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Melbourne Australia 8 October 1982



Volume 43 Numbers 1 & 2

COVER PHOTOGRAPH

Beached Whales.

Photograph courtesy Sun News Pictorial

MEMOIRS
of the
NATIONAL MUSEUM OF VICTORIA
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Memoir 43
Numbers 1 & 2

Director

BARRY R. WILSON

Deputy Director

THOMAS A. DARRAGH

Editor

DOUGLAS M. STONE

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INSTRUCTIONS TO AUTHORS

The National Museum of Victoria was established in 1854 for the purpose of scholarship and education in the fields of natural history and anthropology. The Museum publishes two scientific serials to further these objectives, *Memoirs of the National Museum of Victoria* and *Reports of the National Museum of Victoria*.

The *Memoirs* publishes papers on original research in the natural sciences pertinent to Victoria and/or the museum's collections. All contributions are assessed by an independent referee before publication.

The *Reports* are research documents of sufficient importance to be preserved but which are not appropriate for primary scientific publication. Reports are factual rather than interpretive studies, may be of special local interest or may be larger than a normal scientific paper. Contributions will be refereed if appropriate.

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A KEY TO THE VICTORIAN GENERA OF FREE-LIVING AND RETREAT-MAKING CADDIS-FLY LARVAE (INSECTA: TRICHOPTERA)

BY DAVID I. CARTWRIGHT AND JOHN C. DEAN

Biology Laboratory, Melbourne and Metropolitan Board of Works, Melbourne.

Summary

A key is provided to Victorian genera of free-living and retreat-making Trichoptera larvae of the families Philopotamidae, Polycentropodidae, Hydrobiosidae, Ecnomidae and Hydropsychidae. Twenty-eight genera are included, although some remain unidentified while the status of several others is uncertain. In addition larvae of four genera of Hydrobiosidae cannot be separated, and have been lumped in the key as the *Taschorema* complex.

Introduction

With the great upsurge in environmental and ecological studies over the last few years, there has been an increase in the demand for taxonomic information. For Australian freshwater environments, however, taxonomic information has in general been found completely inadequate. Although the immature stages of caddis-flies represent an important component of many inland water communities, there are very few descriptions of Australian larvae in the literature except at the family level (Riek, 1970; Williams, 1980).

We have been investigating the taxonomy of free-living and retreat-making Trichoptera larvae of the families Hydrobiosidae, Philopotamidae, Polycentropodidae, Ecnomidae and Hydropsychidae. Taxonomic knowledge of the adults of Victorian species in these families unfortunately is incomplete, and this has presented some problems. There are numerous undescribed species and probably several undescribed genera, and in addition in many cases it is not known whether genera described from elsewhere in Australia also occur in Victoria. As a consequence many larval types cannot be allocated to a genus, either because we have not bred them out or because the associated adult cannot readily be accommodated in any described genus. However, since it could be some time before all Victorian genera can be identified, we believe that a preliminary guide is justified, and that the inclusion of unidentified material will enhance the value of the keys. Although the families Hydroptilidae and Glossosomatidae are not considered in this paper, for the sake of com-

pleteness they are included in the key to families.

The keys have been developed for the Victorian fauna, and should be used elsewhere with caution. Erroneous identifications could result in regions where non-Victorian genera occur. It is also possible that species from elsewhere in Australia may exhibit characters which fall outside the range found to define a genus in Victoria, so that when the fauna of the whole of Australia is considered new generic criteria will be required. The keys are primarily for later instar larvae, and difficulties could be encountered in keying out early instars. Terminology generally follows that of Wiggins (1977).

KEY TO THE FAMILIES OF FREE-LIVING AND RETREAT-MAKING TRICHOPTERA LARVAE OF VICTORIA

1. Larvae campodeiform; abdominal prolegs usually long, not fused at base, anal claws terminal; tubercles absent from abdominal segment one; mostly free-living or retreat-makers2
SUPERFAMILIES RHYACOPHILOIDEA and HYDROPSYCHOIDEA
- Larvae eruciform; abdominal prolegs short, fused to form an apparent tenth abdominal segment, anal claws lateral; tubercles present on abdominal segment one; construct portable cases
SUPERFAMILY LIMNAPHILOIDEA (Not considered further)

2. Dorsal sclerotisation on first thoracic segment only (Fig. 33)3
- Dorsal sclerotisation on all three thoracic segments, although incomplete on mesonotum and metanotum in some families (Figs. 27, 28, 41, 51, 52)5
3. Labrum membranous, anterior margin considerably broader than posterior margin (Fig. 23).....
-PHILOPOTAMIDAE
- Labrum sclerotised, anterior margin not greatly broader than posterior margin (Figs. 18, 34).....4
4. Protrochantin distinct and well developed, prothoracic leg simple (Figs. 31, 32)
-POLYCENTROPODIDAE
- Protrochantin reduced, not at all obvious; prothoracic leg modified, either chelate or with femur broadened and with a field of stout spines (Figs. 2, 8, 12, 20) ...HYDROBIOSIDAE
5. Abdomen of final instar swollen, distinctly wider than head and thorax; final instar living in portable purse-like case (Fig. 51)
-HYDROPTILIDAE
- Abdomen not swollen, only slightly wider than head and thorax; not living in purse-like case.....6
6. Mesonotum and metanotum each bearing a pair of small sclerites (Fig. 52); living in dome-shaped portable stone caseGLOSSOSOMATIDAE
- Mesonotum and metanotum with sclerotisation complete or almost complete (Figs. 27, 28, 39, 41)7
7. Abdominal gills present (Figs. 39, 41)
-HYDROPSYCHIDAE
- Abdominal gills absentECNOMIDAE

Hydrobiosidae

The Hydrobiosidae of Australia were revised by Neboiss (1962), who recorded twenty-four species from Victoria contained in nine genera. Since then three additional species have been recorded from the state, *Austrochorema nama*, *Ulmerochochorema onychion* and *Tanjilana*

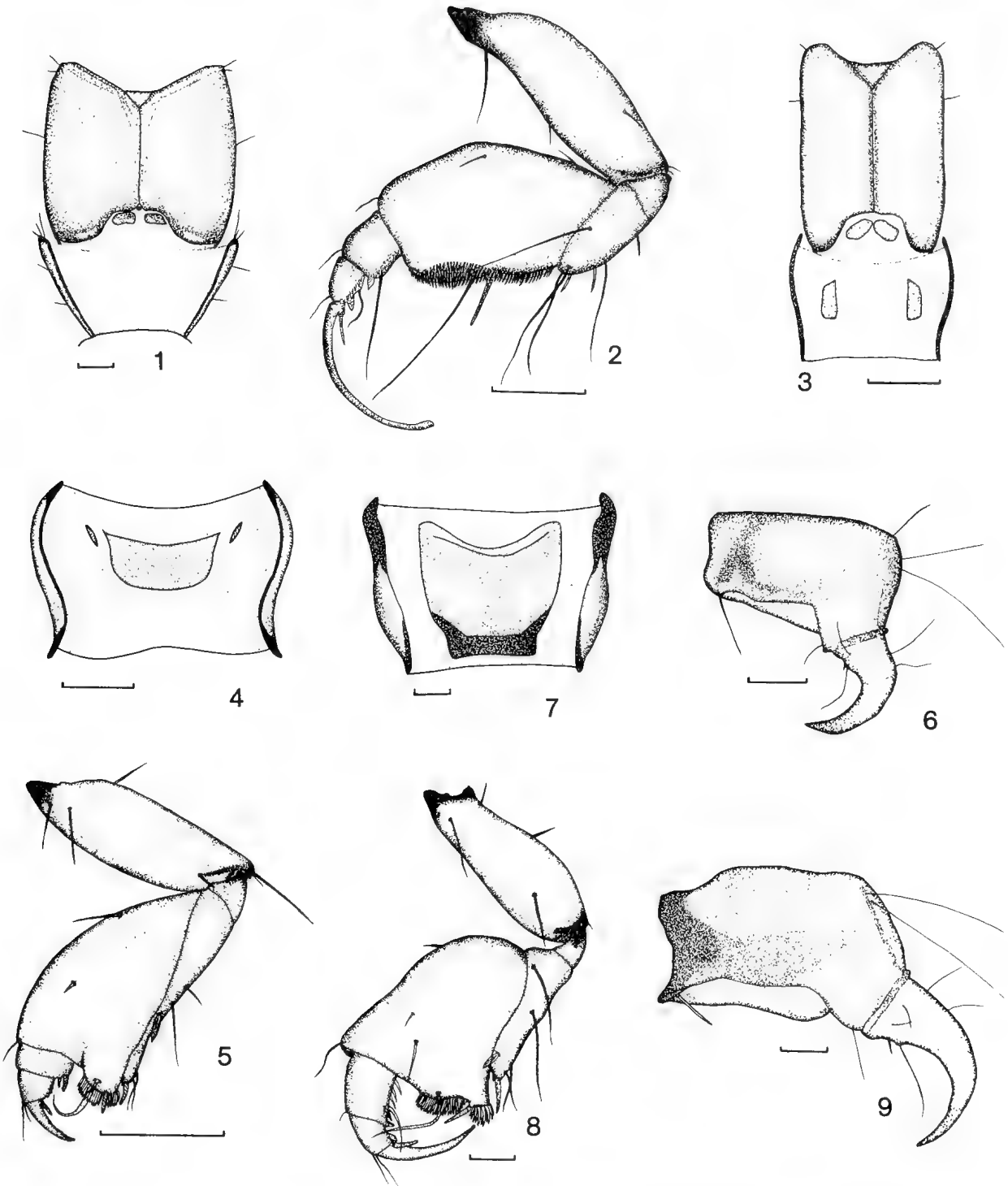
zothecula (Neboiss 1977, personal communication). In addition several species have been transferred from the genus *Taschorema* to two new genera, *Ethochorema* and *Ptychobiosis* (Neboiss, 1977). This is probably one of the few Trichoptera families for which taxonomic knowledge of the Victorian fauna is close to complete.

We have bred through to the adult all known Victorian species of the genera *Apsilochorema*, *Megogata*, *Psyllobetina*, *Koetonga*, *Ethochorema*, *Taschorema* and *Ptychobiosis*, as well as five species of *Ulmerochochorema* and one of the two *Tanjilana* species. Two additional larval types cannot be referred to the above genera, and presumably therefore represent the remaining Victorian genera, namely *Allochorema* and *Austrochorema*. One of these larval types is very similar to confirmed larvae of *Austrochorema pegidion* from Tasmania, and is accordingly included in the key as *Austrochorema*, while the larva we have called 'Genus' A is more similar to *Apsilochorema* than other Victorian genera, and this suggests *Allochorema* as the likely identity.

As mentioned above Neboiss (1977) transferred several species from the genus *Taschorema* to the new genera *Ethochorema* and *Ptychobiosis*. Although we have bred out and are able to recognise all Victorian species involved, we have been unable to identify reliable characters to key out the genera. Likewise we have been unable to key out the genus *Tanjilana*, and as a consequence the genera *Taschorema*, *Ethochorema*, *Ptychobiosis* and *Tanjilana* are lumped in the key as the *Taschorema* complex.

KEY TO VICTORIAN GENERA OF HYDROBIOSIDAE

1. Undersurface of head with pair of small posterior sclerites closely associated with head capsule (Figs. 1, 3).....2
- Undersurface of head without posterior sclerites3
2. Prosternum without sclerites (Fig. 1); tarsal claw of prothoracic leg twice combined length of tibia and tarsus (Fig. 2)*Apsilochorema*



Figures 1-9 HYDROBIOSIDAE

Figs. 1-2. *Apsilochorema*. 1, head and prothorax, ventral; 2, prothoracic leg.
 Fig. 3. 'Genus' A, head and prothorax, ventral.

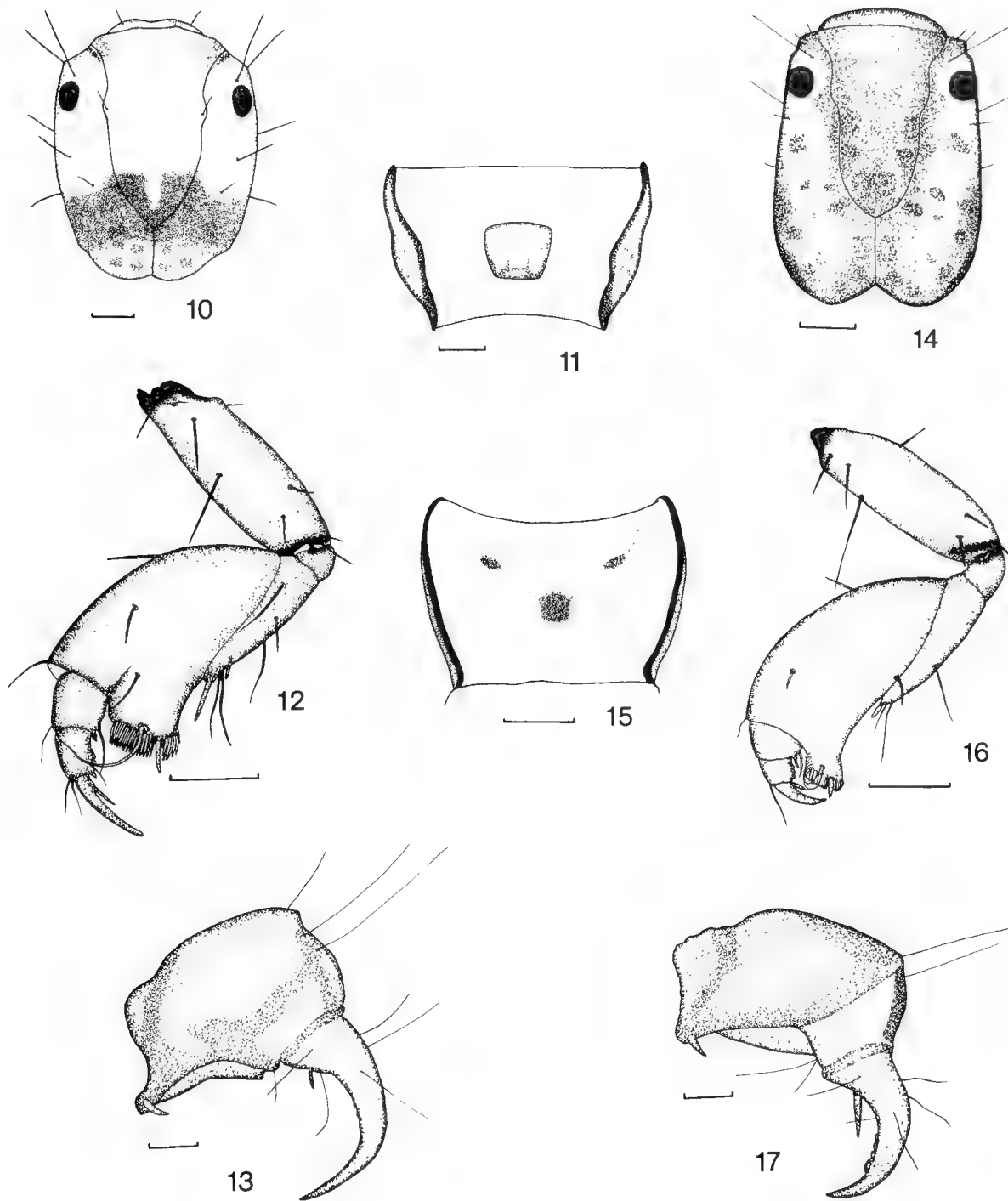
Figs. 4-6. *Austrochorema*. 4, prosternum; 5, prothoracic leg; 6, abdominal proleg.
 Figs. 7-9. *Koetonga*. 7, prosternum; 8, prothoracic leg; 9, abdominal proleg.
 Scale lines: 0.1 mm (Figs. 6, 9); 0.2 mm (Figs. 1-5, 7-8)

- Prosternum with pair of small rectangular sclerites (Fig. 3); tarsal claw of prothoracic leg only slightly longer than combined length of tibia and tarsus 'Genus' A
- 3. Prothoracic leg with femur broadened, trochanter extending at least halfway along ventral margin of femur (Figs. 5, 8, 12, 16); chela absent (Figs. 5, 8, 12) or short and not well developed (Fig. 16); prosternum generally with central sclerite reduced (Figs. 4, 11, 15) although with a single exception (Fig. 7) 4
- Prothoracic leg with femur not broadened, trochanter never extending halfway along ventral margin of femur (Fig. 20); chela long and well developed (Fig. 20); prosternum with single large sclerite (Fig. 19) 7
- 4. Apical spine of protrochanter reaching cluster of spines on apical-ventral angle of femur (Figs. 5, 8); ventral spine at base of abdominal proleg long, slender and straight (Fig. 9) or replaced by a long hair (Fig. 6) 5
- Apical spine of protrochanter not reaching cluster of spines on apical-ventral angle of femur (Figs. 12, 16); ventral spine at base of abdominal proleg short, stout and curved (Figs. 13, 17) 6
- 5. Central sclerite of prosternum twice as wide as long, two small antero-lateral sclerites also present (Fig. 4) *Austrochorema*
- Central sclerite of prosternum about as wide as long, antero-lateral sclerites absent (Fig. 7) *Koetonga*
- 6. Prosternum with single central sclerite, antero-lateral sclerites absent (Fig. 11); frontoclypeus with dark pigmentation in posterior quarter only, pigmentation extended outside frontoclypeus to cover much of posterior third of head (Fig. 10) *Ulmerochorema*
- Prosternum with pair of small antero-lateral sclerites, and in some species also with a central sclerite (Fig. 15); frontoclypeus more uniformly pigmented, dark pigmentation not restricted to posterior third of head (Fig. 14) *Psyllobetina*
- 7. Frontoclypeus long and narrow, length/width ratio greater than 2.0; lateral margins with small conspicuous rounded projections in posterior half (Fig. 21) *Megogata*
- Frontoclypeus not long and narrow, length/width ratio less than 1.7; lateral margins without conspicuous projections in posterior half (Figs. 18, 22) *Taschorema* complex

Philopotamidae

Two genera have been recorded from Australia, *Chimarra* and *Hydrobiosella*. We have bred out two species of each genus from Victoria, and have found the genera readily distinguished on the basis of the processes on the coxa of the prothoracic leg. In *Hydrobiosella* the coxa bears two sclerotised processes, each with a terminal seta, while *Chimarra* has only a single sclerotised process and basal to this a long dark seta arising directly from the surface of the coxa. Utilising these criteria we have been able to recognise additional species of both genera from mainland Australia.

It should be mentioned, however, that we have examined larvae from Tasmania which do not possess sclerotised processes on the coxa, instead having two dark setae arising directly from the surface. Neboiss (1977) has revised the adult Philopotamidae of Tasmania, and recognised nine species all placed in the genus *Hydrobiosella*. He did, however, comment on the presence of three quite distinctive species groups on the basis of male genitalia; the *H. corinna* group with four species, the *H. tasmanica* group with four species, and *H. waddama*. We have bred out *H. waddama* and a species of the *H. corinna* group from Victoria, and both have two sclerotised processes. In the collection of the National Museum of Victoria there is a pupa of the *H. tasmanica* group, and the associated larval parts do not have coxal processes. If this condition is common to all

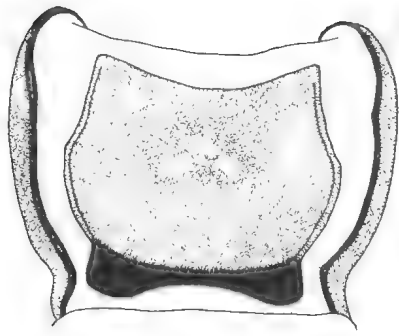


Figures 10-17 HYDROBIOSIDAE

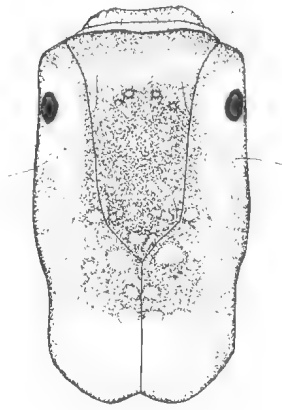
Figs. 10-13. *Ulmerochorema*. 10, head; 11, prosternum; 12, prothoracic leg; 13, abdominal proleg.

Figs. 14-17. *Psyllobetina*. 14, head; 15, prosternum; 16, prothoracic leg; 17, abdominal proleg.

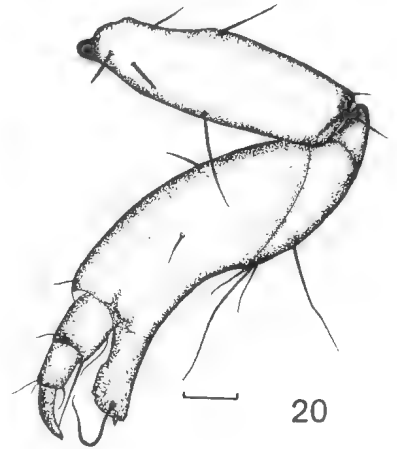
Scale lines: 0.1 mm (Figs. 13, 17); 0.2 mm (Figs. 10-12, 14-16)



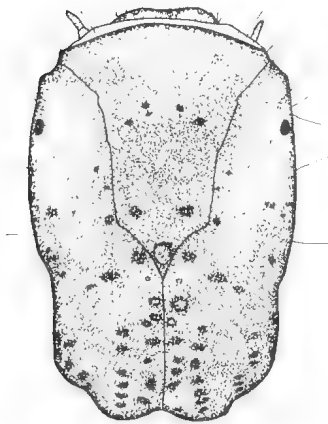
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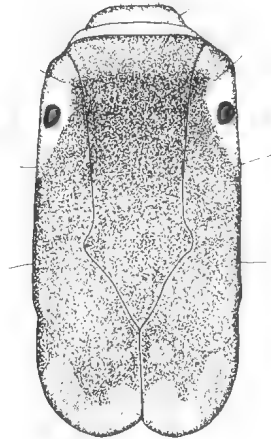
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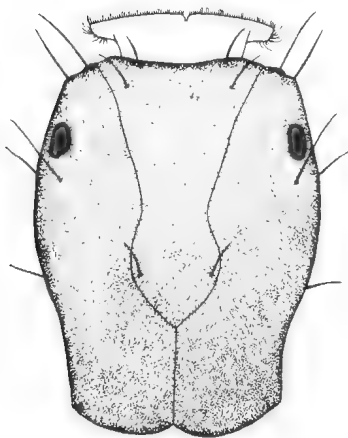
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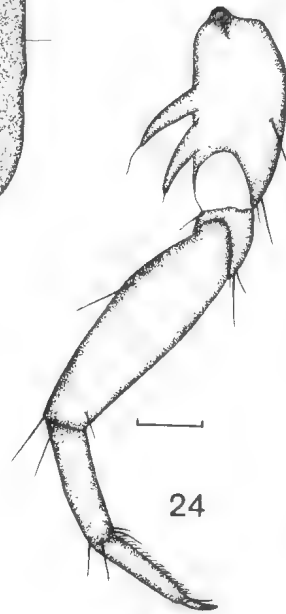
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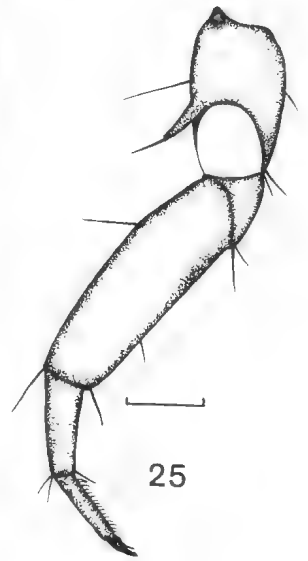
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25

Figures 18-22 HYDROBIOSIDAE

Figs. 18-20. *Taschorema*. 18, head; 19, prosternum; 20, prothoracic leg.

Fig. 21. *Megogata*, head.

Fig. 22. Species of *Taschorema* complex, head.

Figures 23-25 PHILOPOTAMIDAE

Figs. 23-24. *Hydrobiosella*. 23, head; 24, prothoracic leg.

Fig. 25. *Chimarra*, prothoracic leg.

Scale lines: 0.2 mm

species of the *H. tasmanica* group, either our generic concept will have to be broadened or erection of a new genus could perhaps be justified. This, however, is outside the scope of the present study, and since larvae without coxal processes have not been recorded from Victoria they have not been considered in the key below.

KEY TO VICTORIAN GENERA OF
PHILOPOTAMIDAE

1. Coxa of prothoracic leg with two sclerotised processes, each with a terminal seta (Fig. 24) *Hydrobiosella*
- Coxa of prothoracic leg with a single sclerotised process, and basal to this a long dark seta arising directly from the surface of the coxa (Fig. 25) *Chimarra*

Ecnomidae

All described Australian species have been referred to the genera *Ecnomus* and *Ecnomina*. The only Victorian species recorded in the literature are *Ecnomus tillyardi* and *Ecnomina irrorata* (Neboiss 1977, 1978). We have collected at least twelve larval species from the state, and have bred out males of seven of these.

While the species of *Ecnomus* form a well defined group, described species of *Ecnomina* fall into several distinct species groups on the basis of structure of the genitalia and minor details of the wings (Neboiss, personal communication). Future erection of new genera to accommodate some of these species groups is a definite possibility, and such an approach is supported by evidence in the larvae. In addition to species of *Ecnomus*, we have collected larvae of seven ecnomid species which we consider probably represent three different genera. We have bred out adults of two of these presumed genera, and both would be identified as *Ecnomina* using currently available adult taxonomy. Until adult taxonomy has been revised, generic identification of these larvae is not possible, and for this reason they are included in the key as 'Genus' D, 'Genus' E and 'Genus' F.

