3757.

Description. Mature nymph more than 30mm long. Abdomen with distinct pigmentation pattern, preserved only in very immature nymphs, consisting of a central irregularly pigmented area joined to a dark lateral area by an oblique arm on each side of each segment.

Head distinctly wider than pronotum, with large but not bulging eyes, appearing a little wider than long (possibly due to distortion upon compaction); labrum with anterior margin appearing emarginate at meson; maxilla with long styliform terminal processes; mandible with heavily sclerotized terminal tooth; pronotum widening posteriorly but not strongly produced; wing pads extending to posterior of second or third abdominal segment. Legs relatively long; femur much wider than tibia-tarsus; tibia about equal in length to tarsus, with a slight transverse groove close to its base. Abdominal segments with posterolateral corners produced into pointed carinate tips, eighth and ninth segments having strongly produced almost spinose tips, with prominent median carina; gills on each side of first seven segments, broadly lamellar, with strong curved ridge some distance behind anterior margin (closer to margin on first than on other gills), and all subequal not reduced in size on posterior segments; anterior gill sub-elytroid, more heavily sclerotized than posterior gills; each gill consisting

of a broad lamella with basal fibrilliform tuft extending almost entire length of anterior gills and (possibly protruding at caudal margin) reduced on posterior gills; caudal filaments short, less than half abdominal length, with short articles; median filament and inner margins of lateral ones with dense long hairs; lateral filaments with dense fringe of short hairs on outer margin over distal portion but without hairs towards base.

Remarks. The fossil nymph is similar to that of living *Mirawara* (see Riek, 1955b) though there are small but distinct differences. The mouthparts are highly modified, as in *Mirawara*, but the terminal spines on the maxilla are shorter and the terminal tooth on the mandible is shorter than in *Mirawara*. In *Mirawara* the first gill is reduced in size, though in form it is not unlike that of the fossil species. *Promirara* has a broadly expanded area anterior to the longitudinal ridge of the gill whereas *Mirawara* has a strongly sclerotized anterior margin developed apparently as a swimming aid. Lateral caudal filaments of *Promirara* retain the primitive feature of hairs on the lateral margin though the hairs are reduced in length and do not extend to the base of the filament. Hairs are not present on the lateral margin in *Mirawara*, though they do occur to a slight extent in *Tasmanophlebia* Tillyard 1921, another Australian siphlonurid, and in a few other siphlonurid nymphs.

AUSTRALURUS gen. nov.

Etymology. Latin *australis* — southern and [...] — water-bird.

Type species. Australurus plexus sp. nov.

Diagnosis. Nymphs only. Head elongate; mandibles large; antenna long; face above antennal insertions ridged. Legs long and the tibia shorter than tarsus; tarsal claw apparently long. Mesonotum raised and produced caudad; pronotum large. Abdomen with seven pairs unmodified lamellar abdominal gills; gill structure imperfectly known but each gill apparently with strengthened longitudinal ridge at or close to margin and possibly with a fibrillar tuft at base; segments 1 to 9 strongly produced posterolaterally into spines. Caudal filaments with dense fringe of fine hairs except on outer margins of each lateral filament.