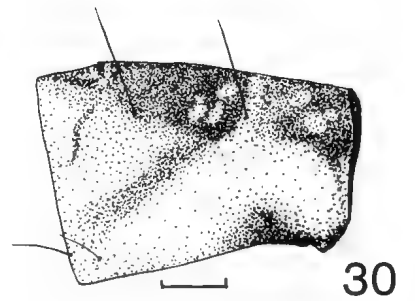
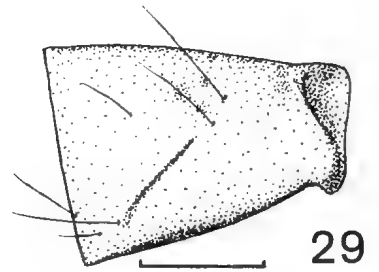
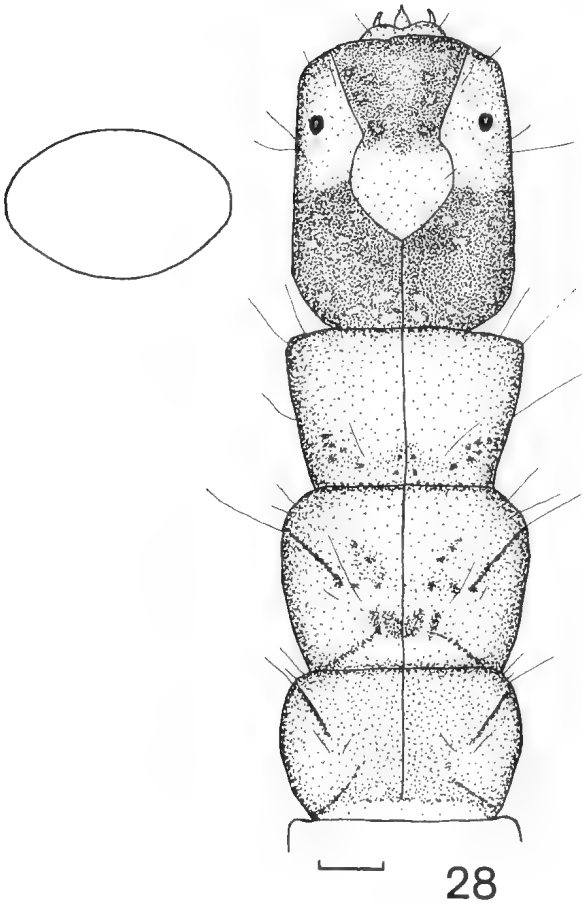
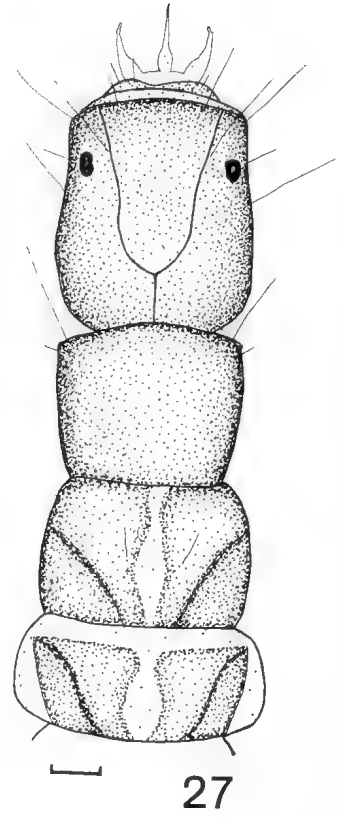
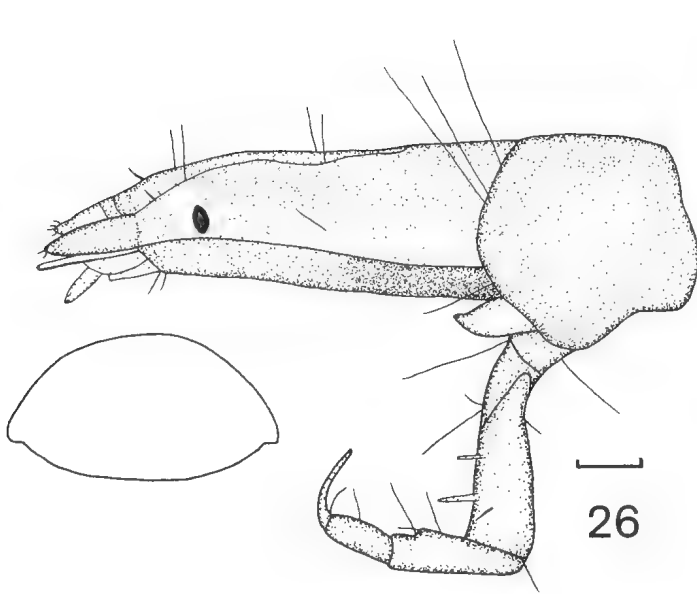
KEY TO VICTORIAN GENERA OF
ECNOMIDAE

1. Head ventrally flattened, lateral margins angular with conspicuous ridge running full length of head capsule (Fig. 26) 'Genus' D
- Head not ventrally flattened, lateral margins rounded and without conspicuous ridge (Figs. 27, 28) 2
2. Frontoclypeus not obviously constricted near middle; mesonotum incompletely sclerotised, membranous along midline (Fig. 27) 'Genus' E
- Frontoclypeus obviously constricted near middle; mesonotum completely sclerotised (Fig. 28) 3
3. Mesonotum usually with broad and ill-defined dark band extending obliquely backwards from antero-lateral corner (Fig. 30), although this band may be absent in some specimens *Ecnomus*
- Mesonotum always with narrow and sharply defined dark line extending obliquely backwards from antero-lateral corner (Fig. 29) 'Genus' F

Polycentropodidae

The Polycentropodidae of Victoria remain virtually uninvestigated. The only records in the literature are *Plectrocnemia australica* and a species of *Nyctiophylax*, both collected during the Dartmouth environmental survey (Smith et al. 1977). Other genera recorded from Australia are *Polyplectropus* from New South Wales, *Tasmanoplegas* from Tasmania and *Hyalopsyche* from North Queensland (Mosely & Kimmins, 1953; Neboiss, 1977, 1980).

We have records of seven distinctive larval species from Victoria, and these are here placed into five 'genera'. We have bred out two species each of *Plectrocnemia* and *Nyctiophylax*, while the other three larval species remain unidentified. The larval type we have designated 'Genus' G is instantly recognizable by its large size and the fused tibia and tarsus in the pro- and mesothoracic legs. We suspect that this larval type will prove to be *Stenopsychodes*. However, until this is confirmed it seems more



appropriately placed with the Polycentropodidae rather than in the family Stenopsychidae. Likewise we have not bred through larvae of our 'Genus' H, which would in fact be identified as a Stenopsychidae using the key in Williams (1980). However, that key is based upon described larvae of the type genus *Stenopsyche*, which is restricted in distribution to Asia and central Africa, and which is not necessarily relevant to the Australian situation. Indeed Schmid (1969) has drawn attention to the considerable differences between *Stenopsyche* and *Stenopsychodes* in adults at least, and has suggested that the two genera should be placed in different sub-families. The status of 'Genus' I has also caused us some concern. We have examined a male pupa of a species from this group, and the genitalia appeared to be of the *Nyctiophylax* type. We have also seen larvae from Tasmania which have ventral processes on the anal claw as well as an accessory dorsal spine, and which therefore cannot be accommodated in the key below. Until a full taxonomic revision of both adults and larvae has been completed generic identity will remain uncertain.

KEY TO VICTORIAN GENERA OF
POLYCENTROPODIDAE

- 1. Pro- and mesothoracic legs with tibia and tarsus fused (Fig. 31) 'Genus' G
- Pro- and mesothoracic legs with tibia and tarsus not fused (Fig. 32) 2
- 2. Frontoclypeus not obviously constricted near middle (Fig. 36); abdominal segments without lateral fringe of fine setae 'Genus' H
- Frontoclypeus obviously constricted near middle (Fig. 34); abdominal segments with lateral fringe of fine setae (Fig. 33) 3
- 3. Anal claw without ventral teeth or processes (Fig. 35) *Plectrocnemia*

Figures 26-30 ECNOMIDAE

- Fig. 26. 'Genus' D, head and prothorax, lateral, cross section of head.
- Fig. 27. 'Genus' E, head and thorax, dorsal.
- Figs. 28-29. 'Genus' F. 28, head and thorax, dorsal, cross section of head; 29, mesonotum, lateral (anterior to left).
- Fig. 30. *Ecnomus*, mesonotum, lateral (anterior to left).

Scale lines: 0.2 mm

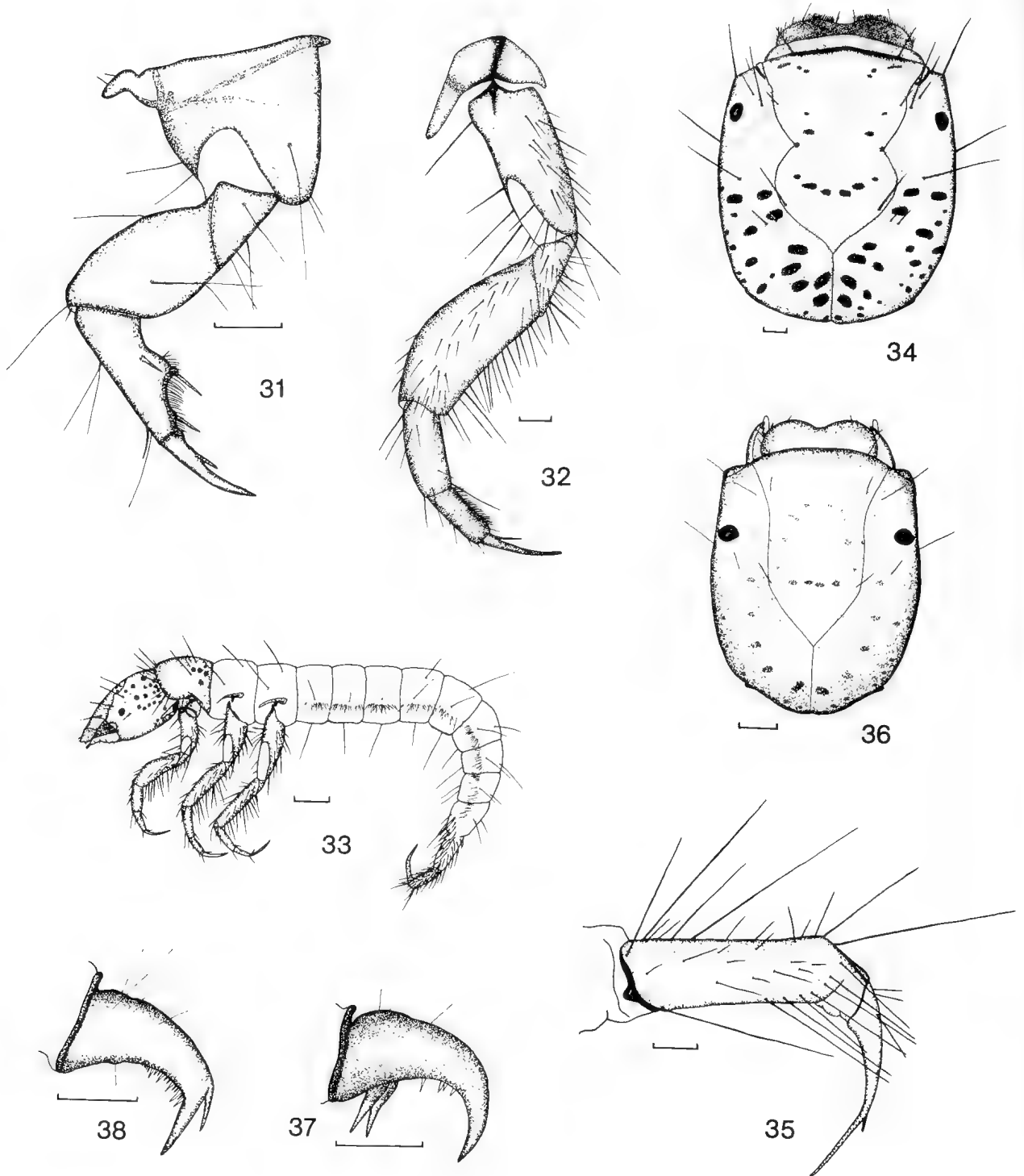
- Anal claw with ventral teeth and/or processes (Figs. 37, 38) 4
- 4. Anal claw with ventral processes near base, without accessory dorsal spine (Fig. 37) 'Genus' I
- Anal claw without ventral processes near base, accessory dorsal spine present (Fig. 38) *Nyctiophylax*

Hydropsychidae

Although eight genera of Hydropsychidae have been recorded from Australia, there are literature records for only four from Victoria. We have examined larvae of at least thirteen Victorian species, and these appear to represent six genera. We have bred out species of the genera *Asmicridea* and *Cheumatopsyche*, while the other larval types remain unidentified.

One of our larval types has been figured by Riek (1970) as *Macronema*. However, since we have not confirmed this the larva is included in the key as 'Genus' J. It should be noted that Korboot (1964) has figured a larva under the name *Macronemum torrenticola*, which obviously is not congeneric with Riek's *Macronema*. A second unidentified larval type, with at least two Victorian species, we have designated 'Genus' K. We have examined specimens of this larval type from both Tasmania and Western Australia, and the only genus known to be common to these two regions for which we have no knowledge of the larva is *Smicrophylax*.

The remaining two larval types from Victoria belong to a group which may be termed the *Dipletrona* complex. This consists of some fourteen described Australian species, which have been referred to the genera *Dipletrona*, *Austropsyche* and *Sciops*. The generic taxonomy of these species is, however, in urgent need of revision. Several species described under the genus *Dipletrona* are obviously congeneric with *Austropsyche victoriana*, while of the two species of *Sciops* one appears to be congeneric with *Austropsyche victoriana* while the second is probably congeneric with other species at present contained in the genus *Dipletrona*. We have separated larvae of this complex on the basis of the presence or absence of a transverse constriction of the pronotum. Proof



Figures 31-38 POLYCENTROPODIDAE

Fig. 31. 'Genus' G, prothoracic leg.

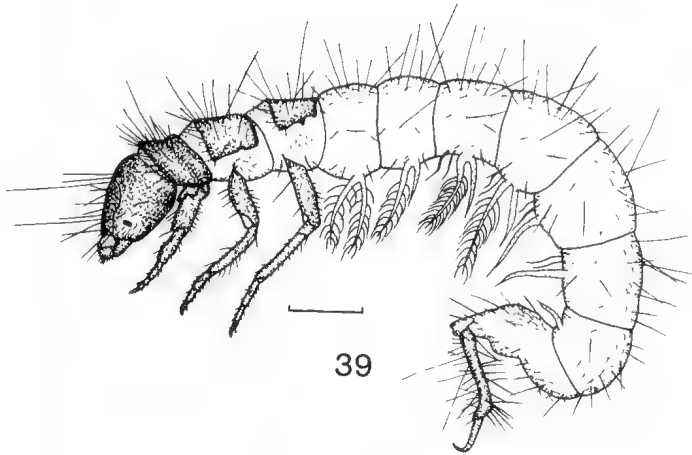
Figs. 32-35. *Plectrocnemia*. 32, prothoracic leg; 33, whole animal; 34, head; 35, abdominal proleg.

Fig. 36. 'Genus' H, head.

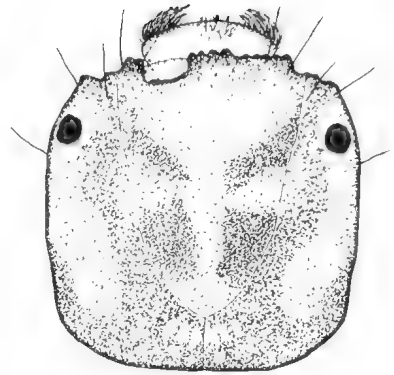
Fig. 37. 'Genus' I, anal claw.

Fig. 38. *Nyctiophylax*, anal claw.

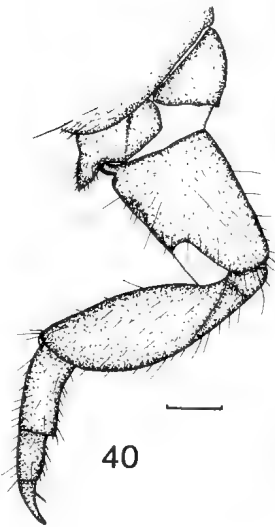
Scale lines: 0.1 mm (Figs. 37, 38); 0.2 mm (Figs. 31, 32, 34-36); 1.0 mm (Fig. 33)



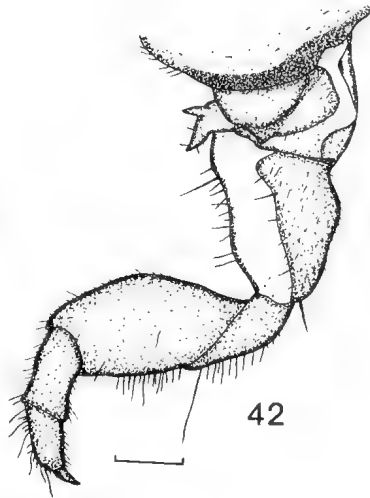
39



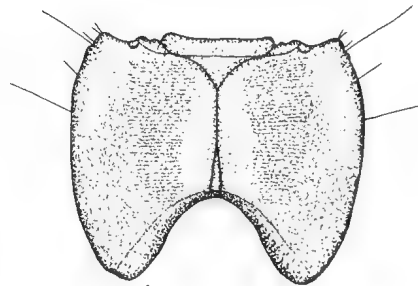
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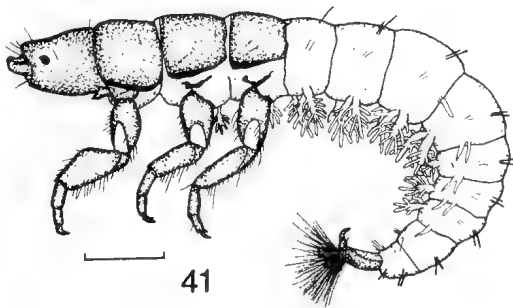
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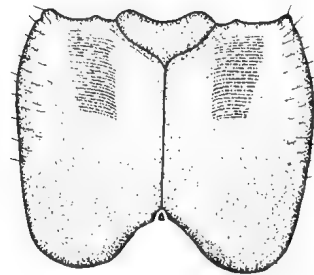
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41



43

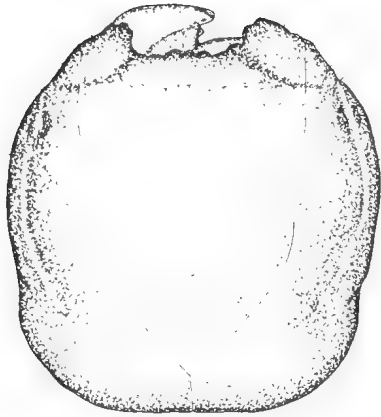
Figures 39-45 HYDROPSYCHIDAE

Figs. 39-40. *'Genus' J.* 39, whole animal; 40, prothoracic leg.

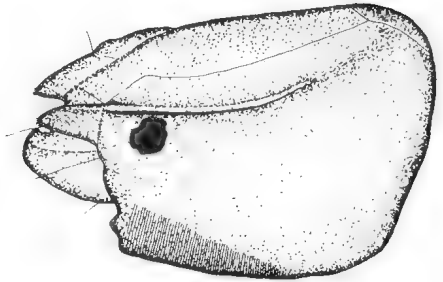
Figs. 41-43. *Cheumatopsyche.* 41, whole animal; 42, prothoracic leg; 43, head, ventral.

Figs. 44-45. *Asmicridea.* 44, head, dorsal; 45, head, ventral.

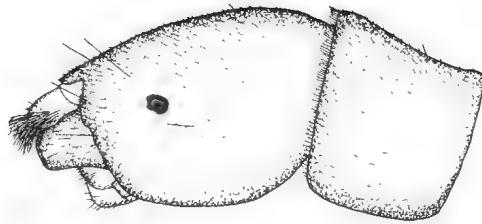
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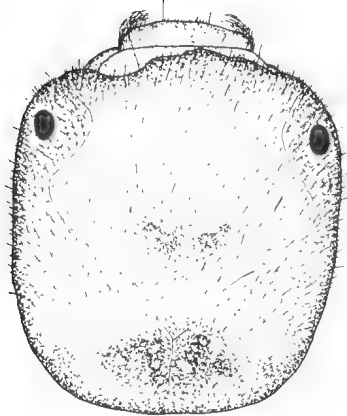
46



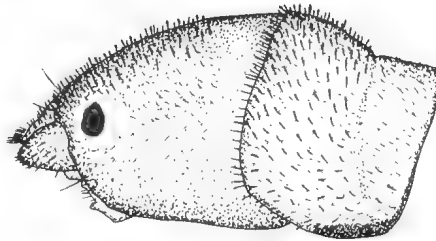
47



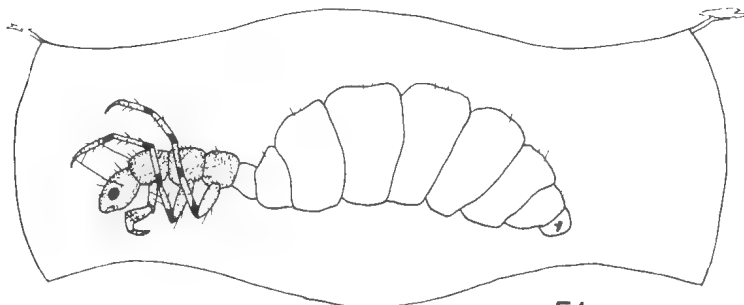
50



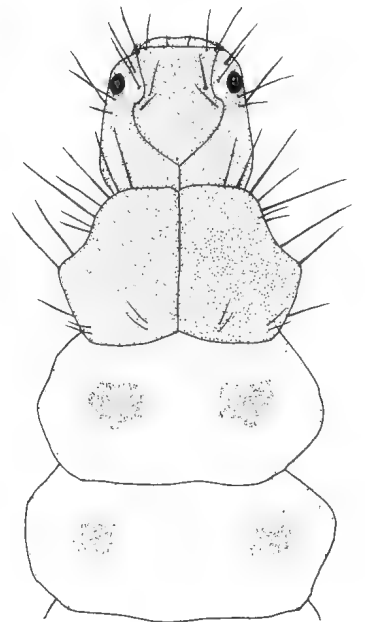
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48



51



52

of the validity of such a division must await extensive breeding out of adults. However, Wiggins (1977) has used the same character to separate North American genera within the subfamily Diplelectroninae. Although we are not prepared to allocate generic names to the two larval types, our 'Genus' L includes *Austropsyche victoriana*, which we have bred out, while larvae of 'Genus' M agree with the description of *Diplelectrona* larvae given by Wiggins (1977).

KEY TO VICTORIAN GENERA OF
HYDROPSYCHIDAE

1. Posterior ventral apotome of head very small, much less than half as long as median ecdysial line linking it with anterior ventral apotome (Fig. 43).....2
- Posterior ventral apotome of head larger, at least half as long as median ecdysial line linking it with anterior ventral apotome (Fig. 45).....3
2. Protrochantin forked (Fig. 42); abdominal gills with branches stout and not linear, gills not feather-like in appearance (Fig. 41).....*Cheumatopsyche*
- Protrochantin simple (Fig. 40); abdominal gills with lateral branches slender and linear, gills feather-like in appearance (Fig. 39).....'Genus' J
3. Frontoclypeus either not constricted in anterior half, or with constriction very shallow (Figs. 44, 46).....4
- Frontoclypeus very obviously constricted in anterior half (Fig. 49).....5
4. Head with well developed carina (Figs. 46, 47).....'Genus' K
- Head without carina (Fig. 44).....*Asmicridea*

Figures 46-50 HYDROPSYCHIDAE

Figure 51 HYDROPTILIDAE

Figure 52 GLOSSOSOMATIDAE

- Figs. 46-47. 'Genus' K. 46, head, dorsal; 47, head, lateral.
 Fig. 48. 'Genus' L, head and prothorax, lateral.
 Figs. 49-50. 'Genus' M. 49, head, dorsal; 50, head and prothorax, lateral.
 Fig. 51. Hydroptilidae, whole animal.
 Fig. 52. Glossosomatidae, head and thorax, dorsal.
 Scale lines: 0.2 mm (Figs. 46, 47); 0.5 mm (Figs. 48-52).

5. Pronotum with transverse constriction in posterior half (Fig. 48).....'Genus' L
- Pronotum without transverse constriction in posterior half (Fig. 50).....'Genus' M

Acknowledgements

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A TAXONOMIC REVISION OF *OCTOPUS AUSTRALIS* HOYLE, 1885
(OCTOPODIDAE: CEPHALOPODA), WITH A REDESCRIPTION OF
THE SPECIES

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Abstract

Octopus australis Hoyle from South Eastern Australian waters is fully redescribed. Several species from New Zealand previously synonymised with it are recognised as distinct and their nomenclatural status is discussed.

Introduction

Octopus australis was described by Hoyle, based on one female and one immature specimen from Port Jackson, N.S.W. Subsequently, Massey (1916), Robson (1929), Benham (1942) and Dell (1952) have described material from New Zealand, which they have synonymised with *O. australis* Hoyle. Dell's synonymy includes *Polypus campbelli* Smith, 1902; *Polypus australis* Massey, 1916; *Polypus* cf *australis* Berry, 1918; and *Robsonella australis* Benham, 1942. Specimens from South Eastern Australian waters match closely with the brief type description, but differ to the descriptions of Smith, Massey, Robson, Benham and Dell. To clarify this situation, the type specimens of *O. australis* were borrowed from the British Museum for comparison with other Australian and New Zealand material.

The identity of the S.E. Australian species is confirmed as *Octopus australis* Hoyle, and a complete redescription is given. The New Zealand species *Polypus campbelli* Smith, *Polypus australis* Massey and *Robsonella*

australis Benham are identified as a separate species group, and their nomenclatural status is discussed.

Measurements and Abbreviations

The measurements and abbreviations used are the same as given in Voss (1963), with the exception of head length. Head length (H.L.) is taken from the junction of the dorsal pair of arms to the midpoint between the eyes. Measurements are given in Table 1, indices are expressed in Table 2. Other abbreviations used are BM(NH)—British Museum (Natural History); NMV—National Museum of Victoria.

***Octopus australis* Hoyle, 1885**

Plate 1—a, b Figures 1-2.

1885a *Octopus australis* Hoyle, p. 224.

1885b *Octopus australis* Hoyle, pp. 98-99.

1886 *Octopus australis* Hoyle, pp. 88-89, pl. 3, figs. 4-5.

Materials examined:

Sex	M.L. (mm)	Reg. No.	Location	Date coll.	Depth (m)
Holotype ♀	22	BM(NH)1889.4.24.28.9	Port Jackson, N.S.W.	April 1874	11-28
Paratype ♂	12	BM(NH)1889.4.24.28.9	Port Jackson, N.S.W.	April 1874	11-28
Other material ♂	16	NMV F25247	Western Port Bay, Vic.	—	—
♂	21	NMV F30860	40°34'S, 144°46'E	4. 2.1981	68
♂	27	NMV F31265	37°55'S, 144°58'E	18. 3.1980	7
♂	37	NMV F31003	32°24'S, 133°30'E	23. 8.1973	49
♂	42	NMV F31265	37°55'S, 144°58'E	18. 3.1980	7

Sex	M.L. (mm)	Reg. No.	Location	Date coll.	Depth (m)
<i>Materials</i>					
♂	45	NMV F21911	38°02'S, 145°04'E	1961	11
♂	45	NMV F21911	38°02'S, 145°04'E	1961	11
♂	46	NMV F31267	32°24'S, 133°24'E	26.10.1973	40
♂	54	NMV F31002	39°38'S, 145°06'E	3. 2.1981	66
♂	56	NMV F21911	38°02'S, 145°04'E	1961	11
♂	67	NMV F31260	32°13'S, 133°52'E	27. 4.1973	8
♂	67	NMV F25436	38°07'S, 145°06'E	1964	—
♂	72	NMV F31002	39°38'S, 145°06'E	3. 2.1981	66
♂	73	NMV F31264	38°03'S, 145°06'E	7. 6.1978	—
♀	9	NMV F31263	38°55'S, 145°55'E	9.11.1972	12
♀	14	NMV F31262	35°23'S, 137°17'E	21. 1.1971	54
♀	17	NMV F25247	Western Port Bay, Vic.	—	—
♀	17	NMV F30927	40°50'S, 146°07'E	4. 2.1981	66
♀	19	NMV F25247	Western Port Bay, Vic.	—	—
♀	25	NMV F31265	35°55'S, 144°58'E	18. 3.1980	7
♀	28	NMV F31265	37°55'S, 144°58'E	18. 3.1980	7
♀	34	NMV F31265	37°55'S, 144°58'E	18. 3.1980	7
♀	34	NMV F31003	32°24'S, 133°30'E	23. 8.1973	49
♀	37	NMV F31265	37°55'S, 144°58'E	18. 3.1980	7
♀	37	NMV F31003	32°24'S, 133°30'E	23. 8.1973	49
♀	41	NMV F24485	37°51'S, 144°57'E	15. 1.1930	—
♀	44	NMV F25245	Western Port Bay, Vic.	1963	—
♀	47	NMV F24492	37°59'S, 145°01'E	10.11.1973	—
♀	49	NMV F31002	39°38'S, 145°06'E	3. 2.1981	66
♀	49	NMV F31002	39°38'S, 145°06'E	3. 2.1981	66
♀	62	NMV F31265	37°55'S, 144°58'E	18. 3.1980	7
♀	88	NMV F24437	38°13'S, 145°02'E	3.10.1957	—

Diagnosis

Size up to 90 mm M.L., arms long, mantle sculpture fine dorsally, smooth ventrally, lateral integumental ridge usually present. 7-8 gill lamellae in outer demibranch; funnel organ with closely opposed, occasionally partially fused VV units. Hectocotylied arm 58-75% of A_{LIII} length; ligula robust, 12-18% of arm length, with double row of fine papillae along median oral excavation.

Description

Mantle globular, quite broad, well demarcated from head; mantle aperture wide; head narrow; eyes small, protuberant (Fig. 1a, Plate 1b). Funnel free for about half its length; funnel organ with two closely opposed V shaped units, ventral and dorsal limbs of approximately equal lengths; units may be partially fused medially (Figs. 1, b-d).

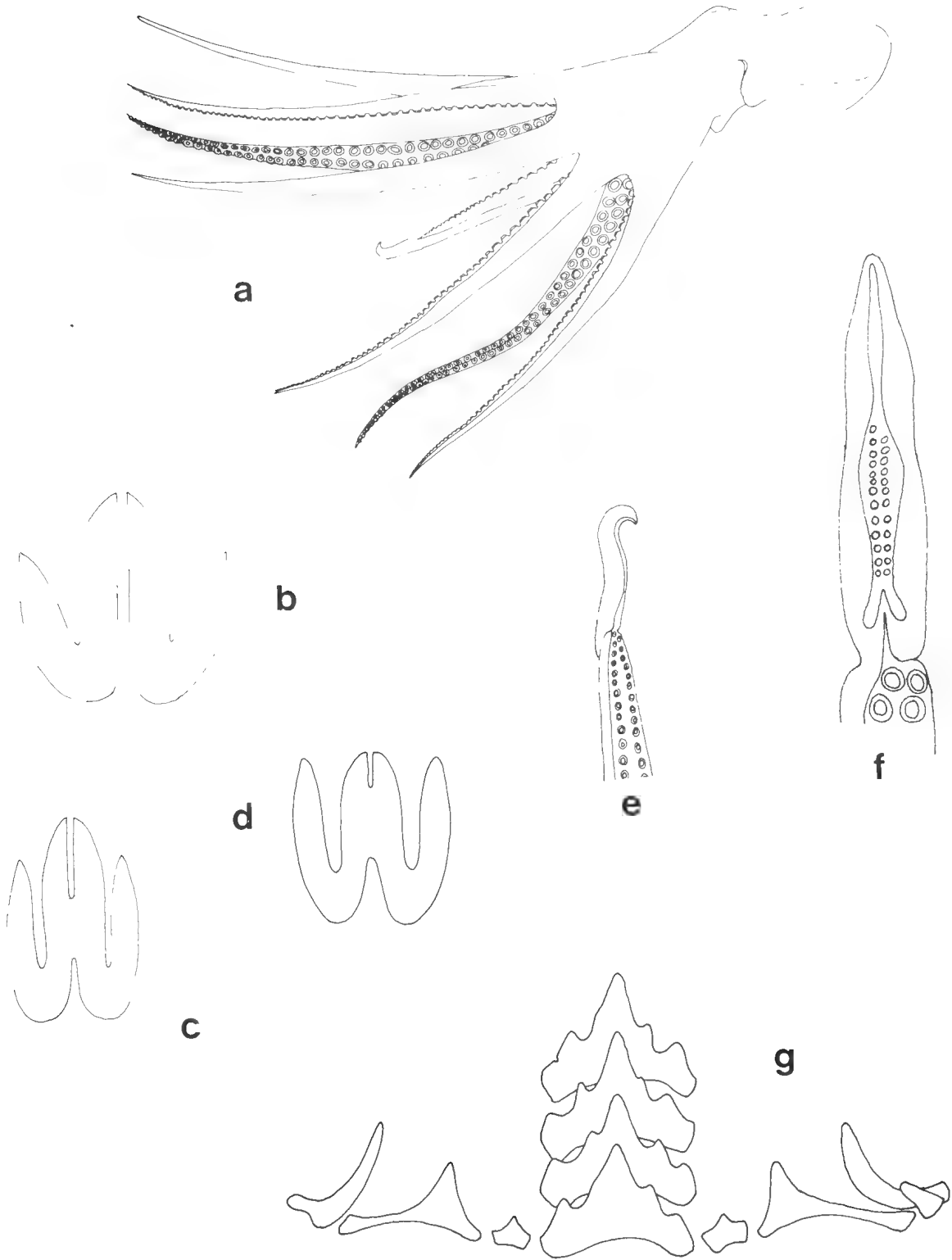
Arms long, subequal, tapering to fine tips; suckers moderate in size, no enlarged suckers in males. Web shallow, extends up the ventral side of the arms for almost their entire length. Web formula D.C.B.E.A. to C.D.B.A.E., dorsal and ventral sectors always shallowest.

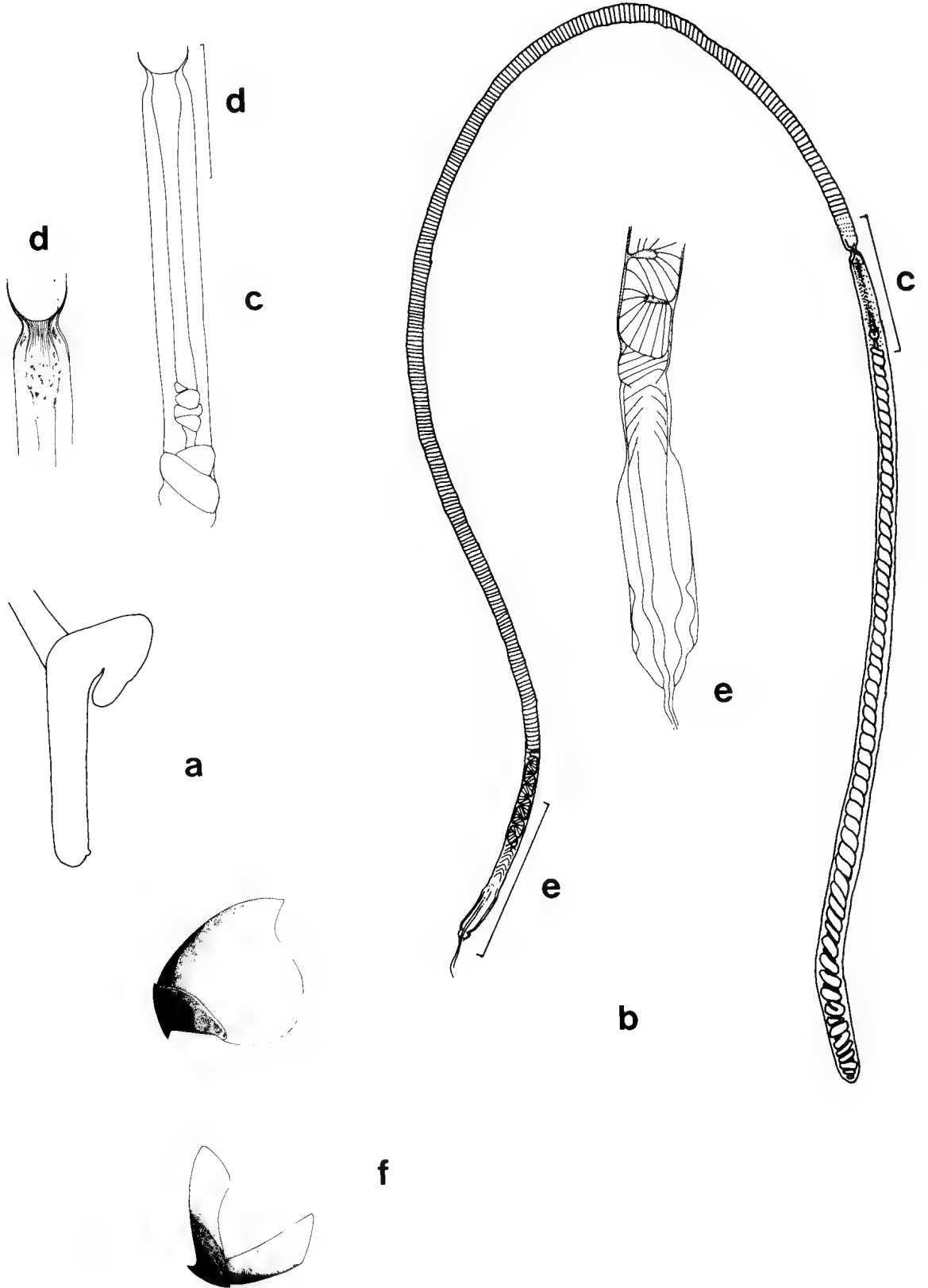
Third right arm of males hectocotylied, 58-75% length of its opposite member; spermatophoral groove well developed but without any conspicuous thickening of the interbrachial web. Ligula large (Figs, 1e, f), deeply excavated, usually curved orally; medially two rows of very small papillae are present along the excavation. Calamus short, acutely pointed.

Gills moderate in length, outer demibranch with 7-8 primary lamellae, plus a terminal lamella.

Reproductive system of males typical of the genus; penis (Fig. 2a) long with a single coiled diverticulum on the right hand side, genital aperture subterminal, on right hand side. Spermatophores (Fig. 2, b-e) long, thin; horn with 2-3 coils close to oral end, oral cap expanded. Female reproductive system without distinctive features; eggs large, length 9-14 mm, attached singly by a stalk approximately 8 mm in length; each clutch of 80-130 eggs (Tait 1980).

Fig. 1. *Octopus australis* Hoyle, 1885, a. Ventral view, male, NMV F31267, 46 mm M.L. b-d. Funnel organs. b. Holotype, female, 22 mm M.L. c. NMV F31265, female, 28 mm M.L. d. NMV F31265, male, 42 mm M.L. e-f. Ligula. NMV F31267, 46 mm M.L. g. Radula. Holotype.





Alimentary canal of normal octopodan type; crop with an anterior caecum of about 10% of its length; posterior oesophagus short; posterior salivary glands elongate, connect to buccal mass by a common duct, ducts to crop separate. Stomach bipartite; caecum strongly coiled; ducts to stomach and caecum originate separately from hepatopancreas, intestine without conspicuous differentiation. Ink sac large, embedded in surface of hepatopancreas, connected to intestine near anus by a short duct.

Beaks (Fig. 2f) typically octopodan; dorsal rostrum curved, wings transparent in small individuals; ventral beak with very blunt rostrum, wings with small anterior protuberances.

Radula (Fig. 1g) with B₃₋₄ seriation (holotype B₄); rhachidian tooth asymmetrical, 1-2 cusps on each side; first laterals with one sharp cusp, second laterals with one cusp, third laterals long, straight or slightly curved; marginal plates oblong, elongate.

Dorsal mantle surface covered by fine tubercles, supraocular cirri often present, ventral surface smooth. Depending on condition of preservation, a ventro-lateral integumental ridge may be present (Fig. 1a, Plate b), most evident adjacent to mantle aperture, often disappearing posteriorly. In live animals this may be extended into a shallow web, or evident only as a fine, light coloured line.

Colour of preserved specimens brown to purplish dorsally, ventral surface cream. Faint pair of roughly circular ocelli present in some specimens posterior to the eyes; each ocellus comprises a dark ring with a lighter centre; they are most apparent in live animals and fade during preservation.

Males have spermatophores in the Needhams Sac when larger than 20-25 mm M.L. (10-13 g), and may reach 70-80 mm M.L. (250 g). Females have large, white and translucent eggs in the ovary when larger than 30-40 mm M.L. (40-60 g), and do not usually grow beyond 50 mm M.L. (100 g).

Fig. 2. *Octopus australis* Hoyle, 1885. a. Penis. NMV F31002, 72 mm M.L. b-e. Spermatophore. NMV F31002, 54 mm M.L. b. Whole spermatophore. c. Cement body. d. Oral end of cement body. e. Oral end. f. Beaks. NMV F31002, female, 49 mm M.L.

Distribution

The collections of the National Museum of Victoria contain specimens of this species from New South Wales, Victorian, Tasmanian and South Australian waters, to depths of 70 m.

Discussion

The confusion relating to the identity of *Octopus australis* Hoyle is due largely to the lack of a mature male type specimen. Although their external morphology is somewhat similar, New Zealand and Australian species may be readily separated by the form of the hectocotylus. Details of the funnel organ, radula, surface sculpture and number of gill lamellae of the holotype indicate that it is conspecific with the Australian material studied.

Of the four species synonymised with *Octopus australis* Hoyle in Dell (1952), detailed descriptions exist for three. Robson (1929) redescribed the holotype of *Polypus campbelli* Smith, from Campbell Island (N.Z.) as having a W-type funnel organ, 10 lamellae in each gill demibranch, enlarged suckers in the male and a L.L.I. of only 8.5%. Massey's (1916) *Polypus australis*, from New Zealand, has a L.L.I. of 11%, a W type funnel organ and symmetrical seriation of the radula. *Robsonella australis*, also from New Zealand, was described by Benham (1942) and Dell (1952). It has a W type funnel organ, stronger cusps on the radula than *O. australis* Hoyle, and eggs of only 2.5-2.8 mm in length (Brough 1965). Further, I have remeasured the five mature males described by Benham and one other from 38°10'S, 147°49'E (NMV F31259) and these have the hectocotylus indices given in Table 3.

TABLE 3
Hectocotylus indices of *Robsonella australis* Benham

	n	mean	S.D.(n-1)	range
HcAI	5*	77.5	3.5	73-81
LLI	6	8.1	1.5	6-10
CLI	6	39.1	7.4	33-53

* A_{LIII} of one specimen regenerating.

These are quite distinct from the corresponding indices given for *O. australis* Hoyle in Table 2. Therefore, all the New Zealand species previously considered to be synonyms of *O. australis* Hoyle appear to be separate and distinct. The description of *Polypus* cf. *australis* from South East Australia, by Berry (1918), is not detailed enough to confirm his tentative identification.

Robson (1929) synonymised *Polypus campbelli* Smith and *Octopus australis* Hoyle by comparing, in part, the ligula of each. Robson's material included the types of *O. australis* Hoyle and Massey's *Polypus australis*. As a mature male type is lacking, Robson's synonymy was therefore based on Massey's material, already shown to be distinct from *O. australis* Hoyle. Furthermore, Robson's description of the radula of the *O. australis* holotype could not have been from the types, as both type specimens had buccal masses intact when loaned by the British Museum.

Nomenclatural Status of the New Zealand Species

The New Zealand species *Polypus australis* Massey and *Robsonella australis* Benham are both junior homonyms of *Octopus australis* Hoyle. This follows the renaming of the genus *Polypus* as *Octopus* by Robson (1929), and the regrouping of *Robsonella* under *Octopus* by Pickford (1955). If the synonymy of these two species and *Polypus campbelli* Smith, as given in Benham (1942) and Dell (1952) is correct, then *Octopus campbelli* (Smith) is the correct senior synonym. However, the differences in the radula of *P. australis* Massey and the enlarged suckers in male *P. campbelli* Smith make it probable that these species and *R. australis* Benham are distinct from each other. *Robsonella australis* Benham and *Polypus australis* Massey must then be renamed to prevent the occurrence of two homonyms of *Octopus australis* in close geographic proximity. A review of this New Zealand species group is urgently required to remove this problem.

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TABLE 1
Measurements (in mm) of *Octopus australis* Hoyle

BM(NH) 1889.4.24.28.9	NMV F25436	NMV F31265
NMV F25247	NMV F31002	NMV F31003
NMV F30860	NMV F31264	NMV F24485
NMV F31265	NMV F31263	NMV F25245
NMV F31003	NMV F31262	NMV F24492
NMV F31265	NMV F25247	NMV F31002
NMV F21911	NMV F30927	NMV F31002
NMV F21911	NMV F25247	NMV F31265
NMV F31267	BM(NH) 1889.4.24.28.9	NMV F24437
NMV F31002	NMV F31265	
NMV F21911	NMV F31265	
NMV F31260	NMV F31265	
	NMV F31003	

Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂
M.L.	12	16	21	27	37	42	45	45	46	54	56	67
Tot. L.	38	47	86	107	170	184	158	163	220	280	200	245
MW	10	12	17	21	29	31	33	27	35	48	35	36
H.L.	3	5	9	10	17	16	17	15	22	20	17	22
H.W.	8	10	12	16	18	21	21	18	27	26	22	23
ARI	20	30	54	72	119	115	—	113	160	190	138	142
ALI	22	30	60	69	120	121	100	110	155	202	120	163
ARII	26	33	63	77	119	115	106	134	158	—	—	179
ALII	24	32	59	76	105	—	106	114	156	230	163	—
ARIII	23	30	51	59	97	101	108	108	96	146	121	138
ALIII	23	31	65	—	140	135	—	—	141	229	—	155
ARIV	22	27	54	70	—	123	118	118	157	202	138	162
ALIV	25	30	56	70	152	125	101	115	172	210	142	150
HcAL	23	30	51	59	97	101	108	108	96	146	121	138
Lig. L.	0.8	3.6	4.0	8.3	16.2	17.5	13.3	14.5	17.0	19.0	19.3	20
Cal. L.	0.1	0.7	0.9	2.1	3.6	3.3	2.8	2.7	3.3	3.4	3.1	4.0
Web A	6	8	13	15	19	23	24	17	33	36	21	28
Web B _R	7	9	16	17	23	26	27	27	39	41	28	32
B _L	7	9	17	17	20	28	23	27	35	47	30	35
Web C _R	8	9	18	16	22	29	35	28	37	45	33	36
C _L	8	9	17	17	22	33	32	28	38	48	32	37
Web D _R	7	10	17	18	22	33	35	30	34	44	37	35
Web D _L	7	10	15	16	25	28	27	29	40	45	33	37
Web E	7	8	11	14	20	24	24	25	32	37	27	27
Web Form.	CBDEA	DCBAE	CDBAE	CDBAE	DCBEA	CDBEA	CDBAE	DCBEA	DCBAE	CDBEA	DCBEA	CDBAE
S normal	1.2	1.5	1.9	2.7	3.3	3.6	3.6	4.0	4.5	4.8	4.5	4.8
Sp. L.	—	—	—	—	—	—	—	36.0	31	—	49	42
Sp. R.L.	—	—	—	—	—	—	—	16.5	14	—	20	18
Sp. R.W.	—	—	—	—	—	—	—	1.6	1.1	—	1.0	1.3
Penis L.	2	3	3	—	10	—	—	16	17	14	13	17
Gill No.	8	7	7	7	7	8	7	7	8	7	8	7

Sex	♂	♂	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
M.L.	67	72	73	9	14	17	17	19	22	25	28	34	34
Tot. L.	250	395	285	29	57	57	75	57	87	88	82	121	140
MW	49	65	37	9	12	14	14	14	19	19	26	22	24
H.L.	20	22	24	3	7	6	7	8	7	10	11	13	12
H.W.	29	34	25	7	10	11	10	12	13	15	16	18	16
ARI	172	326	201	15	37	31	—	—	47	56	65	—	86
ALI	175	—	—	16	38	33	52	37	50	59	65	78	79
ARII	187	325	202	18	37	32	35	43	55	62	—	85	—
ALII	206	368	229	19	40	35	43	44	58	—	76	86	109
ARIII	—	205	162	18	39	37	57	40	59	59	65	86	101
ALIII	205	352	215	18	43	36	50	42	58	65	76	76	110
ARIV	—	285	190	18	33	36	53	41	—	61	—	83	101
ALIV	186	300	—	18	39	34	53	—	54	59	73	80	92
HcAL	—	205	162	—	—	—	—	—	—	—	—	—	—
Lig. L.	—	27.6	21.8	—	—	—	—	—	—	—	—	—	—
Cal. L.	—	3.5	2.6	—	—	—	—	—	—	—	—	—	—
Web A	38	55	40	5	10	9	10	10	11	10	15	19	16
Web BR	39	60	42	6	10	10	11	10	15	13	18	22	18
BL	50	61	50	6	12	10	11	10	16	14	18	22	19
Web CR	38	60	44	6	10	12	12	11	17	19	19	25	20
CL	65	60	50	6	12	11	14	12	18	17	20	26	21
Web DR	40	54	46	6	12	10	12	12	17	17	16	24	23
DL	55	55	52	6	11	11	14	13	16	17	20	22	24
Web E	38	43	40	5	11	9	11	9	14	14	16	18	18
Web Form.	CDBAE	BCDAE	DCBAE	DCBAE	DCBEA	CDBAE	DCBEA	DCBAE	CDBEA	CDBEA	CDBEA	CDBAE	DCBEA
S normal	6.7	7.1	5.4	0.7	1.3	1.6	1.4	1.7	2.4	2.3	2.5	2.8	2.3
Sp. L.	—	—	41	—	—	—	—	—	—	—	—	—	—
Sp. R.L.	—	—	16	—	—	—	—	—	—	—	—	—	—
Sp. R.W.	—	—	1.4	—	—	—	—	—	—	—	—	—	—
Penis L.	16	19	19	—	—	—	—	—	—	—	—	—	—
Gill No.	8	7	7	8	7	7	7	7	7	7	8	8	7

Sex	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
M.L.	37	37	41	44	47	49	49	62	88	—
Tot. L.	152	208	180	162	168	215	250	149	248	—
MW	31	33	24	31	27	37	44	40	32	—
H.L.	11	13	15	14	11	11	14	18	19	—
H.W.	20	21	18	21	18	20	25	23	24	—
ARI	86	136	115	109	100	147	177	120	132	—
ALI	94	140	—	109	—	148	175	122	109	—
ARII	108	159	130	126	119	162	191	141	156	—
ALII	108	156	129	119	113	159	—	133	156	—
ARIII	112	146	131	125	115	162	201	140	166	—
ALIII	106	147	134	117	124	161	198	136	163	—
ARIV	106	132	135	—	113	158	186	126	154	—
ALIV	107	158	—	118	125	157	179	134	162	—
HcAL	—	—	—	—	—	—	—	—	—	—
Lig. L.	—	—	—	—	—	—	—	—	—	—
Cal. L.	—	—	—	—	—	—	—	—	—	—
Web A	20	23	21	26	21	25	35	26	26	—
Web BR	26	31	19	26	28	31	41	29	38	—
BL	27	31	25	30	28	28	35	29	35	—
Web CR	29	35	29	29	30	35	45	28	48	—
CL	27	34	29	29	28	35	47	36	50	—
Web DR	26	33	26	32	27	34	40	29	46	—
DL	25	35	30	25	35	39	46	34	42	—
Web E	23	25	21	23	21	30	31	27	30	—
Web Form.	CBDEA	CDBEA	DCBAE	DCBAE	DCBAE	DCBEA	CDBAE	CDBEA	CDBEA	—
S. normal	2.9	3.4	3.1	3.2	3.1	3.7	4.6	3.8	4.6	—
Sp. L.	—	—	—	—	—	—	—	—	—	—
Sp. R.L.	—	—	—	—	—	—	—	—	—	—
Sp. R.W.	—	—	—	—	—	—	—	—	—	—
Penis L.	—	—	—	—	—	—	—	—	—	—
Gill No.	8	7	7	7	7	7	7	8	7	—

TABLE 2
Means, Standard Deviations and Ranges of Indices of *Octopus australis* Hoyle

	Males				Females			
	n	mean	S.D.(n-1)	range	n	mean	S.D.(n-1)	range
MWI	15	73.3	11.8	51-90	19	75.8	15.2	36-100
HLI	15	35.3	6.6	23-48	19	33.5	7.2	22-50
HWI	15	48.8	9.5	34-62	19	53.0	12.4	27-77
ALI	15	78.5	6.9	68-93	19	75.4	7.7	65-95
WDI	15	24.2	4.8	16-32	19	26.8	3.2	22-32
SI (normal)	15	8.9	0.1	7-10	19	8.1	1.3	5-11
HcAI	6	68.2	6.6	58-75				
LLI	11	14.7	1.9	12-18				
CLI	11	18.5	3.9	12-25				
PLI	10	28.5	4.6	23-37				
SpL (mm)	6	40.7	6.4	31-49				
SpLI	6	73.1	12.8	56-91				
SpRI	6	39.3	6.4	29-46				
SpWI	6	3.1	0.6	2.0-3.9				

Explanation of Plate

PLATE 1

Octopus australis Hoyle, 1885. Holotype, female, 22 mm

M.L. a. Dorsal view. b. Lateral view.

a



b



CEPHALOPOD REMAINS FROM THE STOMACHS OF SPERM WHALES CAUGHT IN THE TASMAN SEA

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Summary

1. Cephalopod remains from the stomachs of 66 sperm whales caught in the Tasman Sea included almost intact cephalopods, detached heads and bodies, 'crowns' of arms, isolated buccal masses and isolated upper and lower beaks (mandibles). 3282 of the 3299 lower beaks were identified to genus and, as far as possible, to species with over 30 species from 14 families.
2. The four species *Octopoteuthis rugosa*, *Octopoteuthis* sp. A, *Taningia danae* and *Histioteuthis atlantica* together comprised over 40% of the lower beaks. Estimates of the weight of flesh represented by beaks of the different taxonomic groups were made from beak size. Three large species *Taningia danae*, *Kondakovia longimana* and an *Architeuthis* species contributed about 80% of the weight of flesh represented by lower beaks. The collection shows that cephalopods contribute an important proportion of the 'standing stock' of nekton in the deep ocean even distant from continental slope areas. Flesh remains in the sperm whale diet suggest that there is a boundary to several squid distributions near 40°S.
3. In 17 species of squids, the size distributions of the beaks collected in the Tasman Sea are closely similar to those of the same species collected off South Africa and Western Australia. In two species, there is a gradual change in size distribution of the beaks across the range from West to East. In the genera *Kondakovia* and *Architeuthis*, the Tasman Sea beaks have different size distributions to those collected further west.

Introduction

This paper describes the cephalopod remains collected from 66 sperm whales caught during commercial whaling activities of a Japanese factory ship in the Tasman Sea while on passage to the Antarctic. The collection is of particular interest since it is from a region in which the cephalopods are very poorly known and because the samples cover a broad latitudinal spread from 31°20'S to 46°56'S and a broad longitudinal spread from 174°28'E to 148°04'E (Fig. 1). The samples comprise both complete cephalopods and parts of cephalopods including a total of 3299 lower and 3335 upper beaks (mandibles). The present study is a useful addition to similar studies made on cephalopods from sperm whales caught off New Zealand (Gaskin & Cawthorn 1967a, b) in the eastern South Pacific (Clarke, MacLeod & Paliza 1976), the North Pacific (Beteshava & Akimushkin 1955; Okutani & Nemoto 1964; Okutani *et al.*, 1976; Kawakami 1976; Clarke & MacLeod, 1980), off Western Australia, the Antarctic and South Africa (Clarke 1980) and in the North Atlantic (Clarke 1962a; Clarke & MacLeod 1974, 1976).