Discussion. This genus differs from the living *Tasmanophlebia* mainly in the general form of abdominal gills which occur, as is general for the family, on the first seven abdominal segments, but the first gill is not modified into a cover for succeeding gills as in *Tasmanophlebia*. This would seem to indicate that the fossil nymphs did not
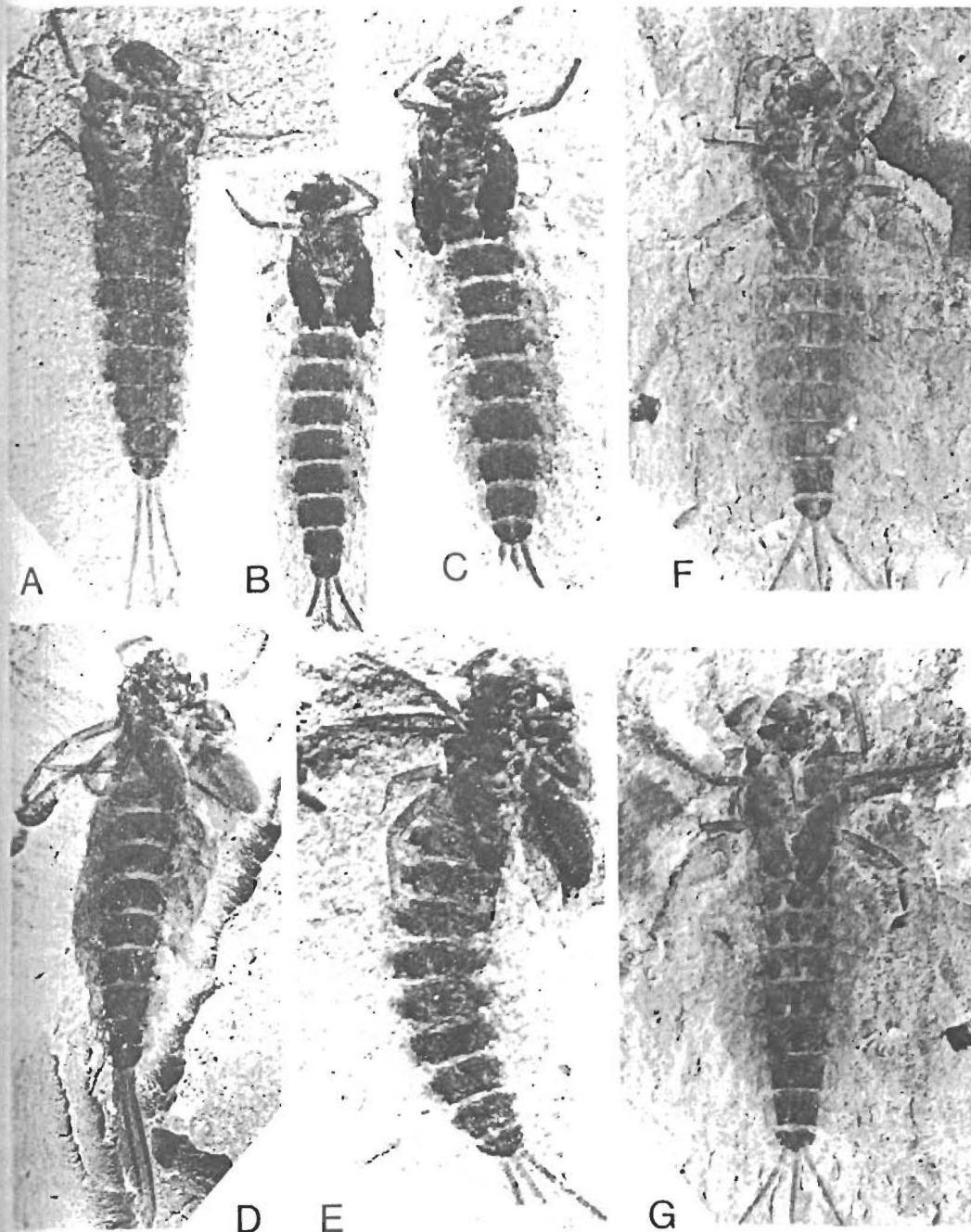
Fig. 4. *Australurus plexus* gen. et sp. nov. All in dorsal view. A, paratype NMVP102475, ×7. B,C, part and counterpart of paratype NMVP22398, ×8 and ×9, respectively. D, paratype MUGD3748B, ×7. E, paratype NMVP52550B, ×8.5. F,G, counterpart and part of holotype NMVP102450B and 102450A, respectively, ×8.

partly bury themselves in sand or silt as is the habit of nymphs of *Tasmanophlebia*. *Tasmanophlebia* lives either at the margins of lakes or in sandy backwaters and some silty areas of small, well-aerated streams; the species are all cold-adapted.

Although the mesonotum is extended in the fossil there is no suggestion of dorsal median spines on the basal abdominal segments as in nymphs of *Tasmanophlebia*. There is no suggestion of a dense marginal fringe on the outer margin of the cercus in the fossil species; such a fringe is present in *Tasmanophlebia*. Although the fossil species is similar to *Tasmanophlebia* it is probably not directly ancestral because, although most of the specialized features of *Tasmanophlebia* occur in more generalized form in *Australurus*, the cerci, lacking a lateral fringe, are more specialized and have developed to the condition that is of almost uniform occurrence throughout the Siphlonuridae.

The fossil nymph can also be compared with the nymphs of Baetidae, especially *Centroptilum* Eaton 1869 which occurs in similar habitats along the margins of present day lakes, but the fossil species is markedly larger, has well-developed pleural spines, relatively large gills, a broad clypeus and labrum, and the labrum is apparently not deeply emarginate at the apex.

Jurassic siphlonurids discussed by Sinitshenkova (1985) from Siberia and Mongolia bear certain similarities to *Australurus* but each may be distinguished by the combination of its features. *Australurus* differs from *Mesobaetis* Brauer, Redtenbacher & Ganglbauer 1889 by its spinose pleural tips, its more slender femora, its elongate mandibles only slightly tapering and its abdominal pigmentation pattern and from *Mogzonurella* Sinitshenkova 1985 in its spinose pleural tips, more elongate head, relatively longer and more slender legs and relatively shorter caudal filaments. The specimens figured by Hong (1982a, pl. 18, figs 2,3) as *Ephemeropsis trisetalis* Eichwald from Upper Jurassic strata in the Neimenggol Autonomous Region of China also bear resemblance to *Australurus* particularly in the short caudal filaments but their pleural tips do not appear to be spinose, their gills appear to be strongly supported and features of the head are not evident.

AUSTRALURUS PLEXUS sp. nov. (Figs 4-6)

Etymology. From Latin *plexus* — braided or interwoven.

Material. Holotype NMVP102450, a mature female nymph almost complete, except for apex of caudal filaments and apical parts of hind legs. Paratypes NMVP22398, 48610, 52550, 102455-

102457, 102465, 102475, 102476, 102478, 102479, 102486, 102492, 102538, 102619, 102893, 103120, 103222, MUGD3747, 3748, 3754. This is an extremely common species and a further 100 or more specimens are housed in the Museum of Victoria.

Diagnosis. As for genus.

Description. Length of mature nymph (with dark wing-pads) 9-10mm. Abdomen with distinct pigmentation pattern consisting of a median and a pair of lateral longitudinal bands joined at the anterior margin of each segment. Median longitudinal band indistinct on two caudal segments. Lateral regions unpigmented. Vertex of head apparently deeply pigmented or heavily sclerotized. Wing-pads on almost mature nymphs with four main pigmentation lines corresponding to R, M, CuA and A.

Head elongated, often preserved with mandibles displaced laterally; mandibles large, with transverse groove or ridge about middle, distinctly longer than wide, tapering only slightly to apex; antennae widely separated, first and possibly second segment enlarged, flagellum distinctly longer than distance between antennal insertions; face, above antennal insertions, with an oblique curved ridge from just mesal to antennal insertions to inner margin of eye; eye large, oval, extending to caudal margin of head; vertex slightly produced caudally at meson; clypeus relatively long; labrum apparently not deeply emarginate at meson.

Pronotum, seen better in lateral compression, long, apparently slightly raised at meson caudally; posterolateral margin not strongly produced; mesonotum large, posteriorly obviously raised and produced at apex almost to a point; margin rimmed, with a ridge close to and converging meson to the apical rim so that the apical region of the notum appears to have two grooves on each side converging to apex; wing-pads not extending beyond apex of third abdominal segment, converging slightly to apex; inner margins straight, apex almost pointed. Legs long and thin; coxa expanded; trochanter small; femur not twice as wide as tarsus; combined tibia-tarsus (with claw) longer than femur; tarsus of fore and mid legs about 1.5 times as long as tibia; tibia and tarsus tapering slightly; tibia with a deep transverse groove on upper surface close to joint with femur; tarsal claw stout, tapering regularly, length not fully preserved though apparently long.