While cephalopods of the Tasman Sea have been very neglected the works of Dell (1952) for

New Zealand and Rancurel (1970, 1976a, b) for New Caledonia give useful systematic descriptions from the general area. Cephalopods have been described from stomachs of birds at New Zealand (Imber 1975, 1976, 1978; Imber & Russ 1975) and fish at New Caledonia (Rancurel 1970, 1976a, b).

Material and Methods

Samples of the stomach contents of 66 sperm whales including 20 females, 43 males and three with no data were collected during commercial whaling of a Japanese whale factory ship in November 1970 by arrangement with Dr S. Ohsumi of the Far Seas Fisheries Research Laboratory, Japan Fisheries Agency, Shimizu, Japan. The positions given in Fig. 1 are those of the factory ship, and probably all the whales, from which samples were taken, were killed within 100 miles of the factory. The isobaths on Fig. 1 should only be considered a rough guide since there are considerable inconsistencies between various recent bathymetric charts of the region.

The samples included relatively intact cephalopods, detached heads and bodies, 'crowns' of arms, isolated buccal masses including beaks and isolated upper and lower

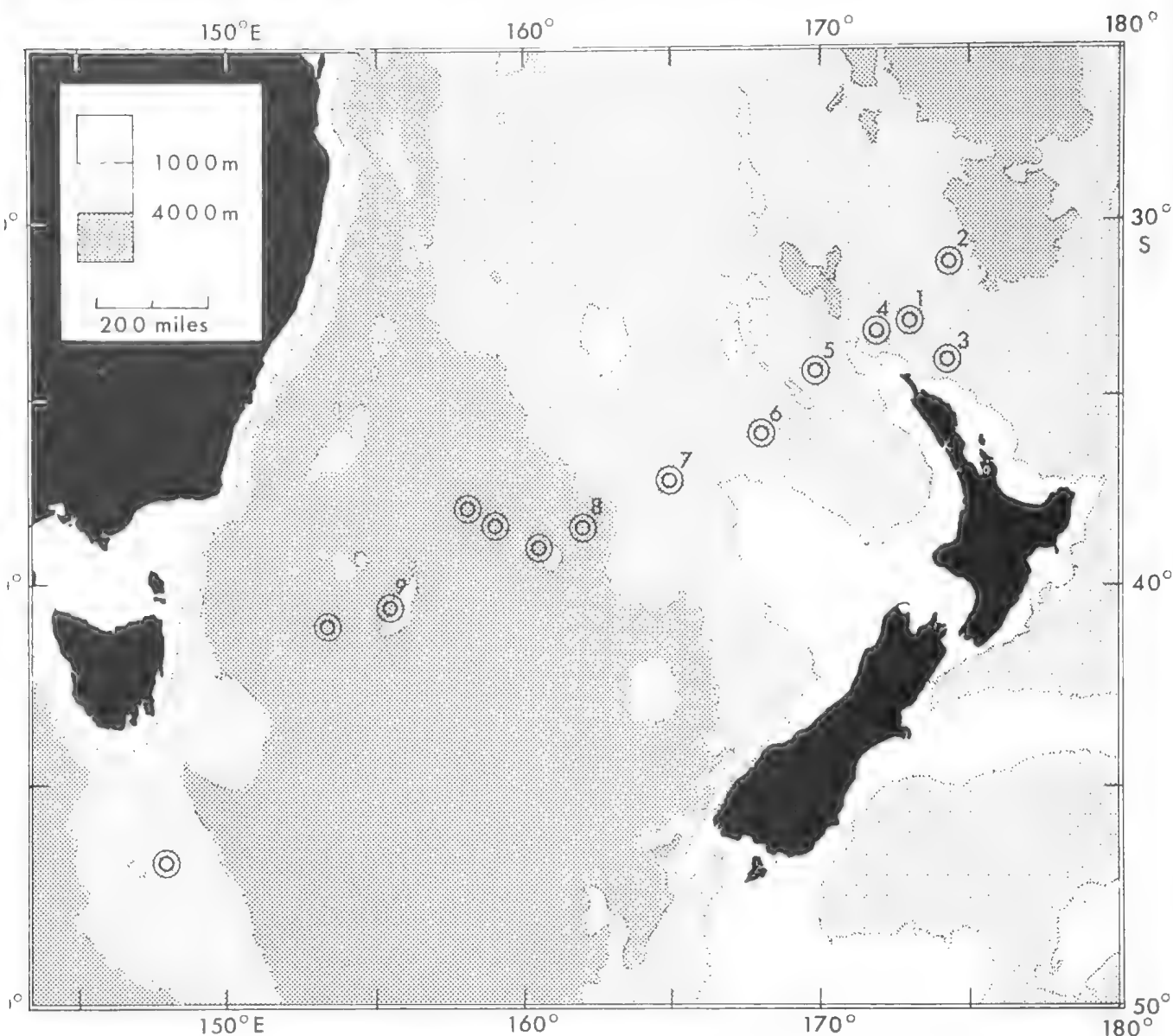


Fig. 1. Position of the factory ship when the sperm whales from which stomach contents were collected were killed. The positions of the catchers when they killed the whales was probably within 100 miles of these factory positions. Isobaths E of 150°E are taken from New Zealand Journal of Geology and Geophysics 13 (1) 1970 and those W of 150°E from International Chart 601 N.Z. 4601, 1971. Beak collections were made at positions 1-9. Flesh of cephalopods was collected at all positions except 4.

beaks. As much information as possible was obtained from the relatively intact specimens and pieces of flesh and the beaks were then sorted. Upper beaks were counted and lower

beaks were sorted into groups and the lower rostral lengths (LRL) or, in the octopod *Alloposus*, the hood lengths were measured with vernier calipers to an accuracy of 0.005 cm. Identification of lower beaks was carried out using criteria and methods described elsewhere (Clarke 1962b, 1980). Weights of the cephalopods from which the lower beaks came were estimated from the LRLs and hood lengths using graphs published elsewhere (Clarke 1962b, 1980). The size at which the 'wings' of the lower beaks became darkened is noted since this indicates a stage between im-

maturity and 'maturity' which is useful in comparisons between beaks from different geographical regions. If beaks have flesh attached it is certain that the squid was living in the vicinity in which the whale was captured and noting the occurrence of flesh is important in the study of cephalopod distribution. The presence of beaks of Antarctic species is relevant to an understanding of whale migration (Clarke 1972). Female whales normally go no further south than 40°S and the difference between the squid species represented by beaks in female and male stomachs is relevant to an understanding of cephalopod distribution (Clarke 1980). Comparisons are drawn between the present beaks and similar collections made from sperm whales caught off the western side of South America (Clarke, et al., 1976), South Africa, Western Australia and the Antarctic (Clarke, 1980). Samples off South Africa and Western Australia did not include samples in November, when the present collection was made.

Results

Cephalopods present in the region

The samples include 3299 lower and 3335 upper beaks. The number of lower beaks of each taxon collected from whales at each station is shown in Table 1. Almost half the taxa were found at more than 75% of stations.

Five taxa, *Histioteuthis atlantica* (Hoyle, 1885) (B3), *H. miranda* (Berry, 1908) (A3), *Taningia danae* (Joubin, 1931), *Pholidoteuthis boschmai* Adam 1950 (A) and *Galiteuthis armata* Joubin, 1898, were present at all nine stations. Seven taxa, *Octopoteuthis* spp., *Megalocranchia* sp., *Ancistrocheirus lesueuri* (d'Orbigny, 1839), *Pholidoteuthis boschmai* Adam, 1950 (B), *Lepidoteuthis grimaldii* Joubin, 1895, *Octopoteuthis* B and *Cyclotheuthis akimushkini* Filippova, 1968, were present at eight out of nine stations.

The percentage contribution and the estimated contribution by weight of each taxon represented by beaks are shown in Table 2.

Over 30 species from 14 families are represented by lower beaks and over 40% of the lower beaks were from the four species *Octopoteuthis rugosa* Clarke, 1980, *Octopoteuthis*

sp. A, *Taningia danae* and *Histioteuthis atlantica* (B3).

All taxa except *Moroteuthis* A and *Vampyroteuthis infernalis* Chun, 1903 were present in both male and female whales; these were only present in female whales.

Notes on the Material

Family OCTOPOTEUTHIDAE

Four species belonging to this family are represented by lower beaks. *Octopoteuthis rugosa* and *Taningia danae* are also represented by reasonably intact specimens, crowns, etc. The separation of the two smallest of the three *Octopoteuthis* species is not always possible from beak structure but they have distinct LRL peaks and little error will be introduced if these species are separated at an arbitrary LRL of 1.15 cm (Fig. 2).

Octopoteuthis sicula Rüppell, 1844 was reported by Rancurel (1970) in stomachs of *Alepisaurus ferox* caught off New Caledonia. Otherwise the genus is not known from the region.

Flesh of *Octopoteuthis* was found between 31°S 174°E and 47°S 148°E (Figs. 1 & 3).

Three hundred and eighty-six of the lower beaks grouped as *Octopoteuthis* A are indistinguishable from *O. rugosa* except for the latter's smaller size. Similar beaks with the same size range and with peaks at the same LRL were present in samples collected at Albany, Western Australia but were not found in South Africa (Clarke, 1980) or off Peru and Chile (Clarke et al., 1976).

Forty-nine of the beaks belong to a third, much larger, species of this genus, *Octopoteuthis* B. Beaks with LRLs of 1.05, 1.15 and 1.5 cm have undarkened wings and are from young members of this species. One buccal mass of the species was found at 37°S 165°E.

The LRL range and peak of these beaks is similar to beaks described as *Octopoteuthis* sp. B from whales caught off Iceland (Clarke & MacLeod 1976). A specimen believed to be this very large *Octopoteuthis* has been caught by a trawl off the United Kingdom and will be described elsewhere.

TABLE 1
The lower beaks collected from whales caught near the positions in the Tasman Sea shown in Fig. 1

Family	Species	Station (No of samples in parentheses)									No Data	Total
		1 (1)	2 (1)	3 (1)	4 (4)	5 (4)	6 (7)	7 (6)	8 (5)	9 (1)		
Octopoteuthidae	<i>Octopoteuthis rugosa</i> }	125	102	242	0	92	11	41	98	2	2	715
	<i>Octopoteuthis</i> sp. A. }	1	1	3	0	9	15	10	7	2	1	49
	<i>Octopoteuthis</i> sp. (giant) B	40	29	35	5	59	65	34	51	8	22	348
	<i>Taningia danae</i>	2	0	22	0	1	0	3	0	0	0	28
Histioteuthidae	<i>Histioteuthis</i> A1 ? <i>meleagroteuthis</i>	0	0	19	0	1	86	20	2	4	11	143
	A2 <i>bonnellii corpuscula</i>	2	2	55	1	21	14	4	13	6	3	121
	A3 <i>miranda</i>	0	0	136	2	74	22	36	25	0	3	298
	A4 <i>dofleini</i>	0	2	11	0	1	2	0	0	1	0	17
	A spp.	16	16	86	6	89	53	27	61	15	1	370
	B3 <i>atlantica</i>	0	0	2	0	6	1	1	0	2	0	12
	B4	0	0	6	0	1	0	1	7	1	0	16
	B spp.	0	2	23	2	13	76	25	68	13	24	246
Cranchiidae	<i>Megalocranchia</i> sp.	2	6	5	2	6	26	5	12	4	0	68
	<i>Galiteuthis armata</i>	0	0	0	3	2	2	5	9	0	0	21
	<i>Taonius pavo</i>	0	5	3	0	1	0	1	5	0	0	15
	<i>Galiteuthis</i> sp. B	2	0	1	0	0	1	1	5	1	0	11
	<i>Mesonychoteuthis hamiltoni</i>	0	4	8	0	12	23	13	68	1	6	135
Onychoteuthidae	<i>Moroteuthis robsoni</i>	0	0	0	0	0	0	0	10	0	0	10
	<i>Moroteuthis</i> A	0	0	0	2	12	57	13	11	2	5	102
	<i>Kondakovia longimana</i>	2	1	6	1	7	18	13	35	7	0	90
Pholidoteuthidae	<i>Pholidoteuthis boschmai</i> A	0	2	15	3	19	14	5	17	6	1	82
	B	2	0	11	5	13	41	13	26	2	3	116
Enoploteuthidae	<i>Ancistrocheirus lesueuri</i>	11	7	3	0	3	9	8	11	1	4	57
Lepidoteuthidae	<i>Lepidoteuthis grimaldii</i>	0	0	2	0	2	13	18	8	3	8	54
Architeuthidae	<i>Architeuthis</i> spp.	0	0	12	0	1	0	3	0	0	0	16
Chiroteuthidae	<i>Chiroteuthis</i> ? <i>joubini</i>	1	2	10	0	2	6	4	4	0	1	30
	sp. C	4	3	16	1	5	3	0	6	0	0	38
Ommastrephidae	<i>Todarodes</i> sp.	0	1	5	2	7	3	4	3	2	2	29
Cycloteuthidae	<i>Cycloteuthis akimushkini</i>	0	1	16	0	3	0	1	1	0	0	22
	? <i>Discoteuthis</i>	0	0	1	1	1	6	2	4	0	1	16
Mastigoteuthidae	<i>Mastigoteuthis</i> A	0	0	1	0	0	3	2	0	0	0	6
Alloposidae	<i>Alloposus mollis</i>	0	0	1	0	0	0	0	0	0	0	1
Vampyroteuthidae	<i>Vampyroteuthis infernalis</i>	0	1	3	1	8	0	3	0	0	1	17
Others		210	187	759	37	471	570	316	567	83	99	3299
Totals												

Flesh of *Taningia danae* is present at nine stations between 33°S and 47°S (Figs. 1 & 3) but it would appear to be more common to the south and west of the area since 58% of male whales with flesh contained the species to the south of 38°S and west of 162°E and only 9% of males contained it to the north and east of this position. 43% of 37 male whales and 8% of 13 female whales containing flesh included flesh of this species.

It seems likely that the genus *Taningia* is composed to two species, one not yet described,

but until more specimens become available we shall keep both size groups under the one species heading.

Family HISTIOTEUTHIDAE

Beaks in this collection, within this family, fall into eight main groups named for convenience *Histioteuthis* A1-A4 and B1-B4 (Fig. 4) according to size and structure. Beaks of six of these groups have already been described and several positively identified (Clarke 1980). There are 33 beaks which are very probably of

TABLE 2

The importance by number and weight of cephalopods represented by lower beaks from stomachs of sperm whales sampled in the Tasman Sea expressed as a percentage of samples containing flesh

Species	No.	%	Estimated weights			Family		% of whales in which found	% of samples with flesh
			Mean (g)	Total (kg)	Total (%)	No. %	Wt. %		
<i>Octopoteuthis rugosa</i>	329	10.0	337	110	0.9	33.7	45.3	65	18
<i>Octopoteuthis</i> sp. A	386	11.7	526	203	1.7				
<i>Octopoteuthis</i> sp. (giant) B	49	1.5	1 781	87	0.7				
<i>Taningia danae</i>	348	10.5	14 378	5 004	42.0			97	33
<i>Histioteuthis</i> A1	28	0.8	92	3	—	30.4	1.8	16	—
A2	143	4.3	152	22	0.2			48	48
A3	121	3.7	598	72	0.6			58	—
A4	298	9.0	310	61	0.5			61	—
A spp.	17	0.5	155	3	—			—	—
B3	370	11.2	148	55	0.5			90	12
B4	12	0.4	258	3	—			23	—
B spp.	16	0.5	126	2	—			—	—
<i>Megalocranchia</i>	246	7.5	320	79	0.7			11.0	3.6
<i>Galiteuthis armata</i>	68	2.1	251	17	0.1	68	14		
<i>Taonius pavo</i>	21	0.6	405	9	0.1	39	2		
<i>Galiteuthis</i> sp. B	15	0.5	113	2	—	19	—		
<i>Mesonychoteuthis hamiltoni</i>	11	0.3	28 909	318	2.7			29	—
<i>Moroteuthis robsoni</i>	135	4.1	2 007	271	2.3	7.5	22.7	77	—
<i>Moroteuthis</i> A	10	0.3	3 539	35	0.3			6	—
<i>Kondakovia longimana</i>	102	3.1	23 433	2 390	20.1			61	—
<i>Pholidoteuthis boschmai</i> A	90	2.7	1 653	149	1.3	5.2	3.5	58	15
B	82	2.5	3 179	261	2.2			65	—
<i>Ancistrocheirus lesueuri</i>	116	3.5	1 468	170	1.4	3.5	1.4	84	40
<i>Lepidoteuthis grimaldii</i>	57	1.7	2 500	143	1.2	1.7	1.2	58	10
<i>Architeuthis</i> spp.	54	1.6	41 164	2 223	18.7	1.6	18.7	65	12
<i>Chiroteuthis ?joubini</i>	16	0.5	68	1	—	1.4	—	10	—
sp. C	30	0.9	142	4	—	—	—	35	—
<i>Todarodes</i> sp.	38	1.2	2 913	111	0.9	1.2	0.9	39	—
<i>Cycloteuthis akimushkini</i>	29	0.9	1 126	33	0.3	1.6	0.4	45	4
<i>?Discoteuthis</i> sp.	22	0.7	692	15	0.1			16	—
<i>Mastigoteuthis</i> sp.	16	0.5	1 906	30	0.3	0.5	0.3	39	—
<i>Alloposus mollis</i>	6	0.2	612	4	—	0.2	—	10	—
<i>Vampyroteuthis infernalis</i>	1	—	—	—	—	—	—	3	—
	17	0.5	1 001	17	0.1	0.5	0.1	26	—
	3 299	100.0	3 609	11 907	99.9	100.0	99.9		

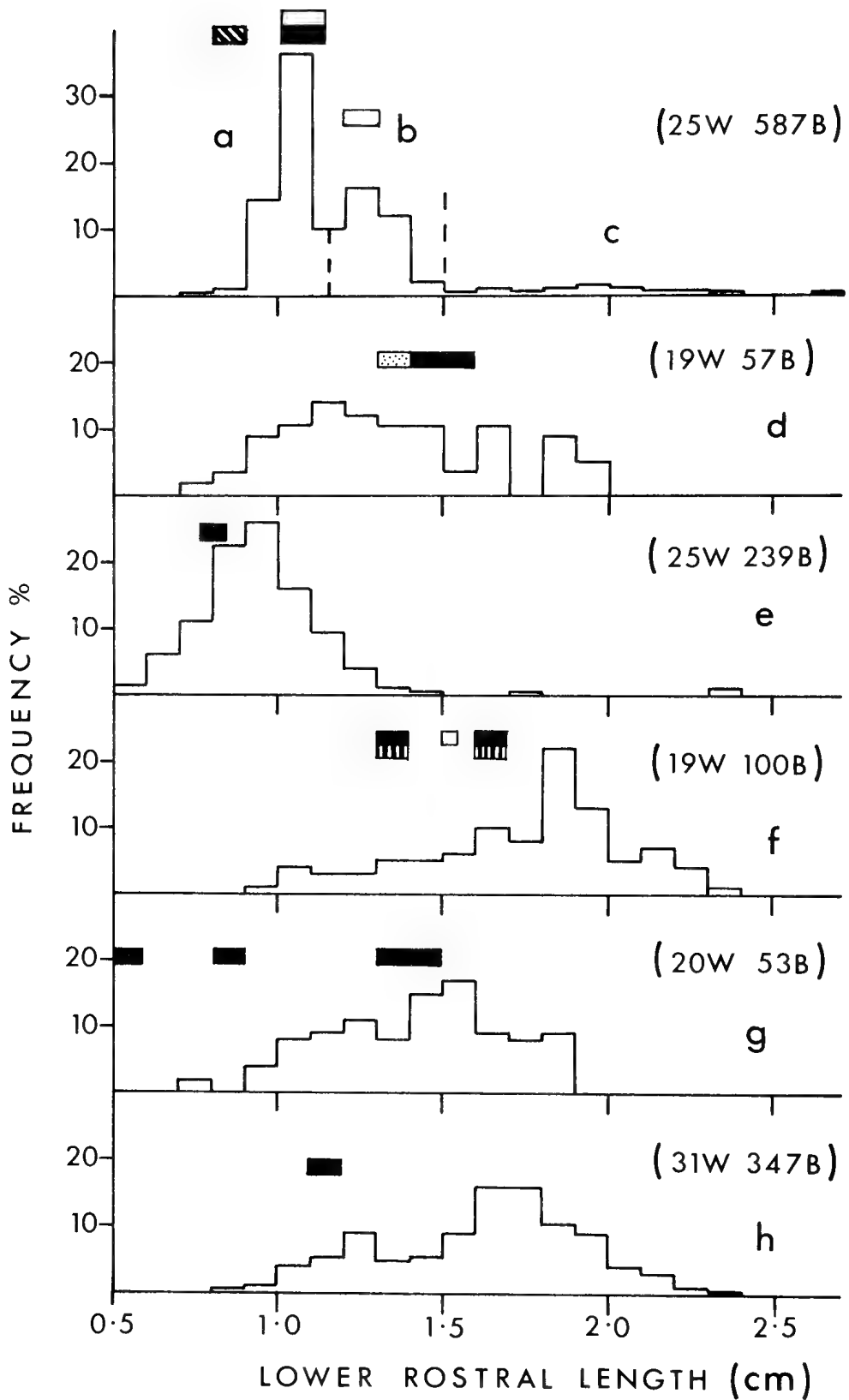
several, as yet undescribed species, which are dealt with under two headings, *Histioteuthis* A & B spp.

The size group of beaks identified as *Histioteuthis* A1? *meleagroteuthis* (Chun, 1910) was rarely found at Durban or in Western Australia and it is possible that this represents a different species from that found off Donkergat.

Beaks of *Histioteuthis bonnellii corpuscula* Clarke 1980, A2 were present from 34°S 170°E to 40°S 155°E. One crown and a complete

specimen were collected at 36°S 168°E and 38°S 158°E respectively.

Beaks of *Histioteuthis miranda* (Berry 1908) (A3) occur in samples extending across the entire geographical range sampled (Table 1). One male and three female whales had flesh of the species in their stomachs which included three crowns and one complete specimen. Beak sizes are closer to the South African than to the Western Australian beaks of this group. While this may suggest more than one species is included here, the almost intact squids show that



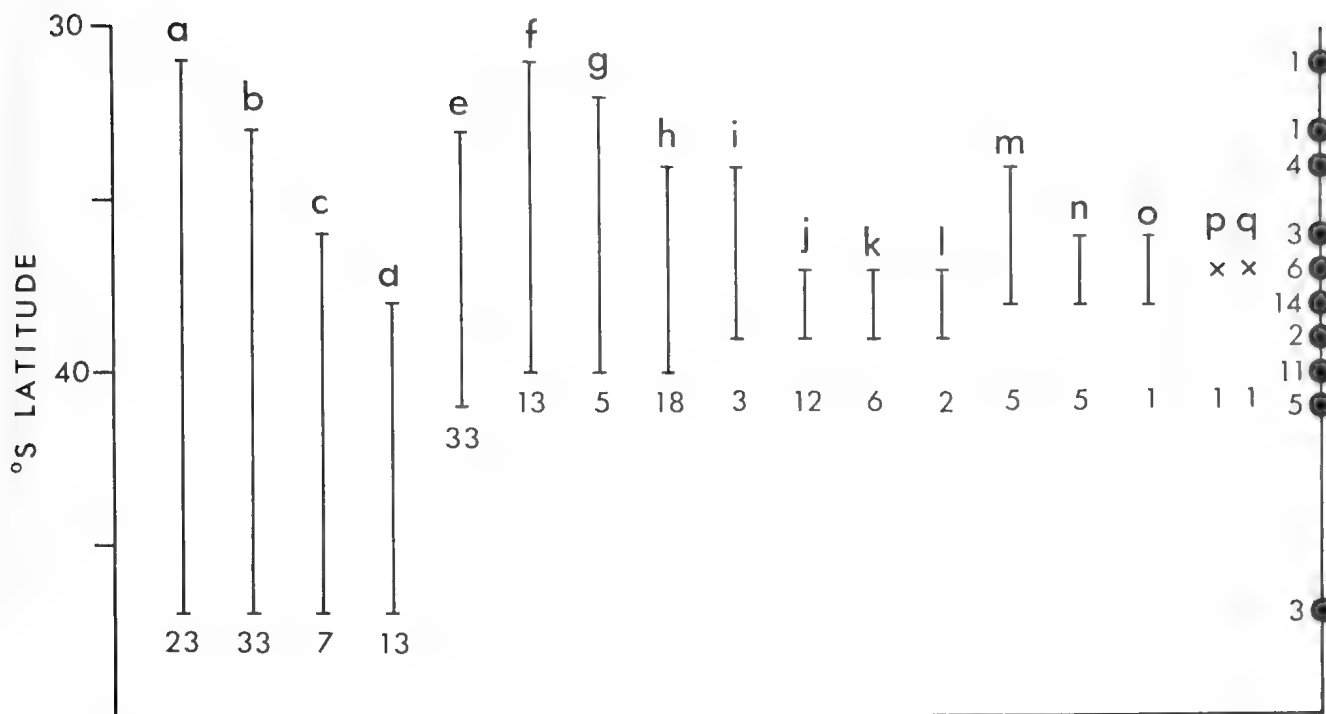


Fig. 3. The latitudinal distribution of cephalopod groups as shown by flesh collected from the stomachs of sperm whales caught in the Tasman Sea. To the right the latitudinal positions of the factory ship and the number of samples at each position are given. The cephalopod groups are arranged in order of their most southern occurrence. Numbers along the bottom show the number of cephalopods

in each group represented by flesh. a, *Octopoteuthis*; b, *Taningia*; c, *Moroteuthis*; d, *Pholidoteuthis*; e, *Ancistrocheirus*; f, *Galiteuthis* sp. A; g, *Lepidoteuthis*; h, *Megalocranchia* sp.; i, *Histioteuthis* A3; j, *Histioteuthis* B3; k, *Architeuthis*; l, *Cycloteuthis*; m, *Histioteuthis* B4; n, *Chiroteuthis*; o, *Histioteuthis* A2; p, *Taonius pavo*; q, *Octopoteuthis* B.

H. miranda is found from South Africa to the Tasman Sea and the evidence, so far, supports the conclusion that the size variation of beaks is merely a reflection of the size variations of a single species.

Beaks of *Histioteuthis* ? *dofleini* (Pfeffer 1912) (A4) are present in samples taken from 34°S 174°E to 38°S 162°E. Some beaks with LRLs up to 0.73 cm have undarkened wings.

Seventeen of the *Histioteuthis* A beaks appear to differ from all the above groups and are probably from several unrecognized species.

Flesh of *Histioteuthis atlantica* (B3) was found in whales from 37°S 165°E to 38°S 158°E and in one female and several male whales. Beaks of the species from whales caught off New Zealand were slightly larger with a peak at 0.5-0.6 cm (Gaskin & Cawthorn 1967). A beak measuring 0.41 cm has undarkened wings.

Beaks identified as *Histioteuthis* species B4 (Clarke 1980) contributed over 7% of the beaks in whales caught off Western Australia.

Sixteen beaks are of the *Histioteuthis* B type but cannot be referred to a species.

Family CRANCHIIDAE

The beaks of this family fall into five groups, three of which have been described elsewhere (Clarke 1980). While these groups have been given species names certain reservations about the specific identity are held which are stated here or elsewhere. (Voss 1974; Clarke 1980).