Abdomen with basal 9 segments subequal, first segment as long as second; segments 2-9 with posterolateral margin produced to a long, slender spine; lateral margins of abdomen convex; abdomen widest at segments 4 and 5; first

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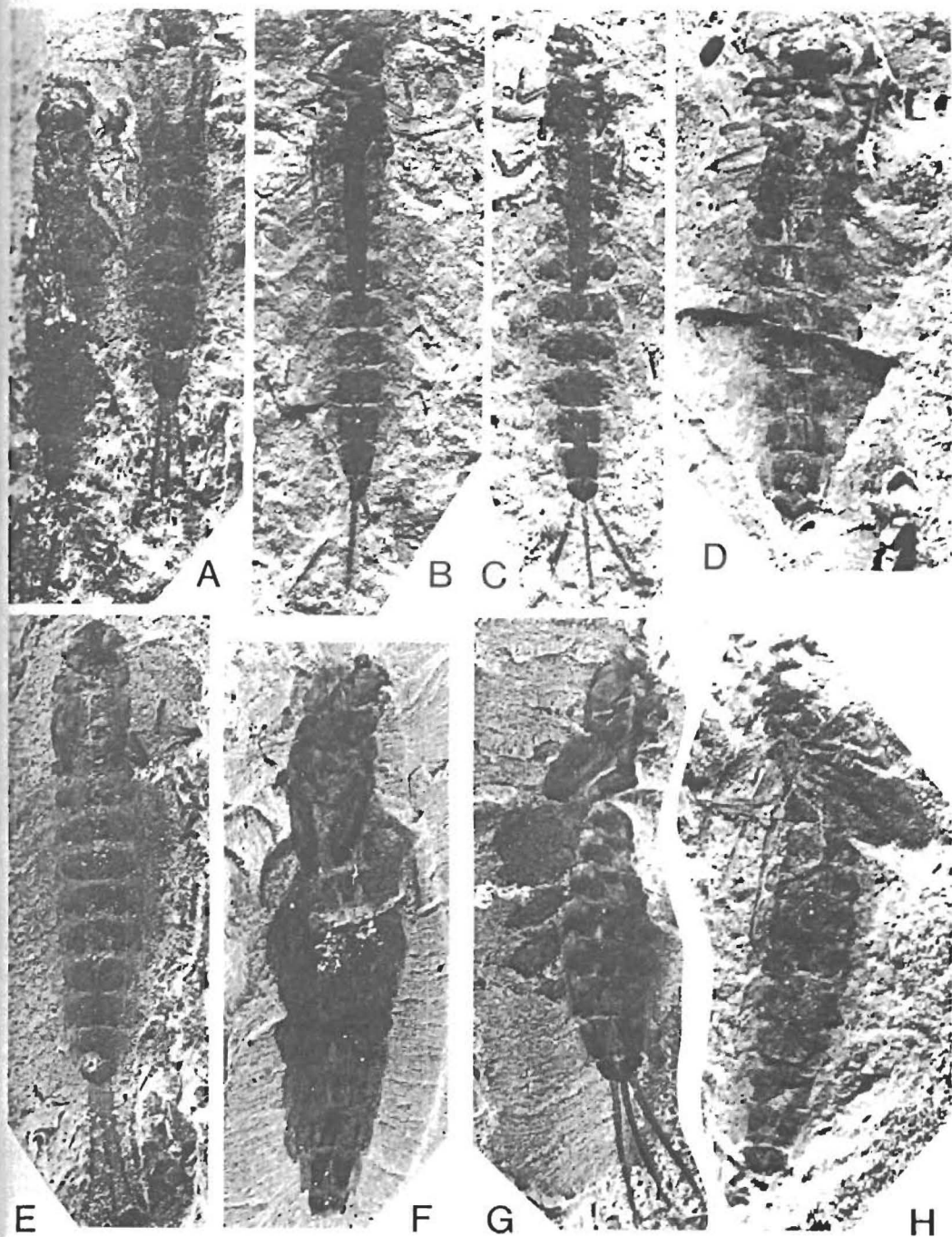ansverse
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Fig. 5. *Australurus plexus* gen. et sp. nov. All in dorsal view. A, two paratypes NMVP102457 (left) and NMVP102456, ×6. B,C, part and counterpart of paratype showing dark central organ through abdomen (probably alimentary canal) NMVP102492A and 102492B, respectively, ×6. D, incomplete paratype NMVP103222, ×10. E, paratype NMVP102478, ×7. F, paratype NMVP102538B, ×8. G, paratype NMVP102486A, ×8. H, paratype NMVP102455, ×10.

segment about 0.5 as long as ninth, its apex rounded though slightly produced; sternum of ninth segment not produced over tenth segment; gills on segments 1-7, lamellar, with strengthened fore margin, held laterally and slightly dorsal, and either with a gill tuft at base or with a branched tracheal trunk; caudal filaments only about 0.5 as long as abdomen, with very short articles, with dense marginal fringes on median filament and inner margin of each lateral filament; outer margin of lateral filaments without obvious fringe even at apex.