Fig. 2 Percentage frequency histograms of the rostral lengths of lower beaks. a, *Octopoteuthis rugosa*; b, *Octopoteuthis* sp. A; c, *Octopoteuthis* sp. B; d, *Lepidoteuthis grimaldii*; e, *Megalocranchia*, sp.; f, *Kondakovia longimana*; g, *Architeuthis* sp.; h, *Taningia danae*. The number of whales (W) and beaks (B) are indicated. Horizontal bars indicate peaks of beaks of the same species from whales caught off South Africa (black), Western Australia (white), South America (hatched), New Zealand (shaded) and in the Antarctic (vertical hatching).

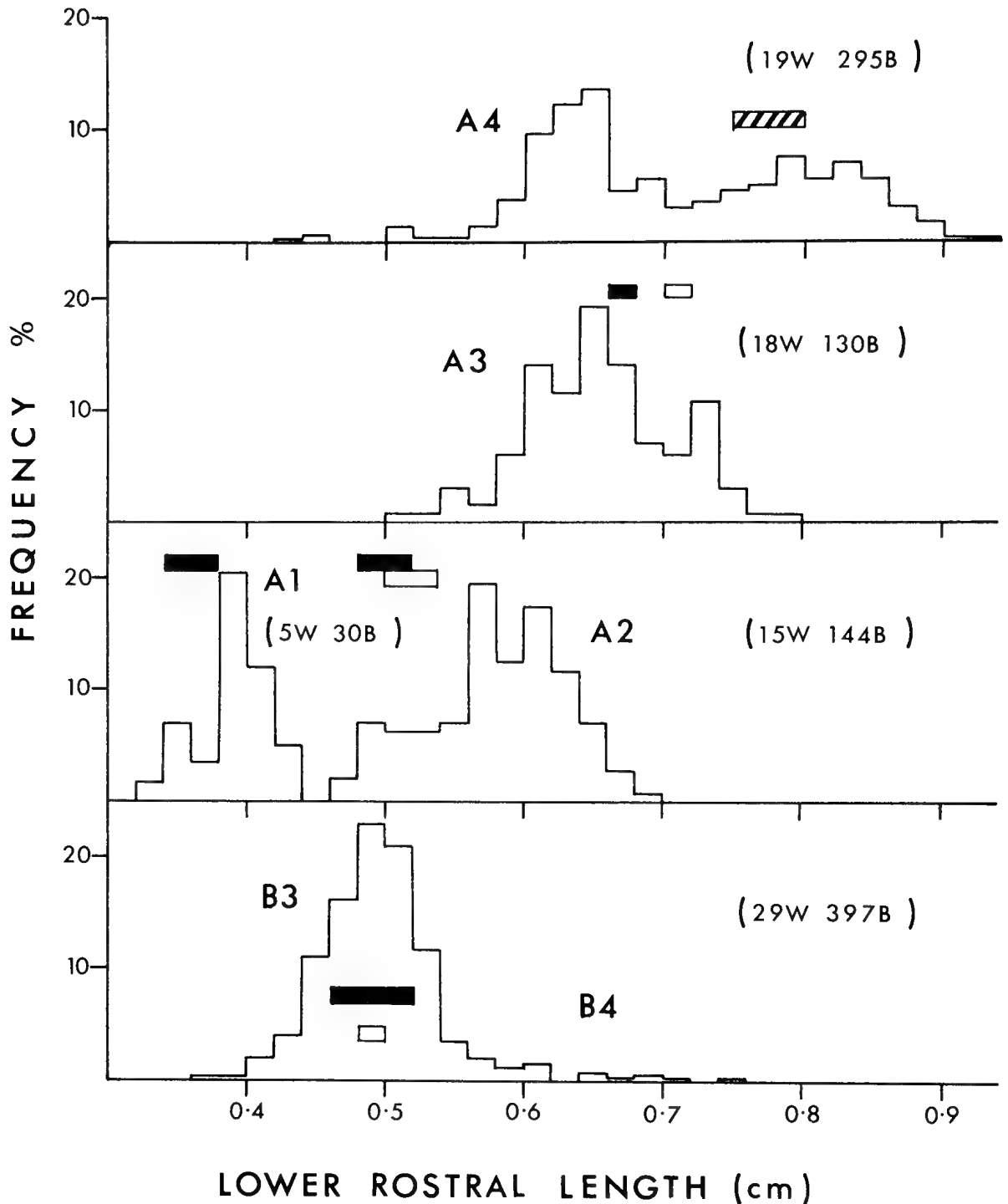


Fig. 4. Percentage frequency histograms of the rostral lengths of lower beaks of *Histioteuthis* A1-A4, B3 and B4. The number of whales (W) and beaks (B) are indicated. Horizontal bars indicate peaks of

beaks of the same species from whales caught off South Africa (black), Western Australia (white) and in the Antarctic (hatched).

Two hundred and forty-six of the lower beaks cannot be distinguished from beaks of *Megalocranchia* sp. (described as *Phasmatopsis cymoctypus* by Clarke 1962c, 1980; Voss (1980) synonymised this genus with *Megalocranchia*) (Voss, 1974), and are found in whales throughout the sampling area (Table 1). Flesh of the species is present in both male and female whales extending from 34°S 170°E to 40°S 155°E (Fig. 3). Three beaks (LRLs 1.7, 2.30, 2.38 cm) apparently of this species, extend the size range to 2.38 cm (Fig. 2).

The flesh of this species consists of twelve crowns, six of which have undarkened or only partly darkened wings on lower beaks with a range of 0.56-0.71 cm. Features of the species which could be distinguished from four of these crowns are as follows. Arm length formula in three crowns is I < IV < II < III. In one of these the arm lengths are 18.5 (I), 23 (II), 26 (III) and 21.5 cm (IV) and the tentacle length is 37.5 cm with a club length of 7.5 cm. Suckers on the middle of arm III are much bigger, with a diameter of 0.76 cm, than on other arms, at 0.47 cm (specimen with a LRL = 0.85 cm). The arms have elongated cirri down their borders and attenuated, whip-like ends. The tentacle manus bears four rows of suckers with elongated, trumpet-shaped outer segments. The carpus is distinct with 10-12 suckers and about the same number of pads.

Beaks of *Galiteuthis armata* are closely similar to beaks described elsewhere from *Teuthowenia megalops* (Prosch, 1849) (called *Taonius megalops* by Clarke 1980). They are present over the entire geographical range sampled and from both male and female whales. Flesh is in samples from 31°S 174°E to 40°S 155°E (Figs. 1 & 3) and is present in both male and female whales.

Five crowns of this species were collected but only one of them, with a LRL of 0.79 cm was in sufficiently good condition to provide useful information. This crown, collected at 31°S 174°E has arms which bear suckers and no hooks and measure 11.0 (I), 13.0 (II), 15.5 (III) and 14.5 cm (IV). The tentacle is 22 cm long with a club of 3 cm and has a distinct, large, single tentacular hook. These features prevent this species from being a *Taonius* as previously

thought from beaks collected off South Africa and Western Australia and it should be grouped in *Galiteuthis*.

Beaks of *Taonius pavo* (Lesueur 1821) which were described by Clarke (1980) are in samples from 34°S 174°E to 38°S 162°E (Fig. 1). Flesh is only present in one whale, a male caught at 37°S 165°E and consists of a crown in very poor condition with incomplete arms and no tentacles.

Beaks identified as *Galiteuthis armata* were found in beak samples extending from 31°S 174°E to 38°S 162°E (Fig. 1) from both male and female whales. No flesh was collected.

No flesh of *Mesonychoteuthis hamiltoni* Robson, 1925 was collected.

Family ONYCHOTEUTHIDAE

Beaks of this family fall into three distinct groups which have been described elsewhere (Clarke 1980), *Moroteuthis robsoni* Adam, 1962, *Moroteuthis* A and *Kondakovia longimana* Filippova, 1972.

Flesh of *Moroteuthis robsoni* occurs from 36°S 168°E to 47°S 148°E (Figs. 1 & 3) and only in male whales. All the beaks have darkened wings; beaks from elsewhere darken at a LRL of 0.5 cm.

Beaks identified as *Moroteuthis* A (Clarke 1980) only occur in two samples, both from female whales caught near 38°S 162°E and one of them contains nine of the ten beaks. No flesh was collected.

Beaks of *Kondakovia longimana* are present in samples collected between 34°S 174°E and 40°S 155°E (Fig. 1) from thirteen male and five female whales. The species was very much rarer than this in female whales off South Africa because it is an Antarctic species which, from evidence collected so far, was not thought to extend far enough north to be eaten by female whales (which do not normally go further south than 40°S). Its presence in so many female whales shows that it must extend either further north or the female whales must go further south than in the Indian Ocean and Atlantic sectors. No flesh was collected. Although we have expressed its weight as a percentage of the diet it must be remembered that this species is, as far as we know, a high latitude species which

contributes considerably more to the diet when the whales are in the Antarctic and nothing in most of the region sampled here i.e. in latitudes lower than 40°S.

Family PHOLIDOTEUTHIDAE ?

The beaks of this family fall into two distinct groups which have been described by Clarke (1980). However, specimens containing these two types of beak could not be distinguished and have all been referred to *Pholidoteuthis boschmai*. Taxonomic difficulties and lack of any tentacles on specimens described by Clarke from whales' stomachs, which are much larger than any collected in other ways, places some doubt on the inclusion of these beaks in *Pholidoteuthis* and the family Pholidoteuthidae. However, the beaks and the squids are very distinctive and it is only the correct name and systematic position which are in any doubt.

Beaks identified as *Pholidoteuthis boschmai* A occur throughout the entire range of sampling (Fig. 1) and in samples from both male and female whales. Flesh was collected from whales killed between 38°S 162°E and 47°S 148°E. It includes five almost complete but damaged specimens (three mantles of the species were also found but could be either A or B). Measurements which could be taken are given in Table 3.

Beaks identified as *Pholidoteuthis boschmai* B are present in whales caught throughout the region sampled (Fig. 1). Flesh is present in samples from 38°S 159°E to 41°S 153°E (Fig. 3). It comprises one complete squid and two crowns. A female with a DML of 33 cm has nidamental glands 9.5 cm long which suggests she was not actively laying eggs.

Family LEPIDOTEUTHIDAE

Flesh of *Lepidoteuthis grimaldii* came from whales killed between 33°S 172°E and 40°S 155°E (Fig. 3) and from both male and female whales. The flesh includes a head and separate body. The LRL is 1.75 cm and the DML is 54 cm.

This species was previously collected from the stomachs of *Alepisaurus ferox* caught at 16°27'S, 166°22'E between the New Hebrides and New Caledonia (Rancurel 1970).

Family ARCHITEUTHIDAE

Taxonomic difficulties make the naming of species within the single genus of this family, *Architeuthis*, very difficult (Dell 1970). Flesh of *Architeuthis* includes a complete female with a LRL of 0.78 cm and a DML of 41.5 cm (Table 3). While the specimen is in too poor a condition to provide much detail, its proportions supplement those few given for specimens collected in South Africa. The arms bear several large subequal suckers which have a diameter of 0.6 cm on arms I, II & III and 0.4 cm on arm IV and the suckers gradually decrease in size to the ends of the arms. No sucker rings are present. There are 30 large suckers on the tentacular club which increase in size to the seventh from the proximal and from 7th to 17th they are approximately the same size. This is an immature female with undarkened wings on the lower beak and nidamental glands 2.2 cm in length. *Architeuthis kirki* Robson, 1887 has been redescribed by Dell (1970) from a specimen stranded in New Zealand, and it seems likely that the beaks described here belong to the same species.

Family CHIROTEUTHIDAE

Beaks tentatively identified as *Chiroteuthis joubini* Voss, 1967 (see Clarke 1980) are present in 10% of beak samples taken from two female and one male whales between 34°S 174°E and 37°S 165°E (Fig. 1, Table 1). No flesh was collected. Beaks of a closely similar species from whales caught off Peru (called '*Chiroteuthis* A' in Clarke *et al.*, 1976) had a very marked peak at 0.50-0.60 cm. Beaks referred to *Chiroteuthis* sp. C (see Clarke 1980) came from throughout the region sampled. Flesh of the species was collected from 36°S 168°E to 38°S 158°E (Fig. 3). The flesh includes one complete specimen and two crowns but few measurements could be obtained because of their poor condition (Table 3).

Family OMMASTREPHIDAE

Beaks of *Todarodes* sp. (see Clarke 1980) were collected from whales caught at all stations south to 38°S (Table 1). No flesh was collected and this is surprising considering the

species is very muscular and flesh was well represented in South African whales.

Beaks of the related genus *Nototodarus* which were collected from sperm whales caught off New Zealand had a peak at 0.80-0.90 cm. (Gaskin & Cawthorn 1967).

Family CYCLOTEUTHIDAE

Beaks belong to two genera in this family. The first, *Cycloteuthis*, is easily distinguished by the lower beaks. The second group is thought to be *Discoteuthis* but lack of comparative material from large animals makes this identification less certain (see Clarke 1980).

Beaks of *Cycloteuthis akimushkini* (see Clarke 1980) were collected from whales throughout the region sampled. Only two male whales contained flesh of the species and these were caught at 37°S 165°E and 39°S 160°E (Fig. 3).

Beaks tentatively identified as ?*Discoteuthis* (see Clarke 1980) occurred in samples from 31°S 174°E to 38°S 162°E (Fig. 1). No flesh was collected.

Family ?MASTIGOTEUTHIDAE

Beaks of ?*Mastigoteuthis* B (See Clarke 1980) are present in samples from 34°S 174°E to 38°S 162°E (Fig. 1). No flesh was collected.

The largest beak with a LRL of 2.08 cm is well outside the range for the group at South Africa and is possibly another species.

Family ALLOPOSIDAE

Beaks of *Alloposus mollis* Verrill, 1880 (see Clarke 1980) were present in two males and a female whale caught from 34°S 174°E to 37°S 165°E. No flesh was collected.

Family VAMPYROTEUTHIDAE

One beak of *Vampyroteuthis infernalis* Chun, 1903 was collected at 34°S 174°E from a 40 ft (12.2 m) female whale.

Other Species

Seventeen or 0.5% of the beaks included several species which could not be identified. LRLs varied from 0.40 to 1.80 cm. Even the family of the largest beak could not be ascer-

tained although it must have come from a large squid weighing perhaps over 9 kg (from curve X Clarke 1962b).

Distribution within the Region

Fig. 1 shows the stations (numbered 1-9) from which beaks and flesh were collected from whale stomachs. Fig. 3 shows the limits of latitude from which flesh of each taxon was collected. As digestion in sperm whales is probably rapid and the whales do not move far between ingestion and digestion, the occurrence of flesh indicates the distribution of the taxa (Clarke 1980).

The percentage of samples which contained flesh of each taxon is given in Table 2.

Although the samples containing flesh of cephalopods have a longitudinal spread of 25°, oceanic variations which influence distribution on a large scale are greatest from north to south and the composition of the cephalopods in these samples is probably most influenced by their latitude. In Figure 3 many species seem to have a southern boundary near 40°S. Flesh of all these species except for *Histioteuthis* B4 was also collected in South Africa at 30-35°S (Durban and/or Donkergat; Clarke 1980). The present collection gives strong support to the conclusion made previously (Clarke 1980) that there is a boundary to many squid distributions near 40°S. Some squids such as *Histioteuthis bonnellii corpuscula*, A2 and *H. atlantica* B3 appear to be restricted to a rather narrow latitudinal distribution (Fig. 3) but, as flesh was collected in South Africa as far north as 30°S, this cannot be a general feature and must be treated with caution in interpreting the Tasman Sea collection.

Four groups extend further south than the 40°S limit of some distributions. Of these *Taningia danae* and *Moroteuthis robsoni* are known to live off South Africa and Western Australia and to extend much further south to South Georgia at about 55°S (Clarke 1980). *Pholidoteuthis boschmai* does not appear to live off South Georgia but, although it extends as far north as Durban at 30°S, it is more numerous at Donkergat and Western Australia at about 35°S and it does seem that this species may have a centre of distribution near the

latitude of 40°S which seems to act as a limit to some species. *Octopoteuthis* flesh considered here is a mixture of *O. rugosa* and *Octopoteuthis* sp. A. The former was present off South Africa and absent off South Georgia and this, together with the present material, suggests the southern limit of distribution is between 47°S and 55°S, possibly at the Antarctic Convergence.

Perhaps the most southerly extension of *Octopoteuthis*, *Taningia*, *Moroteuthis* and *Pholidoteuthis* (Fig. 3) shows that these species can extend much closer to the Subtropical Convergence than the other species which may be less tolerant of short term fluctuations in water conditions which might be expected close to a region of convergence.

Comparison with other regions

Comparison of sizes

The lower rostral length (LRL) distributions for all the taxa are given in Figs. 2, 4-6. In each figure the position of the peaks of similar distributions are indicated where possible for the same taxa collected from whales caught off South Africa, Western Australia, New Zealand, South America and in the Antarctic.

The following 17 groups have peaks which are at very similar LRLs in the areas in which they occur and any difference is not considered significant from the evidence available: *Octopoteuthis rugosa*, *Octopoteuthis* sp. A, *Lepidoteuthis grimaldii*, *Megalocranchia* sp. (all in Fig. 2), *Histioteuthis ?meleagroteuthis* A1, *H. miranda* A3, *H. atlantica* B3 (Fig. 4), *?Discoteuthis* sp., *Taonius pavo*, *Galiteuthis armata* (when compared with *Taonius megalops* see Clarke 1980), *Ancistrocheirus lesueuri*, *Moroteuthis robsoni* (Fig. 5), *Chiroteuthis* sp. C, *Mastigoteuthis* A, *Moroteuthis* A, *Todarodes* sp. and *Pholidoteuthis boschmai* B (Fig. 6).

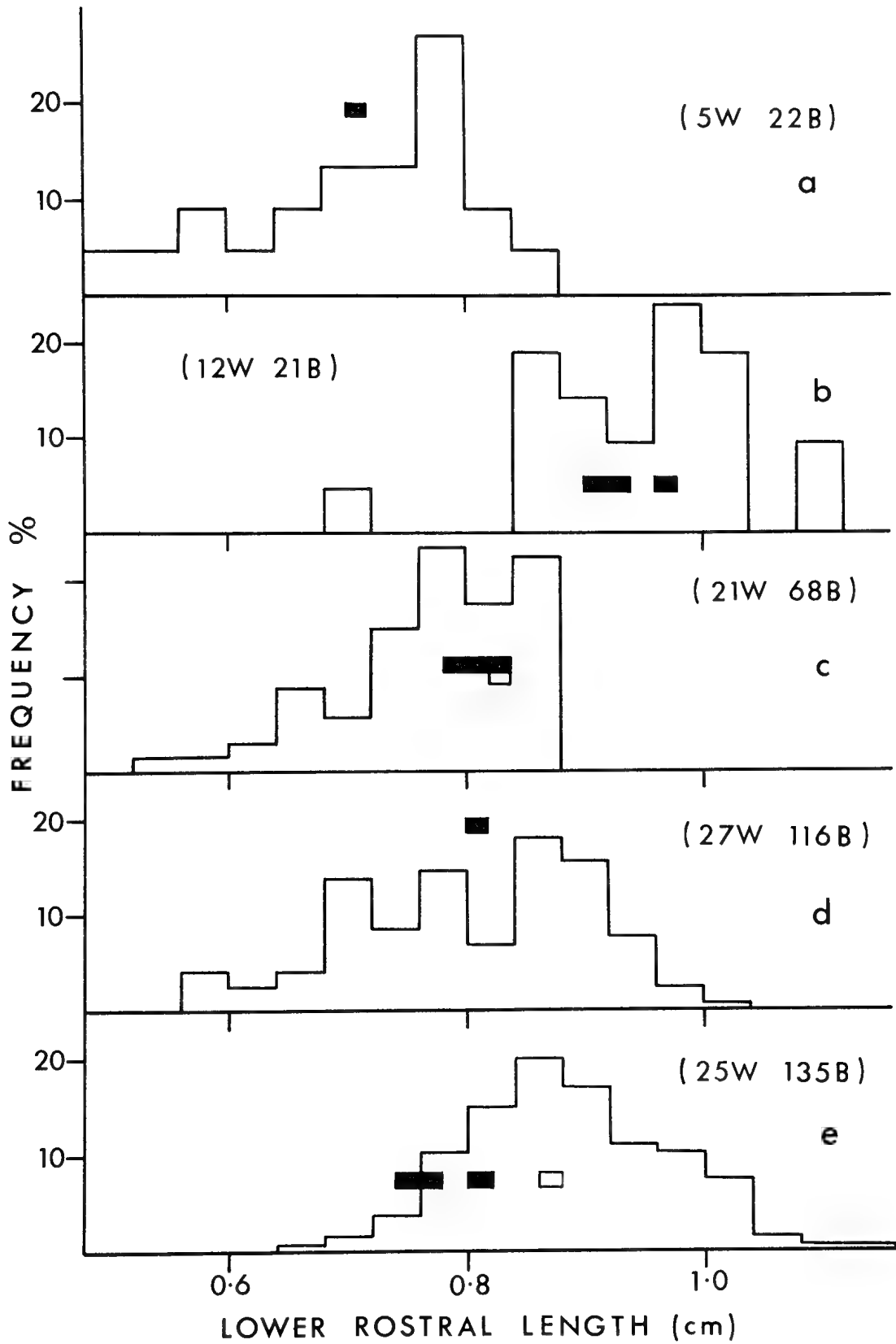
The LRLs of *Kondakovia longimana* have a range of 0.93-2.4 cm and a peak at 1.8-1.9 cm (Fig. 2). The upper limit of the range is higher than elsewhere where the maximum is 2.15 cm and there are 13 beaks larger than 2.15 cm in this collection. In addition, the peaks of the LRLs in whales caught off South Africa and in the Antarctic lie at both 1.3-1.4 and 1.6-1.7 cm

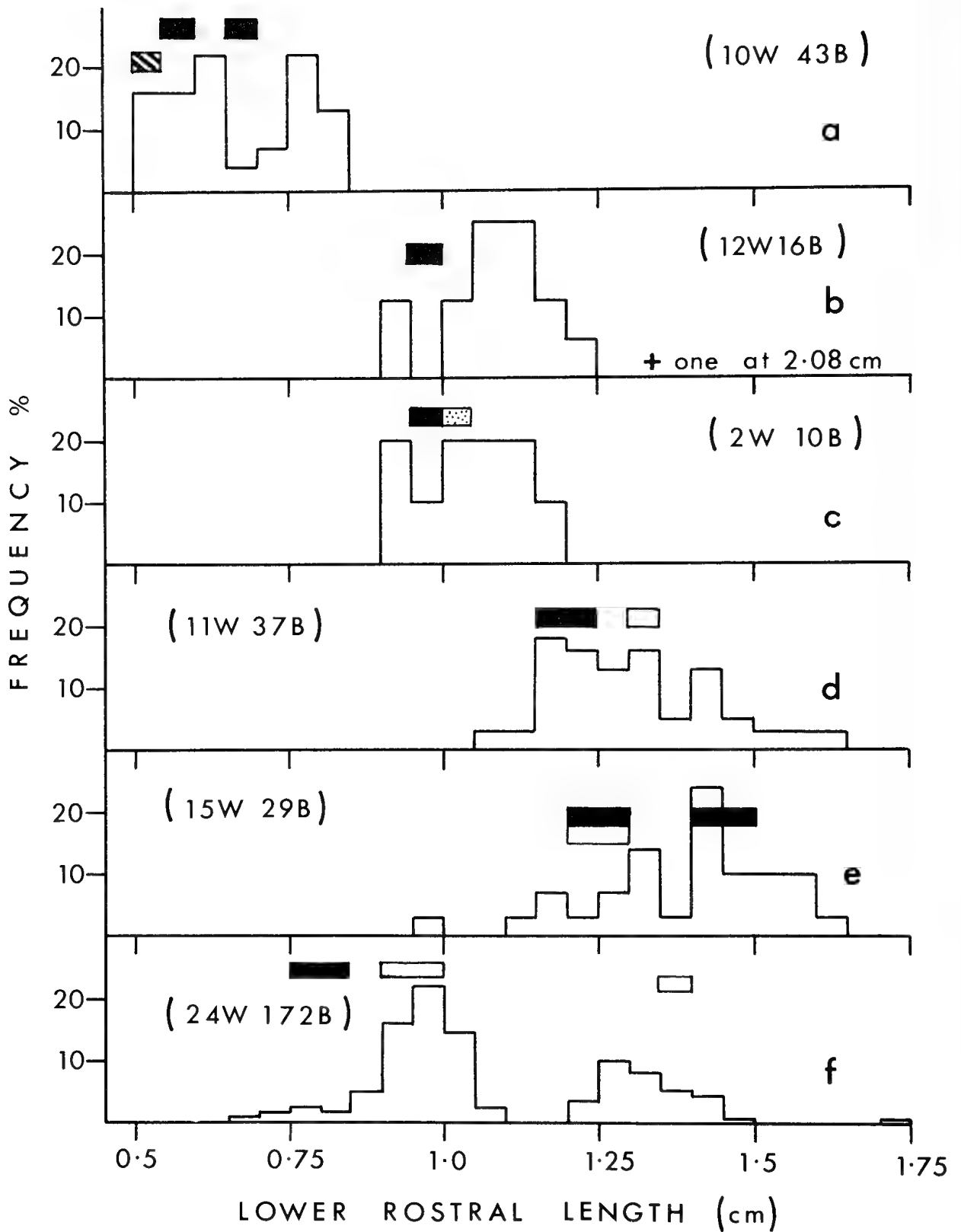
and the peak for the small sample off Western Australia is 1.5-1.55 cm. Clarke (1980) showed that there is a marked change in size of the beaks through the year and interpreted this as a reflection of a two year growth to spawning and death. From July to November the LRL under the peak decreases and larger beaks become scarcer, presumably because the spawners are dying off. The peak of the present beaks is at the LRL which would be expected if the spawners continued growing or if some individuals did not spawn but continued growing. Thus we have the possibilities that in the Antarctic sector south of the Tasman Sea there may be a stock (or perhaps a different race or species) growing to a larger size than in sectors to the west as far as South America or an immigration of spawned and/or large individuals from the sectors to the west.

A beak of *K. longimana* with a LRL of 1.67 cm has undarkened wings and another just over 1.7 cm has no wings (this was probably undarkened in life). Below 1.7 cm 18 beaks have darkened wings and 12 have undarkened wings and darkening takes place between 1.05 and 1.7 cm. Darkening of the beaks in the South African and Atlantic sector of the Antarctic takes place at 0.9-1.2 cm. This is a very important difference between beaks of the Tasman Sea and the more western sectors since it shows that the stock of the Tasman Sea cannot derive merely from migration of large and spawned squids from the west but must be a stock with individuals growing to a larger mature size. Whether it can be regarded as the same species or should be more properly classed as a different species from *K. longimana* will only be clear when flesh can be collected.

LRLs of *Architeuthis* sp. have a range of 0.70-1.90 cm and a main peak at 1.5-1.6 cm (Fig. 2). This is different from the peaks found in beaks from whales caught off South Africa.

Fig. 5 Percentage frequency histograms of the rostral lengths of lower beaks of a *?Discoteuthis*; b *Taonius pavo*; c *Galiteuthis armata*; d *Ancistrocheirus lesueuri*; e *Moroteuthis robsoni*. The number of whales (W) and beaks (B) are indicated. Horizontal bars indicate peaks of beaks thought to be the same species from whales caught off South Africa (black) and Western Australia (white).





At Durban the main peak was at 0.50-0.60 cm with a small peak at 1.40-1.50 cm and at Donkergat the main peak was at 0.80-0.90 cm with just a suggestion of a peak at 1.3-1.4 cm.

The largest beak having undarkened wings has a LRL of 1.4 cm and the smallest one having darkened wings is the same size. This is different from South African beaks where the largest with undarkened wings is 1.1 cm and the smallest darkened is about 0.7 cm.

Differences in LRLs between South African and the present beaks may be caused by the difference in seasonal sampling. Off Durban 63% of the beaks were collected prior to June when most of the LRLs were 0.50-0.60 cm and no beaks were collected after September. Similarly, off Donkergat, only 18% were collected after August. The present beaks were all collected in November and, as beaks of a similar size are present off South Africa it is possible that growth through the year accounts for the difference between the regions and that the same species is involved. However, some doubt is introduced by the size of the beaks when the wings become darkened. This could be a regional difference in one species or merely a sample variation.

The LRL peak of *Taningia danae* at 1.2-1.3 cm is close to, and probably corresponds with, the main peak at 1.1-1.2 cm off South Africa (Fig. 2). The main peak at 1.6-1.8 cm is probably represented in samples from Western Australia (only 30 beaks). In some months in the South African samples there is a suggestion of a peak at a similar size. Wings of the beaks darken at a LRL of 0.8-1.6 cm which is closely similar to the species off South Africa and Western Australia and supports the conclusion that some beaks of the group with large LRLs are present in these regions.

The LRLs of *Histioteuthis bonnellii corpuscula* (A2) have a range of 0.46-0.70 cm and a peak at 0.56-0.58 cm (Fig. 4). These compare with a range of about 0.44-0.58 cm and a peak at 0.48-0.52 cm in South Africa and 0.50-0.54 cm off Western Australia. The difference between the three areas is possibly not significant although the species does seem to become larger from west to east.

The LRLs of *Histioteuthis ?dofleini* A4 have a range from 0.42 to 0.93 cm and peaks at 0.64-0.66 cm and 0.78-0.80 cm (Fig. 4). This compares with a peak at 0.75-0.80 cm in the Antarctic. Many but not all beaks under the peak at a smaller size are immature. This second peak may represent a different size group but we cannot rule out the possibility that another species is present.

LRLs of *Cycloteuthis akimushkini* have a range of 0.95-1.65 cm and a peak at 1.40-1.45 cm (Fig. 6). Beaks from whales caught off South Africa had a rather ill-defined peak at 1.20-1.30 cm. However, in the later half of the year the LRLs are slightly larger and in September the peak is at 1.30-1.40 cm and in October there is a secondary peak at 1.40-1.50 cm. At Albany in April and September combined, the peak is well defined at 1.20-1.30 cm. Thus, the present beaks seem to be slightly larger than those from further west and this could be caused by growth, since these beaks were collected later in the year (November) than elsewhere.

LRLs of *Pholidoteuthis boschmai* A have a range of 0.65-1.10 cm and a peak at 0.95-1.00 cm (Fig. 6). The peak at Donkergat is 0.75-0.80 cm, at Durban 0.80-0.85 cm, at Albany 0.90-1.00 cm (Clarke 1980) and 0.90-1.00 cm in New Zealand (Gaskin & Cawthorn 1967). Thus, beaks to the west and east of Australia are the same size and are larger than off South Africa.

Comparison of species

The percentage contribution of the families represented are compared with collections from sperm whales killed in five areas of similar latitude in Fig. 7 (see Clarke 1980; Clarke, MacLeod and Paliza 1976). Clearly the whales of the Tasman Sea collection eat much more Octopoteuthidae, slightly more Lepidoteuthi-

Fig. 6 Percentage frequency histograms of the rostral lengths of lower beaks of a *Chiroteuthis* sp.; b *Mastigoteuthis*; c *Moroteuthis* 'A'; d *Todarodes* sp.; e *Cycloteuthis akimushkini*; f *Pholidoteuthis boschmai*. The number of whales (W) and beaks (B) are indicated. Horizontal bars indicate peaks of beaks thought to be the same species from whales caught off South Africa (black), western Australia (white), South America (hatched) and in the Antarctic (shaded).

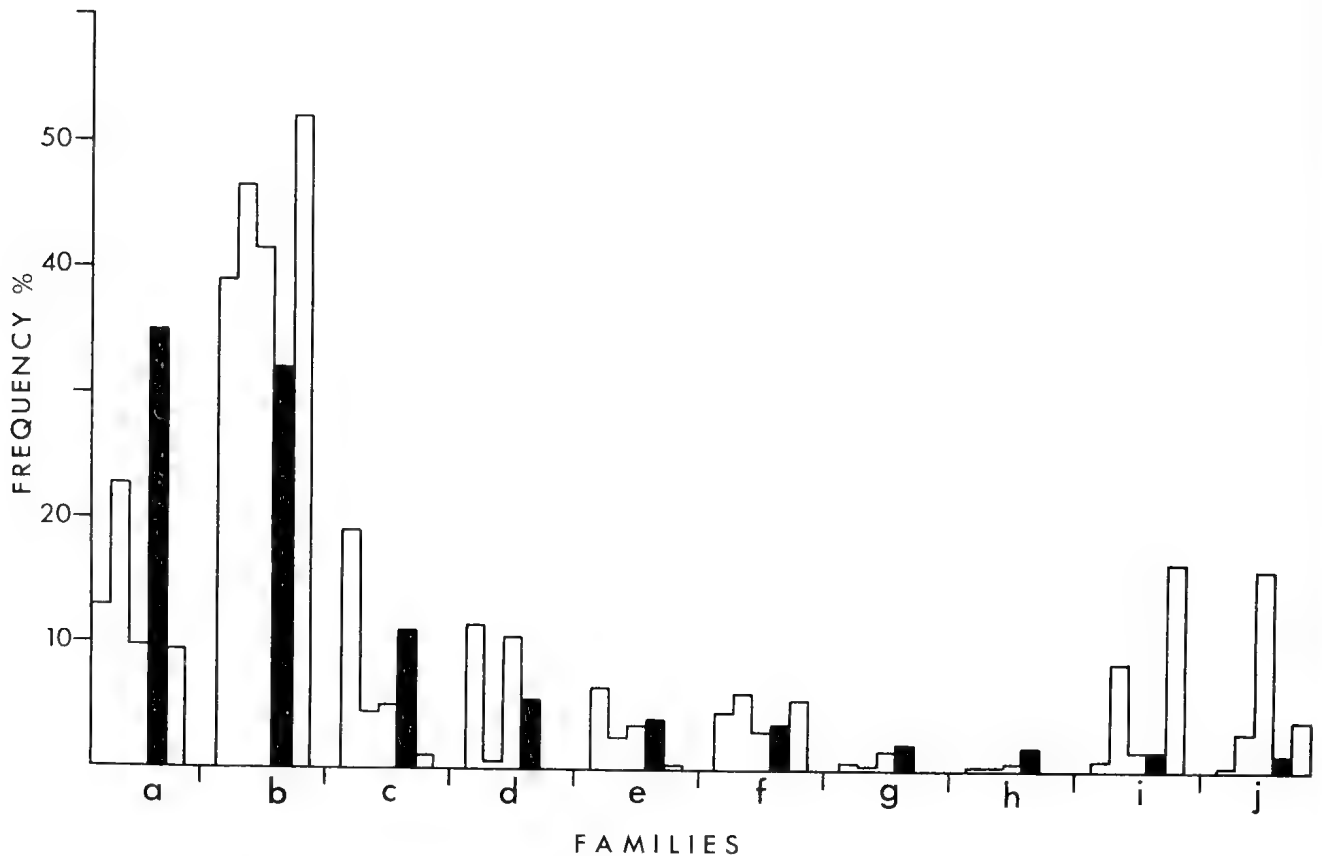


Fig. 7 A comparison of the percentage occurrence of the principal families of cephalopods from stomachs of sperm whales caught in five regions of the southern hemisphere. For each family the columns run from left to right (west to east), Donkergat (South Africa), Durban (South Africa), Albany (Western Australia), Tasman Sea and western South America. Tasman Sea percentages are shown in black. a Octopoteuthidae; b Histioteuthidae; c Cranchiidae; d Pholidoteuthidae; e Onychoteuthidae; f Enoploteuthidae; g Lepidoteuthidae; h Architeuthidae; i Chiroteuthidae; j Ommastrephidae.

dae and Architeuthidae and fewer Histioteuthidae than whales of the other regions.

Whale distribution

While male whales longer than about 37 feet (11.3 m) in length move to and from latitudes higher than 40°S, smaller males and females are rarely encountered south of this latitude (Slijper *et al.* 1964). This is reflected in the composition of beaks in the stomach and the typically Antarctic cephalopod species, *Kondakovia longimana* and *Mesonychoteuthis hamiltoni* are less commonly found and less numerous in

the female and small males than in the large males. In whales caught off South Africa the females and small males (less than 39 ft (11.9 m) in length) had less than 1% and the larger males more than 12% of the beaks of these Antarctic species while, in the Tasman Sea collection, females have 1% and the males 6.3%. 82% of the males and 54% of the females from which beaks were collected have Antarctic species. Beaks of Antarctic species were collected from whales caught at all stations 1-9 except at the most northerly station No. 2 (Fig. 1). At station 6, four of the male whales had a large percentage (10, 26, 27 and 37% respectively) of beaks of Antarctic species which may suggest they were together in a school which had just previously moved north from higher latitudes. 60% of the beaks from Antarctic species from female whales occurred in two females caught at station 8. They were very large females 39 and 41 ft (11.9 and 12.5 m) long and must have been rather far south to pick up so many beaks of Antarctic species.

The smallest male having Antarctic beaks was 39 ft but there was only one smaller than this (38 ft, 11.6 m). Presumably the reason females in general have far fewer beaks of Antarctic species is that they only just cross the northern limit of the Antarctic squids while the males have far more beaks of Antarctic species because they wander right across the Convergence and into higher latitudes.

Discussion

This collection is of particular interest because all the whales containing cephalopod flesh in their stomachs were probably caught where the depth of water exceeds 1000 m and at some stations even 4000 m (Fig. 1). Indeed, many of these samples were collected a great distance from land or a continental slope and, because digestion of the flesh is rapid (Clarke 1980), this must mean that the squids concerned are widespread and not restricted to continental slope areas in the Tasman Sea. A similar wide distribution is also indicated by collections in the Antarctic and South Atlantic and this, together with the widespread occurrence and large population of sperm whales, suggests that cephalopods must form a large proportion of the 'standing stock' of nekton and the reservoir of protein in the deep oceans. This is particularly interesting since net-caught cephalopods

are too few and too small to suggest such a significant role in the food chains of the deep ocean.

In the oceans of the Southern Hemisphere a warm subtropical water mass meets a cold subantarctic water mass at the Subtropical Convergence (Deacon 1937; Rotschi & Lemasson 1967). In the south of the Tasman Sea this convergence extends from near Tasmania to the northern end of New Zealand and therefore lies roughly parallel with and slightly to the south of the line of stations from which samples were taken (Fig. 1). The hydrology or bathymetry of the Tasman Sea does not suggest any obvious discontinuity across the line of stations (Fig. 1) which might act as a barrier to distribution and account for the limits of species collected. We do not know the actual position of the Convergence in November 1970.

Certainly at the longitude of Tasmania the East Australian current pushes the Subtropical Convergence further south than its usual latitude which is nearer 40°S at other longitudes and in November, when the samples were collected, the Convergence is near its most southerly position (Rotschi & Lemasson 1967).

To judge from the absence of flesh of Antarctic squids in the whales caught at 47°S the Convergence was south of the most southerly station (47°S) at that time.

TABLE 3
Dimensions of some squids collected from the stomachs of sperm whales caught in the Tasman Sea (cm)

[] = tips missing

	<i>Pholidoteuthis</i>					<i>Architeuthis</i>	<i>Chiroteuthis</i>		
	1	2	3	4	5		1	2	3
Sex	F					F			
Mantle Length	33	61	56.5	44	40	41.5	≈ 15		
Width						≈ 11			
Circumference			32			26			
Arm Length I						[32]	18	17.5	20.5
II						43.5	25	23.5	
III		24		22	20	49	[30.5]		32
IV	20.5					45.5			
Tentacle Length		71		68		140			
Club Length		16		16		22			
Fin Length		23	21.5	18.5	17	20	6.5		
Width		33	28.5	26	28	8	5.5		
Nidamental gland L	9.5					2.2			
LRL						0.78	0.73	0.70	0.76

All, or very nearly all, the species found in the Tasman Sea collection as flesh or beaks are also represented in collections made off South Africa and Western Australia and it is remarkable that in 17 species the size distributions are closely similar in the three regions.

Where size is quite different in the regions, as in the case of *Kondakovia* and *Architeuthis* in the Tasman Sea collection, there must be a suspicion that more than one species of cephalopod is concerned.

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A REVIEW OF AUSTRALIAN FOSSIL CETACEA

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Abstract

Australian fossil Cetacea are reviewed as a prelude to the revision of previously-described taxa. The fifteen named species and subspecies are based on type-specimens of Oligocene, Miocene and possibly Pliocene age, and represent archaic Mysticeti, Squalodontidae, Physeteridae, Delphinidae, and supposedly Ziphiidae. Only two type-specimens are skulls, while the rest are elements, such as isolated teeth and earbones, which are known from other studies to be often undiagnostic. At least one nominal species of Ziphiidae is a *nomen dubium*. Other specimens which have been described informally or are housed in museums include species of Cetotheriidae, Balaenidae, Balaenopteridae, Squalodontidae, Rhabdosteidae, and Ziphiidae. None of the Australian fossil cetacean faunas is known well enough at present to allow significant paleobiogeographical or paleoecological interpretation.

Introduction

Australia has a small but interesting selection of fossil whales and dolphins (Cetacea). Mahoney and Ride's (1975) index to fossil mammals from Australia mentions 15 species or subspecies from the Oligocene, Miocene and Pliocene, and work under way by the author suggests that other taxa, hitherto undescribed from Australia, are represented in collections. The aim of this article is to outline, in general terms, the current knowledge of Australian fossil Cetacea as a prelude to formal redescriptions planned for the future. Currently-accepted subdivisions of the Cetacea are shown, together with their global and Australian stratigraphic distributions, in Figure 1.

The following abbreviations are used: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; BMNH, Department of Paleontology, British Museum (Natural History), London; MUGD, Department of Geology, University of Melbourne; NMV, National Museum of Victoria, Melbourne; SAM, South Australian Museum, Adelaide.

General Features of Cetacea

Modern cetaceans are completely aquatic mammals whose most conspicuous link with terrestrial mammals is air-breathing. Cetacea are well adapted for life in water. The body is

hairless and streamlined, and hindlimbs are absent. Tailflukes are used in swimming and forelimbs in steering. Different species of Cetacea are externally quite similar to each other but the internal skeleton is very variable. In contrast to most mammals, the anterior, tooth-bearing portion of the skull (rostrum) is long (Figure 2). Teeth are usually multiple, undifferentiated (homodont) and conical. They may be absent in some species with toothed close relatives, and are absent in adult baleen whales. The skull is 'telescoped', that is, the contact relationships of the bones have departed from the normal mammalian condition, and the nares (nasal openings) and blowholes have migrated toward the top of the head. For general reviews of cetacean characters other than those discussed below, see, for example, Gaskin (1976), Harrison and King (1980), Kellogg (1928), Norris (1966) and Slijper (1979).

Three suborders are recognized within the Order Cetacea: Archaeoceti, Mysticeti and Odontoceti (Figure 2). Archaeocetes are primitive, extinct toothed whales, from which living mysticetes (baleen or whalebone whales) and odontocetes (modern toothed whales, dolphins and porpoises) arose. Whereas identification of living cetaceans is based largely on external characters, identification of fossils is based necessarily on the skeleton. Skeletal

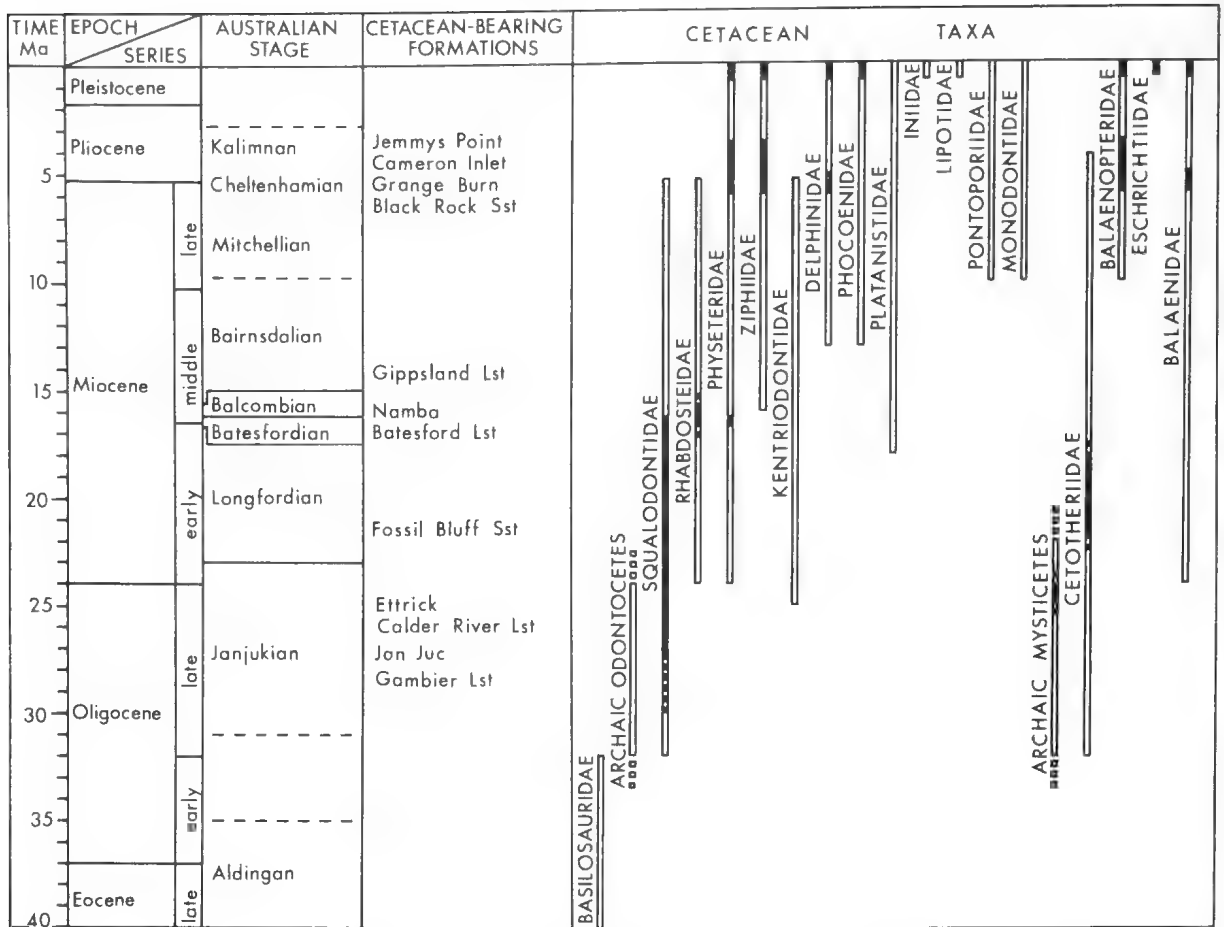


Fig. 1. Correlation of absolute time (millions of years before present, Ma) and international stratigraphic subdivisions with some Australian Tertiary stages, some Australian cetacean-bearing formations, and global records (open bar) and Australian records (infilled bar) of main cetacean taxa.

structures are also used for determining higher relationships (e.g. between genera, families) of living cetaceans. Accordingly, there is a great deal of literature about cetacean comparative morphology. For example, Miller (1923) described the different patterns of telescoping of the maxilla and other skull bones which constitute the primary basis for classification (Figure 2). The functional anatomy and significance of telescoping was considered by Mead (1975a). Fraser and Purves (1960) discussed the morphology and systematic distribution of air-sinuses in the skull. Cetacean earbones, which are common fossils, were

discussed by Yamada (1953) and Kasuya (1973). Teeth, also common fossils, are of little use in determining the relationships of any but the oldest fossil Cetacea (in which the teeth are still differentiated into peg-like anterior teeth and shearing posterior cheek-teeth). Similarly, elements of the postcranial skeleton (vertebrae of the neck, thorax, lumbar region, and tail, ribs, and forelimbs) cannot be used consistently for accurate identifications.

Archaeocetes

Archaeocetes, the oldest, most primitive whales, probably arose from archaic ungulates (Van Valen 1968) by the Early Eocene. The transition from land mammal to aquatic cetacean involved changes in feeding and locomotion, which can be inferred from changes in the skull (such as lengthening of the rostrum, widening of the frontals, loosening of the jaw

articulation) and postcranial skeleton. The most important postcranial skeletal change was modification of the caudal vertebrae, associated with the evolution of tail flukes, although this is not yet recorded in fossils.

The earliest archaeocetes (Family Protocetidae) include specimens from around the ancient Tethys sea (India, Pakistan, Egypt, Nigeria) and Texas (Kellogg 1936, Sahni and Mishra 1975, West 1980). No specimens are known from Australia or anywhere else in the Southern Hemisphere.

More advanced archaeocetes (Family Basilosauridae) probably arose from protocetids, from which they differ in features such as more elaborate cheek-teeth, development of an air-sinus in the basicranium, and more elaborate earbones. All described species of basilosaurids are from the Middle to Late Eocene and probably Early Oligocene of the Northern Hemisphere (Kellogg, 1936, Barnes and Mitchell 1978). The family was revised recently by Barnes and Mitchell (1978), who recognized two subfamilies. The Basilosaurinae (the 'Zeuglodon', *Basilosaurus cetoides*) were gigantic toothed whales of length approaching 20 m. Although they had distinctly elongate vertebrae, they were probably like modern whales in appearance. Basilosaurines, because of their vertebral structure, were too specialised to have given rise to any of the known later Cetacea. The other subfamily of basilosaurid, the Dorudontinae, comprise small, perhaps dolphin-like, species which were taxonomically and ecologically more diverse than basilosaurines. Fossil evidence suggests that both mysticetes and odontocetes arose from this group (e.g. Barnes and Mitchell 1978, Fordyce 1980b), although such an origin is disputed by some authors (e.g. Yablokov 1965, Kuzmin 1980). If the former notion is accepted, then the suborder Archaeoceti, as currently defined, is a nonmonophyletic group (in the sense of Gaffney 1979), for it does not include all descendants of the ancestral member of the group. For further reading on archaeocetes, see Kellogg 1936, Van Valen 1968, Sahni and Mishra 1975, Barnes and Mitchell 1978, Fordyce 1980b, and West 1980.

Very few supposed archaeocetes from the

Southern Hemisphere have been recorded in the literature, and all are known poorly. Bones of 'Zeuglodon' have been collected from the Upper Eocene of Seymour Island, Antarctic Peninsula (Kellogg 1936, Elliot *et al.* 1975) but those described so far give a poor idea of relationships. At least one apparent archaeocete, represented by dorudontine-like teeth, is known from the Upper Eocene of New Zealand (Fordyce 1979: 739). The only Southern Hemisphere record of a supposed archaeocete from the Oligocene is that of the New Zealand Late Oligocene species, *Kekenodon onamata*. Although this species has been mentioned widely in the literature, it is known only from the holotype teeth, earbones, and a fragment of skull (Fordyce 1980a). These are sufficiently different from specimens from elsewhere to warrant continued recognition as a separate genus and species of uncertain suprageneric affinities. The Australian Oligocene species *Mammalodon colliveri* Pritchard, 1939, has been assigned to the Archaeoceti, but it appears to be a proto-mysticete and is discussed below.

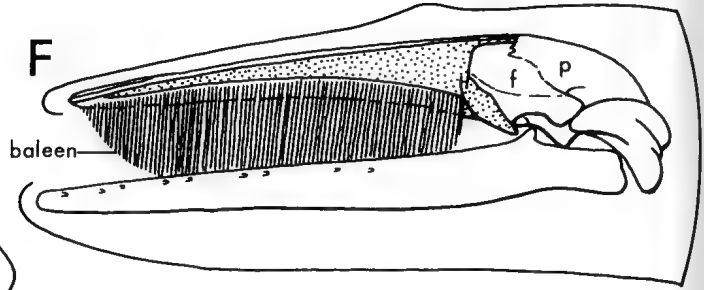
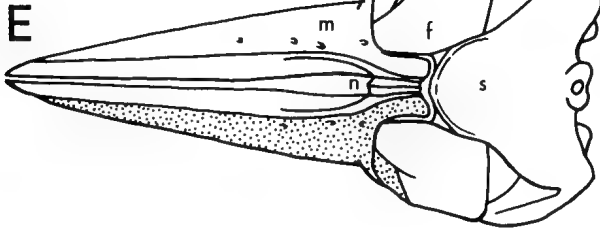
Mysticetes

Living mysticetes or baleen whales are large filter feeders which lack teeth (in all but embryonic stages) and, instead, possess baleen. Baleen consists of a series of thin, fibre-fringed plates which hang from the upper jaw (Figure 2), and functions to sieve food (small fish, plankton) from the water (Pivorunas 1979). Other apparently characteristic features of mysticetes also reflect the filter-feeding habit. These include the long rostrum, broad and dorsoventrally thin maxilla, loosely-sutured rostral bones, well-developed infraorbital process of the maxilla, elongate palatine bones, origin of temporal muscles on the dorsal surface of the supraorbital process of the frontal, presence of a pterygoid fossa primarily within the pterygoid bone, and absence of a bony symphysis in the mandible (based on features discussed by Miller 1923, Fraser and Purves 1960; see Figure 2).

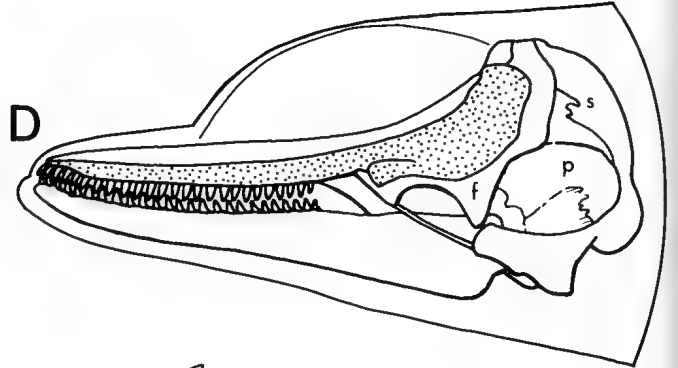
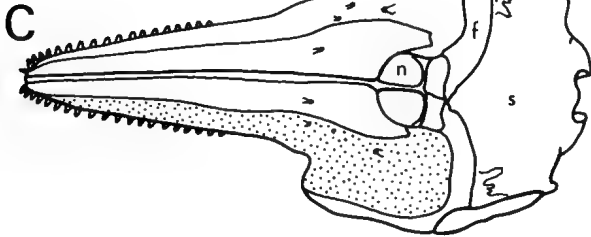
Archaic Mysticetes

Five families of extinct and living mysticetes are recognized (Aetiocetidae, Cetotheriidae, Balaenopteridae, Eschrichtiidae, and Balaeni-

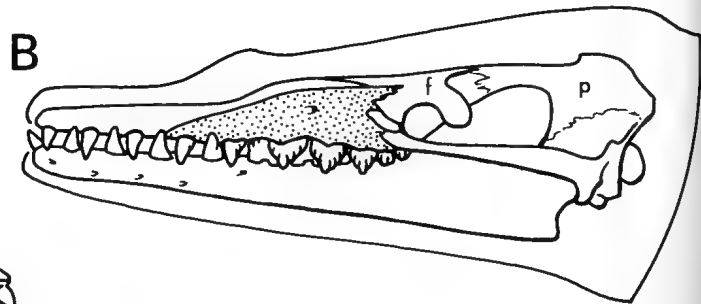
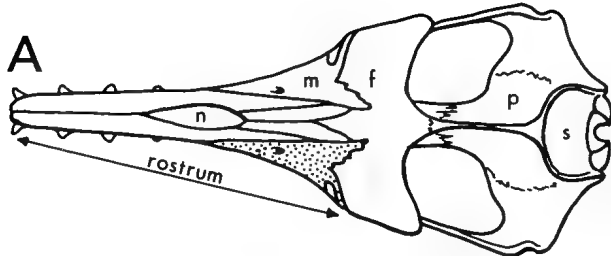
MYSTICETI



ODONTOCETI



ARCHAEOCETI



dae), of which the Family Aetiocetidae is the most primitive. Aetiocetids are represented with certainty only by the Early Miocene *Aetiocetus cotylalveus* Emlong, 1966, from Oregon. Because the species possesses teeth, it was assigned originally to the Archaeoceti, but Van Valen (1968) and Barnes and Mitchell (1978) stressed that it should be included in the Mysticeti because it exhibits derived mysticete characteristics. Although *A. cotylalveus* is the most primitive mysticete yet described, it is a relict species and is not the geologically oldest mysticete known.