Immature nymph with only slightly raised mesonotum and small wing-pads, and nymph usually preserved in lateral view.

Comments on type specimen. Holotype (Fig. 4F,G) a mature female nymph, almost complete, except for apex of caudal filaments and apical portions of hind legs. Numerous paratype specimens, some preserving structures more distinctly than holotype. NMVP22398 (Fig. 4B,C) shows dark wing-pads of the mature nymph and general body form. MUGD3748 (Fig. 4D) is a complete nymph that preserves the gills on both sides of the abdomen though they are not easily discernible on one side where they overlie the thin lateral flange of the segments. The displaced mandible and structure of the legs are also clear. NMVP48610 (Fig. 6D) a lateral compression of an immature nymph showing segmentation of the thorax. The head is particularly well preserved. NMVP102619 (Fig. 6G) shows abdominal gills and head structure.

DULCIMANNA gen. nov.

Etymology. An anagram for Mrs Ilma Duncan, for her support during many years of collecting.

Type species. Dulcimanna sculptor sp. nov.

Diagnosis. Nymph only known, large, markedly elongate body 10 times as long as wide. Head rounded, relatively small, with large bulging dorsal eyes, with entire anterior margin on labrum. Legs with femora of approximately equal length from fore to hind legs, with tibiae and unsegmented tarsi — becoming longer to hind leg, with strong curved relatively long tarsal claw. Abdomen with flat lobate gills on segments 1 to 7, with gently convex internal margins not spinose posterolaterally. Caudal filaments equal, bearing dense comb of

fine long hairs along lateral margins except on outer edges of cerci.

Discussion. This genus, based only on the nymph, is assigned to the Siphlonuridae on its size, the structure of the labrum exposed anteriorly, the abdominal gills and the distribution of hairs on the caudal filaments. Posterolateral corners of abdominal segments are not spinose as in other members of the family but this may be interpreted as the ancestral state for the family. The unsegmented tarsi distinguish it from *Mirawara*, the lack of hairs on lateral margins of the cerci separate it from *Tasmanophlebia* and *Colo- buriscoides* is distinguished by its distinctive gills.

DULCIMANNA SCULPTOR sp. nov. (Figs 3G,H, 7)

Etymology. Latin *sculptor* — a carver. A noun in apposition.

Material. Holotype NMVP102507. Paratype NMVP103341, AMF66758.

Diagnosis. As for genus.

Description. Available specimens each 20mm long (without caudal filaments) and 2mm wide thorax; head subrounded, a little longer than wide separated from pronotum by markedly constricted neck; eyes large, bulging, situated dorsolateral at posterior of head; labrum with entire, convex anterior margin; maxilla gently curved, with spinose tip; mandible broad, with sclerotized anteromedially. Pronotum with gently convex lateral margins; wing pads not extending beyond first abdominal segment; legs stout, with sclerotized longitudinal ridges on femora becoming only slightly longer from fore to hind leg; femora all approximately same length and width; tibiae becoming longer and slightly stouter to hind leg; tarsi unsegmented, becoming longer to hind leg; tarsal claw sclerotized, curved and relatively long.

Abdomen long and slender, with soft evidenced by the many crinkles presumably formed by compression; abdominal gills segments 1 to 7, flat, lobate, with prominent rib running down gill close to anterior margin, markedly sclerotized ring around point of junction with abdomen; three caudal filaments equal without obvious segmentation, with fringe of

Fig. 6. Australurus plexus gen. et sp. nov. A, dorsal view of paratype MUGD3754B, ×11. B, dorsal view of paratype NMVP102893, ×7. C, dorsal view of paratype NMVP22398, ×9. D, lateral view of paratype NMVP48610, ×8. E, lateral view of paratype NMVP103120, ×6. F, dorsal view of paratype NMVP102465A, ×10. G, dorsal view of incomplete paratype NMVP102619A, ×8. H, dorsal view of paratype NMVP102476B, ×10. I, dorsal view of incomplete paratype MUGD3747B, ×8.