Mammalodon colliveri Pritchard, 1939, formerly assigned to the Archaeoceti, appears to be a relict mysticete even more primitive than *Aetiocetus cotylalveus*. The holotype and only described specimen (presently under study by the author) consists of a fairly complete skull, right mandible, right periotic and tympanic bulla, worn teeth, and axis vertebra, specimen MUGD 1874, and a tooth, specimen NMV P17535 (Plate , fig. 6). The holotype was collected from the uppermost Jan Juc Formation (of latest Oligocene age; Abele 1979) at Bird Rock, Torquay, Victoria (Pritchard 1939, Singleton 1945).

Because the holotype has never been described adequately, its affinities have been interpreted variably by different authors. Pritchard (1939) did not refer it to a suborder, although he did consider it to be an 'ancient form . . . showing the closest approach to descent from a mammalian type of ancestor'. A reviewer (Anonymous 1939) described the species as a 'zeuglodon', Camp *et al.* (1942: 262) placed it in the Cetacea *incertae sedis*, Romer (1966: 392) assigned it to the Basilosauridae, while Pledge and Rothausen (1977: 286) implied that the species (for which was used the apparent *lapsus*

calami, *Mammalodon pritchardi*) is a squalodontoid odontocete. Some features of the holotype, for example, the loosely-sutured rostral bones, the relatively broad, flat palate, the externally-convex profile of the upper tooth-row, the fused roots in the cheek-teeth, the absence of a bony symphysis on the mandible, and the absence of a marked sagittal crest, indicate that *M. colliveri* cannot be assigned to the Archaeoceti as usually defined (e.g. by Kellogg 1936). The specimen does not exhibit derived features (e.g. a posteriorly-telescoped ascending process of the maxilla) which would justify assignment to the Odontoceti. The above features of the holotype suggest mysticete affinities, and I provisionally interpret *M. colliveri* as a very primitive and relict mysticete. The possibility that *Mammalodon colliveri* evolved independently from archaeocetes and, thus, is convergent with mysticetes, cannot be discounted yet.

Apart from the holotype, other material is known which may represent *M. colliveri*, e.g., isolated periotics, NMV P48795, P48806, P48850, P48867A-C, P160125, and P160126. Most specimens are from Janjukian (Late Oligocene) sediments exposed along the coast near Torquay, and in Waurin Ponds quarry, Victoria. Despite the fact that a considerable number of specimens is known for *M. colliveri*, new material will significantly help interpretation of this unusual species.

Cetotheres

Cetotheres (Family Cetotheriidae) comprise a diverse range of early mysticetes which have been classified together primarily because they lack characters typical of living families of mysticete, particularly the balaenopterids. For example, they differ from balaenopterids in the lack of an abruptly depressed supraorbital process of the frontal and in the variable retention of the intertemporal constriction and a strong coronoid process. Thus, as regarded at present, they probably constitute a nonmonophyletic group. The oldest accurately dated described mysticetes, from the Late Oligocene of New Zealand and Europe, have been included in the Cetotheriidae. Cetotheres are common in the Miocene, and range into the Early Pliocene.

Fig. 2. Simplified outlines of cetacean skulls showing subordinal variation in telescoping of the maxilla (m; also stippled), frontal (f), parietal (p), and supraoccipital (s), and position of the nares (n). Mandibles not shown in dorsal view. Not to scale. A, an archaeocete, *Zygorhiza kochii*, dorsal view. B, *Z. kochii*, left lateral view. C, an odontocete, *Tursiops truncatus*, dorsal view. D, *T. truncatus*, left lateral view. E, a mysticete, *Balaenoptera borealis*, dorsal view. F, *B. borealis*, left lateral view.

Specimens have been reported from the east and west coasts of North America, Patagonia, Europe, Eurasia, Japan, New Zealand, and Australia.

The only published description of an Australian cetother is that of a specimen which was described by Glaessner (1955: 367-369). This cetother, apparently first mentioned in print by Tate (1885: 41), consists of a skull minus rostrum, of reported Early Miocene age, from Murbko, South Australia. Glaessner provisionally assigned the species to the genus *Aglaocetus*, species of which have been reported previously from Patagonia and eastern North America (Kellogg 1934, 1968). Further study is needed to determine the affinities of the specimen, particularly in the light of its supposed relationship with species of apparently restricted Atlantic distribution. In unusual contrast to New Zealand, where cetotheres are common in the Oligocene, no significant specimens have been reported from the otherwise fairly productive Victorian Oligocene. It is likely, however, that undescribed fragmentary specimens from the Victorian Miocene will be found to represent cetotheres. For further reading on this group, see Kellogg (1928, 1931), Marples (1956), Rothausen (1971) and Fordyce (1980b).

Living Mysticetes

The rorquals or fin whales (Family Balaenopteridae) include the Blue Whale (*Balaenoptera musculus*, the largest mammal ever to have lived) and other large species. Characteristic features of balaenopterids include a relatively broad, flat rostrum, supraorbital processes that descend abruptly from the vertex, and closely approximated rostral elements and supraoccipital (e.g. Figure 2). Fossil balaenopterids are known from the Late Miocene onwards, and even early members appear to have been structurally similar to living forms. Fossils have been reported from North and South America, Europe, and Asia (e.g., Simpson 1945), but none has yet been described from Australia. Specimens are known, however. For example, earbones similar to those of the living humpback whale (*Megaptera novaeangliae*) and rorquals (*Balaenoptera* spp.) have been collected

from the Pliocene of Flinders Island, Bass Strait, and worn earbones from Beaumaris and Grange Burn, near Hamilton, Victoria, probably represent other species of balaenopterid. These specimens have yet to be described formally.

The Family Eschrichtiidae, represented by the living gray whale, has a fossil record only back into the Pleistocene. The family probably arose from balaenopterids. Gray whales have not been recorded from the Southern Hemisphere.

The Right Whales (Family Balaenidae), which include two large, slow-moving living species, have a fossil record back to the Early Miocene (Cabrera 1926; an Oligocene record mentioned by Fordyce 1980b is erroneous). Even early balaenids appear to have possessed the narrow, arched rostrum, posteriorly-inclined supraorbital process, and forward-thrust supraoccipital typical of modern species. The oldest fossils are from South America, while others are from North America, Europe and Australia. Whereas South American specimens include well-preserved skulls (Cabrera 1926), the Australian specimens are less complete, and none has yet been described formally. Gill (1957: 181) stated that an earbone (a periotic, NMV P16195) from Beaumaris had been identified as cf. *Balaena*. Other balaenid periotics (usually worn, but still exhibiting the typical balaenid features of small pars cochlearis and large, swollen anterior process) from Beaumaris and Hamilton are in the collections of the National Museum of Victoria, and it is likely that fragmentary skull bones from these localities also represent right whales. Howchin (1919) identified a Late Pliocene 'tympanic bone' (actually part of a right periotic; SAM specimen P8321) as that of *Balaena*.

Odontocetes

Odontocetes, or 'modern' toothed whales, encompass fossil and living dolphins, porpoises, beaked whales and sperm whales. The oldest accurately dated undoubted odontocetes are from the Late Oligocene although possibly older fragmentary specimens of less certain relationships are known (Whitmore and

Sanders 1977, Fordyce 1980b). Whereas the early evolution of mysticetes involved the development of a baleen filter-feeding system, that of odontocetes appears to have centred on development of sophisticated acoustic mechanisms of the type used by living odontocetes in echolocation (Fordyce 1980b). In living odontocetes, muscles of the face, which are implicated in the production of echolocation sounds, have distinct bony origins. The presence of the same patterns of bone profiles and telescoping in the phyletically and geologically oldest odontocetes suggests that they too echolocated. Apart from these features of the face, diagnostic features of odontocetes include the presence of nasal diverticula, antorbital notches, a reduced contribution of maxilla to orbit, a temporal muscle origin on ventral surface of supraorbital process of frontal, the presence of middle sinus in the ear, the presence of high-frequency adaptations in the ear, and the presence of a 'panbone' in the mandible (based on features discussed by Miller 1923, Fraser and Purves 1960, Kasuya 1973, Mead 1975a, Fleischer 1976; see Figure 2).

Primitive Odontocetes

The best-known early odontocetes probably are the shark-toothed dolphins (Family Squalodontidae, discussed below). Odontocetes more primitive than these were poorly known until recently, and usually were included in the Family Agorophiidae. Despite the fact that agorophiid-like forms gave rise to squalodontids and other more-modern odontocetes, the oldest accurately dated such archaic forms are relicts from the Late Oligocene, contemporaneous with squalodontids and delphinoids. No 'pre-squalodontid' odontocetes have yet been recognized from Australia. It is noteworthy that while primitive 'pre-squalodontid' odontocetes are usually classified in the Agorophiidae, a reappraisal of the Agorophiidae and the study of newly-discovered archaic odontocetes from the north-east Pacific suggest a greater taxonomic and ecological diversity amongst early odontocetes than can be expressed by the use of one family, and it is likely that new families will be described in the near future (Fordyce, 1981a).

Shark-toothed Dolphins

Squalodontids, or shark-toothed dolphins (Squalodontidae) comprise an extinct family known from the Late Oligocene to Late Miocene. They probably exhibited a variety of sizes and external shapes similar to those of the living dolphins (Family Delphinidae), and the skulls of long-beaked species appear much as would primitive beaked whales (Family Ziphiidae, see below) except for the presence of many triangular, denticulate cheek-teeth (hence the name, shark-toothed dolphins). Squalodontids include a few species known from well-preserved skulls, complete tooth complements, earbones and mandibles, but many nominal species (including Australian species) are based only on isolated teeth. Some of these teeth are similar in shape, arrangement of denticles, ornament, and other features, to teeth in identified squalodontid skulls (e.g. as in *Squalodon* spp., discussed by Rothausen 1968) but others are of uncertain affinities and could have come from any one of a number of early odontocetes (not necessarily just Squalodontidae) which exhibit heterodonty. Squalodontids have been reported from the east and west coasts of North America, Patagonia, Europe, Eurasia, Asia, New Zealand and Australia. (For a recent review of Australian species, see Pledge and Rothausen 1977.)

The best-known Australian squalodontid undoubtedly is *Prosqualodon davidis* Flynn, 1923, the holotype of which comprises a skull (now lost) and associated elements, forelimb bones and vertebrae from Fossil Bluff, Wynyard, Tasmania. The elements were described in detail by Flynn (1948) who had earlier (1920, 1923, 1932) given abbreviated descriptions. An artificial cranial endocast was described by Dart (1923). The holotype is from the Fossil Bluff Sandstone, of Longfordian or Early Miocene age (Pledge and Rothausen 1977). The skull is short-beaked and robust, in contrast to the more delicate skulls of the common long-beaked species of *Squalodon* of the Northern Hemisphere Miocene, and carries robust teeth. Perhaps the animal was an active predator—a small equivalent of the living killer whale. Flynn assigned the species to *Prosqualodon* because of its close similarity to the

South American species *Prosqualodon australis* (Plate 2, fig. 2), an earliest Miocene species described by Lydekker (1894; see also references in Flynn 1948). The similarity of *Prosqualodon davidis* to *P. australis* counters the suggestion (Rothausen 1970) that the former should be placed in a different genus.

Other material of *Prosqualodon* is known from the Southern Hemisphere, although no Northern Hemisphere specimens are known yet. Two supposed species of *Prosqualodon*, *P. hamiltoni* Benham, 1937, and *P. marplei* Dickson, 1964, have been recorded from the Late Oligocene Waitakian Stage of New Zealand, but neither seems congeneric with *P. australis* (Fordyce 1980a, 1980b). However, isolated teeth of squalodontids from the New Zealand Waitakian may well represent species of *Prosqualodon*.

Prosqualodon also may be represented in Australia by some isolated teeth, including some described by Hall (1911) and discussed subsequently by Flynn (1948), Glaessner (1955) and Pledge and Rothausen (1977). Those shown in Hall's Figs. 5 and 7 are, respectively, the holotypes of *Parasqualodon wilkinsoni* and *Metasqualodon harwoodi*, discussed below. Specimen NMV P5525, Hall's Fig. 1, was identified by Hall as *?Parasqualodon wilkinsoni*, while Flynn was uncertain of its identity. Its ornament (Plate 2, fig. 5) is unlike that of the *Prosqualodon* teeth figured by Flynn but is reminiscent of the coarse ornament of poorly-preserved the teeth of *Mammalodon colliveri*. The tooth in Hall's Fig. 2 (NMV P5529) is a finely ornamented anterior tooth which Flynn had 'no difficulty' referring to *P. davidis*. However, the ornament on this tooth is much finer than that of *P. davidis*, and close affinity is unlikely. An anterior cheek-tooth (Hall's Fig. 3, NMV P14040; Plate 2, fig. 1), identified by Flynn as *P. davidis*, is similar to teeth figured by Flynn, but the posterior keel of the tooth possesses denticles not seen in *P. davidis*. Accordingly, they may not be conspecific. Flynn regarded the cheek-tooth of Hall's Fig. 4 as that of *P. davidis*, and this was followed by Pledge and Rothausen (1977) who refigured the tooth. This tooth may be that of '*Zeuglodon*' mentioned by Tate (1892). Flynn commented that

the tooth of Hall's Fig. 6 (NMV P5532) could be related to '*Squalodon serratus*', known from a single tooth from the New Zealand Oligocene (Glaessner, 1972, Fordyce 1980a). This is unlikely, as there are marked differences in size, proportions, ornament, and denticles. Pledge and Rothausen (1977: 292) included NMV P5532 with *P. davidis*, but this relationship has yet to be verified.

Parasqualodon wilkinsoni (McCoy, 1866) is known with certainty only from the holotype (NMV P5528), an isolated tooth (Plate 2, fig. 3) probably from the Calder River Limestone (Late Oligocene) near Castle Cove, Aire district, Victoria. The species originally was thought to represent *Squalodon*, and it was only in 1911 that Hall assigned it to a new genus, *Parasqualodon*. Flynn (1948) noted its similarity to *Prosqualodon davidis* but considered that the structure of the tooth argues against close relationship. He considered the tooth to be abnormal. Pledge and Rothausen (1977) mentioned differences in crown structure between teeth of *Parasqualodon wilkinsoni* and *Prosqualodon davidis*, but concluded that the former probably represents a species of *Prosqualodon*. In fact, the possibility of intra-specific variation in teeth and the close geological ages make it possible that these species are conspecific.

Metasqualodon harwoodi (Sanger, 1881) is another tooth taxon, of supposed Squalodontidae, that was poorly understood until reviewed by Pledge and Rothausen (1977). The species is known only from the Late Oligocene holotype and paratype teeth from South Australia. The teeth appear to be those of short-beaked species but, because no skull remains are known, this remains to be demonstrated (as does assignment to the Squalodontidae in the strict sense). Pledge and Rothausen concluded that *Metasqualodon* represents a distinct genus.

'*Squalodon gambierensis* Glaessner, 1955, is based on a single cheek-tooth of early Late Oligocene age, from the Gambier Limestone, South Australia. The tooth was figured by Glaessner (1955) and Pledge and Rothausen (1977). Glaessner (1955) excluded it from described Austral genera and instead assigned it

to 'the widespread genus *Squalodon*' because of its smooth crown, straight roots and strongly developed median cusp. Pledge and Rothausen queried this generic assignment, and it seems unlikely that the tooth represents a species of *Squalodon*, for the keels are sharp, the denticles are relatively large, freestanding and laterally compressed, and the crown lacks ornament (present on even the smoothest crown of teeth of *Squalodon* spp.). It is unlikely that this or other Austral supposed species of *Squalodon* ('*S.* *serratus*' and '*S.* *andrewi*' from New Zealand) actually represent that genus, which is known positively only from the Miocene of the Northern Hemisphere. Until skull remains are found, it is not certain that '*S.* *gambierensis*' even belongs in the Squalodontidae.

Other squalodontid remains are known from Australia, although none is yet formally described. A large squalodontid is represented by an incompletely prepared partial skull, teeth and mandible (MUGD 5101) from Batesford Quarry, near Geelong (Batesfordian, Early Miocene). It differs in the large size of its cheek-teeth from species previously recorded from Australia. Gill (1957: 181) reported that an anterior tooth (NMV P16198) from Beaumaris is probably that of '*Squalodon* cf. *wilkinsoni*', but it is more likely that the tooth is the incisor of a seal. For additional general reading on Squalodontidae, see Kellogg (1923, 1928) and Whitmore and Sanders (1977).

Beaked Whales

Beaked whales (Family Ziphiidae) are medium to large odontocetes with long, narrow, and usually toothless rostra (or beaks), deeply concave facial regions on the skull, and mandibles that are usually toothless or with only one or two pairs of teeth. The fossil record extends back to the Early Miocene, and fossils are well known from North and South America and Europe (Mead 1975b). Fossil ziphiid bones, usually fragments of rostrum and earbones, are resistant to erosion, and may lie on the seafloor for millions of years (Eastman 1906, Fordyce and Cullen 1979). Ziphiids are probably of squalodontid ancestry (Mead 1975b).

One nominal species of fossil ziphiid from Australia, *Ziphius* (*Dolichodon*) *geelongensis*

McCoy, 1882, was based on a specimen thought to be a mandibular tooth, from Waurm Ponds, near Geelong. The holotype actually appears to be an undiagnostic worn fragment of rib, which suggests that the name should be discarded (Fordyce 1981b). The species previously has received occasional incidental mention in earlier literature on Victorian fossils.

McCoy (1879) also recorded worn cetacean tympanic bullae from Waurm Ponds and, unfortunately, established formal species names for these. He used the general name 'Cetotolites', proposed by Owen, as a formal generic name (although in the modern sense of a collective group: an assemblage of identifiable species of which the generic positions are uncertain), and suggested that the bullae represent ziphiids. McCoy recognized four species and subspecies, *Cetotolites leggei*, *C. pricei*, *C. nelsoni* [*nelsoni*], and *C. nelsoni rugosa*, probably all from the Waurm Ponds Member of the Jan Juc Formation of Late Oligocene to earliest Miocene age (Abele *et al.* 1976: Fig. 13). Another supposed species of *Cetotolites*, '*C. baileyi*', was mentioned by McCoy (1883) but was never described. None of the type-specimens is complete enough to be certain of the family to which they belong, let alone to allow assessment of generic and specific relationships. It is likely that when their taxonomic status is reassessed, the names will be considered *nomina dubia* (i.e., names not certainly applicable to any known taxa), and this would warrant discarding them.

Rostra which belong indisputably to Ziphiidae have been found in the Australian Tertiary. Chapman (1917) described two specimens, from Grange Burn, Hamilton district (NMV P13012, specimen A; Plate 2, fig. 12 herein; and NMV P13011, specimen B), which he identified as '*Mesoplodon compressus*, Huxley sp.'. Both are long, narrow, deep, and dense, with mesorostral ossifications and no alveoli. They probably came from the basal Grange Burn Formation, of Kalimnan age (latest Miocene-earliest Pliocene). A third, undescribed rostrum (NMV P21482) also is known from Grange Burn. Glaessner (1947) described a rostrum from the Kalimnan of Lakes Entrance, Victoria, for which he

employed the name *Mesoplodon longirostris* (Cuvier, 1823). Both Chapman and Glaessner listed *Belemnoziphius compressus* Huxley, 1864, as synonyms of the names they employed, whereas Mead (1975b) recognized *B. compressus* as a distinct species which he regarded as the type-species of *Belemnoziphius*. The relationships of these and other as-yet undescribed *Mesoplodon*-like Australian specimens to *Belemnoziphius* and other genera discussed by Mead has yet to be determined. Two other ziphiid records are noteworthy. Scott (1913) described, but did not figure, the postcranial skeleton of a supposed ziphiid from Table Cape, Tasmania. It is possible that, like *Prosqualodon davidis*, this specimen is of Early Miocene age. The affinities of the specimen have not been verified subsequently. Sutherland and Kershaw (1971: 159, Plate 2) figured the rostrum (NMV P23961) of a species of *Ziphius* from the Kalimnan (Pliocene) Cameron Inlet Formation, Flinders Island.

Sperm whales

Sperm whales (Family Physeteridae) encompass both very large and small living species (the sperm whale, *Physeter macrocephalus*, and the pygmy sperm whales, *Kogia* spp.) and many named fossil species of Early Miocene age and younger. The skulls of fossil and recent species typically possess a huge 'supracranial basin', markedly asymmetrical facial bones, and a broad-based rostrum. Few, if any, fossils attain the size of the extant sperm whale. Fossils have been recorded from the east and west coasts of North America, Patagonia, Europe, possibly Eurasia, New Zealand, and Australia, and some of these were reviewed by Kellogg (1925a, 1927).

There are four Australian species of physeterids, none of which has been studied recently. All are based on isolated teeth, and thus are of uncertain relationship. (While older, heterodont Cetacea sometimes can be identified at all taxonomic levels from isolated teeth, this is rarely the case for more modern, homodont odontocetes.) *Physetodon baileyi* McCoy, 1879, for which McCoy established a new genus, is based on pieces of two large teeth NMV P5519, P5520, P5521) from Beaumaris,

Victoria. Chapman (1912) based *Scaldicetus macgeei* on a fairly well preserved tooth (NMV P12889; Plate 2, fig. 4) also from Beaumaris. Its wrinkled crown enamel is similar to that of European species of *Scaldicetus*, but the identity of this genus is uncertain and requires revision. Another nominal species of *Scaldicetus*, *S. lodgei* Chapman, 1917, is known from quite a delicate tooth (NMV P13032) with a small, smooth crown, from Muddy Creek, near Hamilton. The above three species are of Cheltenhamian or Kalimnan age. The holotype of *Scaptodon lodderi* Chapman, 1918, for which a new genus was described, is a weathered tooth (cast, NMV P13042) of uncertain geological age, from Ulverstone, Tasmania. Despite Chapman's assertion, it is not certain that it is a mandibular tooth, for many fossil physeterids possess both upper and lower teeth. The true affinities of the above four species are uncertain, and the holotypes of *P. baileyi* and *S. lodderi* are quite inadequate specimens on which to base new genera. Chapman (1929) referred to *Parasqualodon* and *Metasqualodon* as sperm whales, but this is erroneous.

Other, undescribed, material may give a better insight into Australian physeterids. Gill (1957: 182) mentioned a toothed whale from Beaumaris (NMV P16204-P16207; Cheltenhamian) which consists of the well-preserved apices of both mandibles, teeth, skull fragments and vertebrae of a small sperm whale, unlike any described previously from Australia. Material from near Hamilton includes a well-preserved periotic (NMV P48791; probably Kalimnan) similar to that of the living *Physeter macrocephalus*, and scraps of crania and vertebrae. One physeterid tooth and a fragment of mandible (NMV P48801) from Fyansford, near Geelong, may be of Batesfordian-Bairnsdalian (Early-Middle Miocene) age, somewhat older than the above specimens.

River Dolphins

Four families of small, polydont, long-beaked extant 'river dolphins' are sometimes erroneously united into one family on the basis of external similarities and habits, even though they differ markedly in many cranial features

(Fordyce, MS). The Family Platanistidae is based on the living blind Ganges dolphin, *Platanista gangetica*. It has had fossil species of Middle Miocene age or younger, from North America and Europe, referred to it. The extant South American boto, *Inia geoffrensis*, is placed in the Iniidae, to which Early Miocene to Pliocene species (most of uncertain affinities) from North and South America have been assigned. The Family Pontoporiidae, based on the living franciscana, *Pontoporia blainvillei*, nominally includes fossil species from the Late Miocene and Pliocene of North and South America. The fourth family, Lipotidae, which was established recently for the Chinese dolphin *Lipotes vexillifer*, has not yet had fossils assigned to it. None of these families has yet been recognized in Australia. However, another 'river dolphin' family, the extinct Rhabdosteidae, which also includes small, very long-beaked species, recently was recorded from Australia for the first time (Fordyce, MS). Rhabdosteidae (=Eurhinodelphidae of earlier authors, according to Myrick, 1979, who recently reviewed the family) include fossils from the east and west coasts of North America, Patagonia, Europe, perhaps New Zealand and, very doubtfully, Japan. The group is unusual in that the very long rostrum is partly toothless (Kellogg 1925b). The Australian specimens, which first were thought to be platanistids (Tedford *et al.* 1977), comprise skull fragments, teeth, earbones (Plate , fig. 7), ribs and vertebrae of many individuals of an indeterminate genus and species from the Middle Miocene Namba Formation, Lake Frome area, South Australia. They indicate that the Frome area drained into the sea, and provide the first conclusive evidence of rhabdosteids in the south-west Pacific. This occurrence suggests that rhabdosteids could have been the primary medium-sized, active predaceous endotherms of Australian Miocene fresh waters.

White Whales

White whales (Family Monodontidae) encompass the living narwhal and beluga, and are commonly thought of as Arctic species. Recently, however, Kasuya (1973) assigned the liv-

ing Irrawaddy dolphin (*Orcaella brevirostris*) to the family. In view of its occurrence in northern Australian waters, fossil relatives of this species (as yet unknown) could be discovered here. Fossil white whales are known from Middle Miocene and younger rocks of North America and Europe.

Dolphins

Four dolphin (in the broad sense) families are sometimes united in one superfamily, Delphinoidea. The Acrodelphidae encompasses only extinct species, not considered here, from the Miocene of North America, Europe and Eurasia (e.g., Simpson 1945). Its taxonomy is in serious need of review.

Kentriodontids (Family Kentriodontidae) are primitive dolphins which Barnes (1978) considered ancestral to modern delphinids (discussed below). They are of small to medium size, possess rostra of moderate length, polydont teeth and well-developed basicranial sinuses, and differ from delphinids mainly in their symmetrical skulls and less elaborate airsinuses. Barnes mentioned taxa from the Middle and Late Miocene of east and west North America, Europe, and Eurasia, and other records are known from New Zealand, Europe, Eurasia and perhaps Japan, which include Late Oligocene and Early Miocene specimens. Kentriodontids have not been reported from Australia but could be expected here in Upper Oligocene and Miocene rocks.