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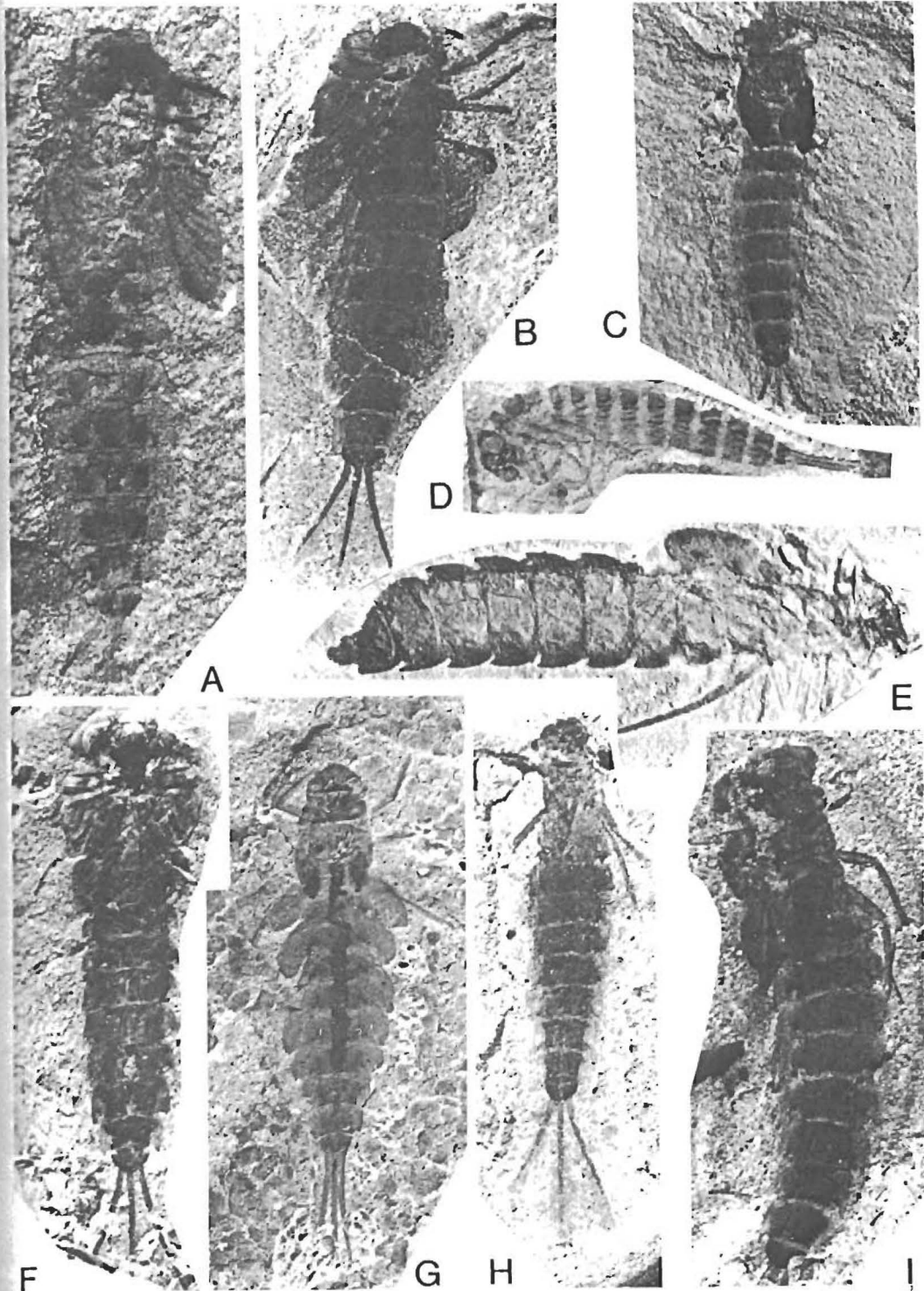*hlebia* and *Colo-
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long hairs on each margin except on the outer margins of lateral filaments.

Remarks. The three available nymphs are not sufficient to provide a complete picture of this species because features such as antennae, some mouthparts and most thoracic features are not clear. However, sufficient detail is available to be confident it does not belong to any previously described genus.

SIPHLONURIDAE? gen. nov. (Figs 2A,B, 3E,F)

Material. NMVP103209 and NMVP103210 both mature nymphs.

Description. Nymph. Length to 6.5mm plus cerci of 2.5mm. Head rounded, mouthparts conspicuous, occupying half area of head in lateral view; eye relatively small; clypeus and labrum small and narrow; labrum rounded at apex, about as long as wide; frons convex in lateral profile; mandible large, subrounded except for tapered apex; maxilla, labium, and labial palps conspicuous below mandible in lateral view, together occupying twice area of mandibles. Pronotum long, with prominent transverse carina towards anterior and posterior margins, not strongly produced posterolaterally, with transverse posterior margin; mesonotum large, strongly extended posteriorly to reach as far as apex of fifth abdominal segment caudally; wing pads conspicuous, apparently separated from one another (i.e. left from right) by extended mesonotum, with eight clearly defined, radiating veins; legs and sternum of abdominal segment 1 not well defined on available material; sternum of abdominal segment 1 not attached to metasternum; segments 2 to 9 increasing regularly in length so that 9 is twice as long as 2; without prominent posterolateral pleural spines except perhaps on segment 9 although some heavier chitinization is evident in the lateral midline; segment 10 short, less than half segment 9; caudal filaments moderately long, slightly more than half length of abdomen. Gills not preserved.

Discussion. The body form of this species resembles the living *Baetisca* Walsh 1862 and *Coloburiscoides* of the Siphlonuridae. Since the latter occurs in Australia whereas the former is only known in cool temperate North America (Edmunds *et al.*, 1976) it would seem much more likely that the similarities with *Coloburiscoides* would prove the more significant.

The lateral midline darkening could reflect pleural spines because the same effect is seen in lateral compressions of *Australurus plexus* where dorsoventral compressions confirm the presence of pleural spines. The gills may all have fallen from the available specimens but this feature is not conclusive.

Order ODONATA (Dragonflies and damselflies)

Suborder ANISOPTERA Selys 1840

Superfamily LIBELLULOIDEA Tillyard 1926

Family MESOPHLEBIIDAE Tillyard 1916

The principal diagnostic feature of the Mesophlebiidae is development of a wide space with at least two rows of cells between R2 and R3. Although it may not be advisable to define a family on one character the fact that adult wing venation is known in each of the assigned genera only from distal fragments and the venation that is known bears little resemblance to other families in matters of fine detail leads us to agree with Tillyard that this group of Australian Mesozoic taxa constitutes a separate family.

Tillyard (1916, p.24) made tentative assignment of this family (as a subfamily) to the Anisoptera but later (1922, p.452) removed it to the Anisozygoptera although the heading of that section indicated the Archizygoptera. This may be assumed to have been a typographical error or perhaps an indication of the uncertainty of its placement. Whatever the intention of Tillyard we consider that his first opinion was correct. The open venation resembles that of the Libelluloidea and Gomphidae; the brace vein continues the line of the base of the pterostigma as in Gomphidae and in Synthemidae; the postnodals are incomplete as in Synthemidae and Gomphidae. The nymphal mask is almost identical with that of many living Libelluloidea.

However the fossil species differs from both Synthemidae and Gomphidae in the cellular development between R3 and IR3. There are three rows of cells towards the margin and four rows the wing margin in the fossil species. There usually a single row in most living anisopter but there is a double row and occasionally irregular third row at the wing margin in some Libellulidae and Corduliidae. The fossil family differs also in not having developed a second intercalary stem between R3 and R4 which present in Libellulidae and Corduliidae but not Synthemidae. On the basis of these comparisons the Mesophlebiidae is tentatively placed within Libelluloidea.

PERAPHLEBIA gen. nov.

Etymology. Greek *pera* — beyond or very; *phlebos* — vein.

Type species. Peraphlebia tetrastichia sp. nov.

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Fig. 7. *Dulcimanna sculptor* gen. et sp. nov. All dorsal views whitened with ammonium chloride. A, paratype NMVP103341, ×4. B–D, part and counterpart of holotype NMVP102507A (C) and 102507B (B,D), ×8, ×6 and ×4, respectively. E–G, part and counterpart of paratype AMF66758A (E,F) and 66758B (G), ×4, ×5 and ×4, respectively.

Plants and invertebrates from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria

Memoir ... of the Association of
Australasian Palaeontologists.

P.A. Jell & J. Roberts editors

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