Dolphins (Family Delphinidae) comprise the most diverse family of living odontocetes. Interpretation of fossil distribution is hindered because many small problematic odontocetes previously have been referred to the family (e.g., Simpson 1945). This has been rectified to some extent by Barnes' (1978) review of kentriodontids. Simpson indicated a stratigraphic range from Early Miocene onwards, but it is more likely Late Miocene to Recent (e.g., Barnes 1977). Fossils have been recorded in North America, Europe, Eurasia, Japan, New Zealand and Australia.

The one supposed fossil delphinid described from Australia, *Steno cudmorei* Chapman, 1917, is based on a worn isolated tooth (NMV P13033; Plate 2, fig. 11) of latest Miocene age,

from Beaumaris. Chapman believed this to be the only known fossil species of the extant genus *Steno*, although two species had been described earlier from the Pliocene of Italy. Another specimen (NMV P48799; Plate 2, figs. 8-10) recently collected from Beaumaris consists of teeth of similar proportion and ornament to the holotype, a periotic, and a tympanic bulla. It is probably conspecific with the holotype. The periotic is quite different from that of the living *Steno bredanensis*, and indicates that the species probably does not belong in *Steno*. The associated bulla is of a type previously collected from Beaumaris, but hitherto not identified. '*Steno*' *cudmorei* does not appear closely related to any extant species of delphinid, although it is not as primitive as kentriodontids.

Other, as yet undescribed, dolphin fossils have been recorded. Longman (1920) mentioned the discovery of a skull of *Delphinus delphis*, of unstated geological age, from Queensland. Scott and Lord (1921) reported that a Miocene 'delphinoid', close to the extant *Globiocephala* spp., had been found near Wynyard, Tasmania, but the identity of this specimen is yet to be verified. Isolated teeth from Beaumaris, with larger and smoother crowns than '*S.*' *cudmorei*, may represent a delphinid. Gill (1965: 4) mentioned that bones of *Delphinus delphis* have been collected from Holocene silts near Melbourne. However, significant finds of delphinid have yet to be made.

True porpoises (Family Phocoenidae) are small, short-beaked odontocetes best known from their living Northern Hemisphere representatives. Some extant species are common around South America, and one (*Phocoena dioptrica*) has been recorded south-east of Australia. Fossil phocoenids have been recorded from the Miocene and Pleistocene of North America and Europe, but have not been recognized in Australia. Marcuzzi and Pilleri (1971: Fig. 77) indicated the presence of a Pleistocene phocoenid in Australia, but this probably refers to the record of *Phocaenopsis mantelli* which is an Early Miocene small odontocete, perhaps a rhabdosteid (Fordyce 1981c), from New Zealand.

Significance of Australian Fossils

Known Australian fossils do not contribute to an understanding of the earliest phases of cetacean evolution: the transition to water before the Middle Eocene, and the Middle-Late Eocene radiation of archaeocetes. Very early archaeocetes may have reached north-west Australia before the eastern Tethys closed, or via the shores of India after that subcontinent contacted Asia, although such specimens are unknown at present. Perhaps the absence of Australian Cetacea older than Late Oligocene reflects the fact that only a narrow seaway was present between Australia and Antarctica until about the middle of the Oligocene when the area of the South Tasman Rise opened enough to allow the establishment of the Circum-Antarctic Current and, presumably, circum-polar provincialism. If there was limited access to the sea, e.g., from the west, and, furthermore, if there were limited shelf areas linking the west with areas of cetacean abundance, then this might account for somewhat depauperate faunas. Because this observation reflects absence of evidence rather than evidence of absence, however, conservative interpretation is necessary. At this stage in our knowledge, it is noteworthy that only one good specimen of Early Oligocene age or older from the southern edge of Australia could allow radical reinterpretation of Austral cetacean history.

The few late Early and many Late Oligocene Cetacea from New Zealand (Fordyce 1980a, 1980b) provide unusual contrast with the few known Australian species of that age. It is uncertain whether this reflects real differences in paleobiogeography, differences in the relative amounts of potentially fossiliferous outcrop, or both. The abundance of specimens in New Zealand may reflect the presence of more-favourable habitats, caused by increases in oceanic currents, cooling, and productivity increases around Antarctica from the earliest Oligocene onwards. In fact, it is plausible that these climate changes triggered the evolution of both odontocetes and mysticetes (Fordyce 1980b). In view of the presence of sequences potentially favourable for preservation of Cetacea, the relative paucity of Australian Oligocene records could reflect relatively less

hospitable marine environments around southern Australia than around New Zealand. Again, however, absence of evidence requires conservative interpretation.

There is no doubt that early odontocetes (e.g. *Metasqualodon harwoodi*, *Parasqualodon wilkinsoni*) inhabited Australian waters during the Late Oligocene. The absence of mysticetes is puzzling in view of their abundance in New Zealand. *Mammalodon colliveri* provides an interesting record of a relict archaic mysticete contemporaneous with more modern taxa, and similar occurrences are known also in New Zealand and the north-east Pacific (Fordyce 1980c).

The presence in Australia, New Zealand and South America of earliest Miocene *Prosqualodon* spp. indicates that some taxa achieved circum-polar distribution by this time. A diverse Early Miocene cetacean fauna, like that known from South America (Cabrera 1926) has not yet been recognized in Australia or New Zealand.

Latest Miocene Cetacea are well represented in south-east Australia. Sequences at Beaumaris and near Hamilton, Victoria, which are known to be of similar age to each other, possess similar cetacean faunas. Nodule beds at each locality have produced balaenids, balaenopterids, delphinids, physeterids, and ziphiids. A similar range of taxa has been collected from the Middle Pliocene of Flinders Island, Bass Strait, but it is premature to speculate on the palaeoecological significance of faunal similarities.

In conclusion, it is noteworthy that although Australia does not have a large fossil cetacean fauna, its fossils include some relatively well-preserved specimens (the holotypes of *Mammalodon colliveri* and *Prosqualodon davidis*) that are important to cetacean systematics. It is likely that other relatively complete and well preserved specimens will be found in future, and these, like other Austral specimens, could elucidate problems hitherto unresolved by the detailed study of Northern Hemisphere fossils.

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Explanation of Plate

PLATE 2

- Fig. 1. NMV P14040, *Prosqualodon* cf. *dauidis*, anterior cheek-tooth, lingual view, $\times 1$.
- Fig. 2. BMNH M7249, *Prosqualodon australis*, skull, dorsal view, $\times 0.15$.
- Fig. 3. NMV P5528, *Parasqualodon wilkinsoni* holotype, isolated posterior cheek-tooth, buccal view, $\times 1$.
- Fig. 4. NMV P12889, *Scaldicetus macgeei* holotype, isolated tooth, posterior view, $\times 0.5$.
- Fig. 5. NMV P5525, indeterminate cetacean (?*Mammalodon colliveri*), isolated tooth, buccal view, $\times 1$.
- Fig. 6. NMV P17535, *Mammalodon colliveri* holotype, cheek-tooth, buccal view. $\times 1$.
- Fig. 7. AMNH 102194, Rhabdosteidae genus and species indeterminate, right periotic, ventral view, $\times 1$.
- Fig. 8. NMV P48799, "*Steno*" *cudmorei*, left tympanic bulla, dorsal view, $\times 1$.
- Fig. 9. NMV P48799, "*Steno*" *cudmorei*, left periotic, dorsal view, $\times 1$.
- Fig. 10. NMV P48799, "*Steno*" *cudmorei*, tooth, buccal view, $\times 1$.
- Fig. 11. NMV P13033, "*Steno*" *cudmorei* holotype, isolated tooth, buccal view, $\times 1$.
- Fig. 12. NMV P13012, *Mesoplodon* sp., rostrum, right lateral view, $\times 0.25$.



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TRIPLECTIDES OF AUSTRALIA
(INSECTA: TRICHOPTERA: LEPTOCERIDAE)

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Abstract

The caddisfly genus *Triplectides* is revised for Australia, with descriptions and keys provided for males of all 26 Australian species and subspecies and for females of the 18 species for which the sexes have been associated. Ten species and one subspecies are described as new to science. *T. cephalotes* and *T. gilolensis* probably do not occur in Australia and should be removed from its faunal list. Five closely related species, *T. australis*, *T. helvolus*, *T. magnus*, *T. parvus* and *T. volda*, are viviparous. The typical size of the compound eyes of southern males of *T. similis* often is twice that of northern males; the eye size ranges do not overlap although the forms are broadly sympatric, suggesting a single-gene variation in this character.

Introduction

Ulmer (1907) and Mosely (1936) provided the latest comprehensive revisions of the long-horned caddisfly subfamily Triplectidinae. Scattered publications since 1936 have brought the number of species to 82 in 14 genera. About half of these species (43) have been included in the nominal genus *Triplectides*. Mosely and Kimmins (1953) published the most recent review of Australian *Triplectides*, indicating 15 species and one subspecies in its fauna. Since then, Neboiss (1977) synonymised *T. dubius* Mosely (but, strictly speaking, not *T. dubius subalbidus* Kimmins) with *T. elongatus* Banks, transferred *T. albanus* Mosely to *Westriplectes* (Neboiss, 1982), and described 4 new species (Neboiss 1977, 1982). In this work, we remove *T. cephalotes* (Walker) and *T. gilolensis* (MacLachlan) from the list of Australian species, synonymize *T. dubius subalbidus* with *T. elongatus* and describe 10 new species and one new subspecies, bringing the total to 25 species and 1 subspecies of Australian *Triplectides*.

The original plan for this work as envisaged by the late Dr Herbert H. Ross and JCM was to infer the phylogenetic history for the species of Triplectidinae, facilitating resolution of questions concerning their most appropriate tribes and genera and permitting a reconstruction of their historical, transantarctic distributions. Our revision here represents the first stage

toward those goals. Subsequent stages will include our revision of the remaining species of Australian triplectidines, a study of extra-Australian species, and, finally, the phylogenetic treatment with its reassessment of triplectidine tribes and genera and their historical biogeography.

The different species of *Triplectides* occur in a wide variety of ecological conditions, including cold and warm, unpolluted to moderately polluted, permanent and temporary lakes, ponds, rivers and creeks. Apart from 3 Baltic Amber fossils, the various species of this genus are distributed in Asia from India to Japan; in Indonesia, Papua-New Guinea, and Australia south to Tasmania; on South Pacific Islands including New Hebrides, New Caledonia, and New Zealand; and in South and Central America. The genus is ubiquitous in Australian waterways, including even temporary aquatic habitats in the centre of the continent, and is often the most common caddisfly genus encountered in benthic surveys.

Morphological terminology used in this work is patterned after the studies by Nielsen for male (1957) and female (1981) caddisfly genitalia and by Betten (1934) and Hamilton (1972) for wing venation.

During the course of our study, we examined specimens from the National Museum of Victoria in Melbourne (NMV), the B.P. Bishop Museum in Honolulu (BPBM), the Austra-

lian National Insect Collection in Canberra (ANIC), the University of Queensland Insect Collection in Brisbane (QU), the Queensland Museum in Brisbane (QM), and the Australian Museum in Sydney (AM). Types of species described herein are deposited in these institutions or in the British Museum of Natural History in London (BMNH) or Institut für Pflanzenschutzforschung, Eberswalde (IPE), formerly Deutsches Entomologisches Institut (DEI), Berlin as indicated.

Complete bibliographies, including synonyms, of each of the following taxa described before 1961 can be found in the catalogue by Fischer (1965, 1972). Only the principal taxonomic references are provided below.

All dissected specimens are identified by a note book number with a prefix PT-; wing venation drawings are prepared from detached wings mounted in glycerol as temporary mounts; genitalia are drawn from cleared specimens, macerated in KOH and transferred to glycerol for storage.

The terminology used for wing venation is indicated on Fig. 1, and the following abbreviations have been used:

Longitudinal veins:

C—costa	Cu—cubitus
Sc—subcosta	P—plical
R—radius	E—empusal
S—sector	A—anal
M—media	JB—jugal bar

Crossveins:

s—sectoral
m-cu—medio-cubital
acc m-cu—accessory medio-cubital (Fig. 26)

Other structures:

arc—arculus
ny—nygma
dc—discoidal cell
tc—thyridial cell

Figures 54-82 illustrate male genitalia; each view is indicated by letters a-g respectively; a—left lateral view of genitalia except phallus; b—ventral view of inferior appendages and tip of phallus; b'—same as b except setae and baso-

ventral lobe omitted; c—left lateral view of phallus; d—dorsal view of terga IX and X; e—dorsal view of phallus, more enlarged; f and g—ventral views of genitalia from varieties.

Abbreviations in terminology used are shown in Fig. 54.

ap do—apico-dorsal lobe of inferior appendage
bv—baso-ventral lobe of inferior appendage
har—harpago or second segment of inferior appendage
me lo—mesal lobe of inferior appendage
ph sc—phallosomal sclerite
sup app—superior appendage
X—tergum X

Figures 83-100 illustrate female genitalia showing: a—lateral view, and b—ventral view. Abbreviations of terms used in female genitalia are shown in Fig. 83.

do se—dorsal setose lobe
go pl—gonopod plate
lam—lamella
s-b p—sensilla-bearing process
sp sc—spermathecal sclerite

The scale is indicated by a line representing 1 mm for the entire wing figure and 0.1 mm for male and female genitalia figures, except Fig. 77e.

Triplectides Kolenati, 1859

Triplectides Kolenati, 1859, p. 247.

The diagnostic character for this genus is the apically broadened discoidal cell (dc) in the forewing (Fig. 1), its lower distal angle produced toward the medial vein (M) and, in the males of some species, closely parallel with it for a short distance. The closing sectoral crossvein (s) for this cell is usually curved basad. The thyridial cell (tc) is long and narrow, always longer than the discoidal cell. In some species, the apex of this cell is narrow, or separated from the rest of the cell by an accessory crossvein (acc m-cu Fig. 26) or its anterior and posterior veins may be fused for a short distance. As evidenced by the position of the

nygma (ny), forks 1, 2 and 5 are present in the male forewing; 1, 2, 3 and 5 in the female forewing. In the hindwing, forks 1, 2, 3 and 5 are present in both sexes, except that fork 1 is usually absent in *T. volda* Mosely. The forewing is longer and narrower than the hindwing and usually slightly widened beyond the arculus (arc). The hindwing posterior region is usually broad, especially in males, giving it a somewhat triangular appearance.

Tibial spurs are 2, 2, 2 or 2, 2, 4 on the 3 legs of one side from foreleg to hindleg, respectively.

Diagnostic characters in the male genitalia (Fig. 54) include a pair of superior appendages flexible at the base, more or less fused sclerites on tergum X, a pair of 2-segmented inferior appendages, and an apparently 1-piece phallus, all of whose lengths and shapes vary according to the species. The basal segment of each inferior appendage bears an apico-dorsal, semi-membranous lobe (ap do) which extends beyond the harpago (har), a baso-ventral lobe (bv) which is flexible at its base, and a mesal lobe (me lo) (possibly the 'phallic guide' mentioned by Morse, 1975) which is fused only basally with that of the opposing inferior appendage and which apparently serves as a clasp for the movable harpago. The phallus consists primarily of a tubular phallobase with a large phallotremal sclerite (ph sc) in its apico-dorsal membranes. No phallic shield or parameres are present. A long, more-or-less sclerotized strip extends along the dorsal midline from the phallic apodeme to the apex, supported by partially eversible membranes, and may represent the primitive phallicata. The ejaculatory duct opening is situated on a short projection between the broad, sometimes convoluted, lateral arms of the phallotremal sclerite, giving this sclerite a somewhat trident-like appearance from dorsal or ventral perspectives.

The female genitalia (Fig. 83) externally include a pair of long, dorsal setose lobes (do se) (area IXc of Nielsen, 1981), flexible basally in some species. A pair of semi-membranous, sensilla-bearing processes (s-b p) is usually present, each generally situated on the ventral edge of its respective setose lobe. Below these arise a pair of lamellae (lam) (IXd of Nielsen, 1981)

which often have longitudinal striae on their mesal face. The ventral gonopods form a flat plate (go pl), completely fused on the midline and fused laterally with segment IX for much of its length. The plate usually has transverse striae apically. Internally, the shape of the spermathecal sclerite (sp sc) may be used to distinguish some groups of *Triplectides* species. Type species: *Mystacides gracilis* Burmeister (subsequent selection of Mosely, 1936).

Australis Group

The five Australian species included in this group are all viviparous, with the females bearing live first-instar larvae through ruptured ventral membranes between segment VIII and the gonopod plate. The pleural abdominal membranes are expanded in these species and the unruptured ventral membranes beyond segment VIII, when fully extended, may reach the second or third abdominal segment (Fig. 83c). A total of 661 larvae were found in one specimen of *T. australis* Navás although it is possible that some larvae had already escaped. Neboiss (1957) estimated 300-350 in another. We suspect that this reproductive strategy may be responsible, at least in part, for the remarkable success of these species in temporary waterways in the drier parts of the continent.

Diagnostic characters include the sharp posterior angle of the discoidal cell clearly separated from the thyridial cell by a short base of vein S_4 (Figs. 1-10), and the 2, 2, 2 tibial spur formula. In males, segment X lacks sharp dorsal or ventral carinae, distinguishing them from *T. ciuskus* and *T. similis* males, which they resemble in the above characters. Harpago usually with 2 or 3 apical teeth. Segment IX of males has a weakly sclerotized strip laterally, below which a broad lobe extends mesad to the phallus. Besides the expanded membranes discussed in the preceding paragraph, the females have greatly enlarged, sometimes sclerotized, sensilla-bearing processes below the conspicuous, dorsal setose lobes. The ventral lamellae are shorter, less conspicuous and much more weakly sclerotized than in other *Triplectides* species, and are often covered by the telescoped sternum VIII. The spermathecal sclerite is generally longitudinally rectangular.

***Triplectides australis* Navás**
(Figs. 1, 2, 54, 83)

Triplectides australis Navás, 1934, p. 93.

Triplectides australis, Neboiss, 1957, pp. 51-53, figs. 1-5; ♀ lectotype designated.

Triplectides australis, Neboiss, 1978, p. 836, fig. 28; ♂ first described.

Triplectides cephalotes, Mosely and Kimmins, 1953, pp. 204-206; misidentification for Australian specimens.

Triplectides cephalotes, Neboiss, 1982, p. 304, figs. 74, 75; misidentification for SW Australian specimens.

Pale to dark brown or grey. Male genitalia (Fig. 54) with distinctively tapered apex of phallus in ventral view. Harpago with subapical teeth. Mesal lobe of inferior appendage broadly rounded, with blunt lateral corner. Female sensilla-bearing lobe semi-membranous, slender, acute (Fig. 83).

This species may be the one described as *T. viviparus* (Wood-Mason, 1890) from India and the species misidentified by various authors as *T. magnus* (Walker, 1852) in Asia from India to New Guinea to Japan.

Length of anterior wing: ♂ 11-15 mm; ♀ 13-16 mm.

Type material: Type ♀, Sydney, NSW; Collection Luddemann, (IPE).

Other material examined: Numerous specimens from many Australian localities including records from lagoons in Central Australia and Northern Territory near the Gulf of Carpentaria; rivers in Western Australia including the Kimberley region; south-west Australian localities are listed in detail by Neboiss (1982) under the name of *T. cephalotes*. Large numbers of specimens were available from localities in Queensland, New South Wales and Victoria. Specimen PT-849 ♂ from Jindabyne, NSW and PT-864 ♀ from Molong, NSW figured (NMV).

Distribution: Australia except Tasmania.

Habitat: larger, slow flowing rivers and lentic water basins.

***Triplectides helvolus*, n. sp.**
(Figs. 3, 4, 55, 84)

Body and wings pale yellow. Male genitalia (Fig. 55) with segment IX as discussed for species group, long dorsally. Superior appendages nearly as long as tergum X. Tergum X rounded apically, incised on midline. Inferior

appendages with short apico-dorsal lobe 1.5X as long as harpago; baso-ventral lobe extending only $\frac{2}{3}$ distance to base of harpago; mesal lobe very narrow, finger-like; and harpago without subapical teeth. Phallus short, gradually curved ventrad, somewhat tapered apically in ventral view, but not as much as in *T. australis*.

Female genitalia (Fig. 84) with dorsal setose lobes long, broad, rounded apically in lateral view, at least 2X as long as sensilla-bearing lobes. Sensilla-bearing lobes sclerotized, truncate apically with row of short, stout setae. Lamellae semi-membranous. Spermathecal sclerite rectangular, broadly rounded posteriorly.

This species most closely resembles *T. australis*, but is distinguishable by its paler colour, and, in the male, by the less markedly tapered tip of its phallus, the lack of subapical teeth on the harpago, the shorter apico-dorsal and baso-ventral lobes of the inferior appendage, and the narrower mesal lobe of the inferior appendage. In the female, it is distinctive in the shorter, truncate, sclerotized sensilla-bearing processes.

Etymology: *helvolus*—(Latin) yellow, pale-yellow.

Length of anterior wing: ♂ 11-12.5 mm; ♀ 12-14.5 mm.

Type material: Holotype ♂ Lambells Lagoon, Humpty Doo, NT., 19 Aug. 1979, J. Blyth (NMV, T-7510); paratypes 11 ♂ 5 ♀, collected with holotype (specimen PT-866 ♀ figured) (ANIC; NMV); 1 ♂ 3 ♀, 5 km NNW Cahills Crossing, East Alligator River, 12°23' S 132°57' E, 8-9 June 1973, J. C. Cardale (specimen PT-842 ♂ figured) (ANIC; NMV); 1 ♂ 4 ♀, Howard Creek, 3 km E of Howard Springs, NT., 17 Aug. 1979, J. Blyth (NMV); 2 ♂ 14 ♀, McCaddy's Lagoon, Reynolds River, 80 km SW of Darwin, NT., 22 Aug. 1979, J. Blyth (NMV); 1 ♂ 1 ♀, Goose Lagoon, 15 km SW by S of Boorooloola, NT., 16°10'S 136°15'E, 31 Oct. 1975, J. C. Cardale (ANIC); 1 ♂, Drysdale River, 15°02'S 126°55'E, WA., 3-8 Aug. 1975, I.F.B. Common & M. S. Upton (ANIC).

Other material examined: **Northern Territory**—3 ♀, 16 km E by N of Mt. Cahill, 13 June 1973, J. C. Cardale (ANIC); 2 ♀,

Nourlangie Creek, 14-17 June 1973, J. C. Cardale (ANIC); 3 ♀, Cooper Creek, nr. Borradale, 3-6 June 1973, J. C. Cardale (ANIC); 1 ♂, Howard Springs, 9 Sept. 1980, D. King (NMV); 1 ♂, 48 km E of Darwin (no date), G. F. Hill (BPBM) (head missing); **North Queensland**—1 ♂, Tinaroo Pines Caravan Park, 9 Apr. 1972, N. McFarland (NMV); 1 ♀, Shipton Flat 15°45'S 145°14'E, 17-19 Oct. 1980 J. C. Cardale (ANIC); 1 ♀, Moses Creek, 4 km N by E of Mt. Finnigan, 14-16 Oct. 1980, J. C. Cardale (ANIC); 1 ♀, Peach Creek Crossing, 25 km NNE of Coen, 4-5 Jul. 1976, G. B. Monteith (ANIC); **North West Australia**—1 ♀, Carson escarpment, 14°49'S 126°49'E, 9-15 Aug. 1975, I.F.B. Common & M.S. Upton (ANIC).

Distribution: N-Qld.; NT.; NW-Australia.

Habitat: usually lakes and lagoons.

Triplectides magnus (Walker)

(Figs. 5, 6, 56, 85)

Leptocerus magnus Walker, 1852, p. 73.

Triplectides magna, MacLachlan, 1866, p. 257, pl. 19, figs. 3a-e.

Triplectides magna, Mosely, 1936, p. 100-103, figs. 2, 23-25.

Triplectides magna, Mosely and Kimmins, 1953, p. 200-204, figs. 134-136.

Triplectides magnus, Neboiss, 1977, p. 128, figs. 694-696.

Usually larger and darker than other Australian species of this group. Apex of male phallus parallel-sided (Fig. 56). Harpago short, with subapical teeth. Apico-dorsal and basoventral lobes of inferior appendage of variable length, but shorter than in *T. australis*. Mesal lobe of inferior appendage very broad, but with its blunt corner clearly situated beyond the rest of the lobe.

Female dorsal setose lobes (Fig. 85) relatively smaller than in the 2 preceding species. Sensilla-bearing processes short, sclerotized, triangular. Anterior edge of each lamellae thick, angled laterally (best seen in ventral view).

The species identified by various authors as *T. magnus* from Asia, New Zealand and other locations outside southeastern Australia is probably some other species, possibly *T. Australis*.

Length of anterior wing: ♂ 15-18 mm; ♀ 17-18 mm.

Type material: Type ♂, 'Van Dieman's Land. Dr. Hooker's Collection' (without other data) (BMNH).

Other material examined: **Tasmania**—Hobart, Lake Pedder, Olga River, Condominion Creek—dates between end of October and mid-February; **Victoria**—Creswick, Tabilk, Latrobe River, Lake Barracoota—dates between end of October and end of February. Specimen PT-314 ♂ and PT-825 ♀ from Lake Pedder, Tas. figured.

Distribution: Tas.; S-Vic.

Habitat: lakes and sluggish rivers, possibly also small creeks.

Triplectides parvus (Banks)

(Figs. 7, 8, 57, 86)

Notanotolica parva Banks, 1939, p. 485, pl. 1, fig. 4, pl. 7, fig. 62.

Pale grey to pale brown. Male genitalia (Fig. 57) with parallel-sided phallic tip. Harpago with subapical teeth. Superior appendages somewhat shorter and broader than in other species of this group. Apico-dorsal and basoventral lobes shorter than in *T. australis*. Distinctive mesal lobe of inferior appendage usually concave apically with rounded mesal projection extending beyond acute lateral corner (Figs. 57b, 57f), but few in Northern Territory with lobes (Fig. 57a) approaching those of *T. volda*.

Female genitalia (Fig. 86) with relatively small, dorsal setose lobes. Sensilla-bearing processes very broad, usually rectangular, sclerotized, without small mesal finger-like projections sometimes seen in *T. volda*. Pleural region of segment IX usually with well-defined secondary carina distad from primary one. Anterior edge of each lamella thick, angled laterally. Both sexes usually with fork no. 1 present in hindwing, but exceptions exist.

Length of anterior wing: ♂ ♀ 10-13 mm.

Type material: Type ♂, Ravenshoe, Atherton Tableland, N-Qld., 27 Apr. (1932) Darlington, Harvard Expedition. MCZ Type no. 22077 now in ANIC (specimen figured).

Other material examined: **North-Queensland**—Iron Range, Upper Jardine River, McIvor River, Cooktown, Mt Webb (specimen PT-832 ♀ figured), Cairns, Atherton

Tableland, Gordonvale, Mareeba—dates throughout the year except February, March and April; **Northern Territory**—Holmes Jungle and Howard Springs near Darwin (March and June); **SE-Queensland**—Kenilworth (specimen PT-823 ♂ figured), Manchester Dam (February and April).

Distribution: NT (Darwin area); N-Qld.; SE-Qld.

Habitat: associated with moderately fast flowing creeks.

***Triplectides volda* Mosely**

(Figs. 9, 10, 58, 87)

Triplectides volda Mosely, in Mosely and Kimmins, 1953, pp. 210-212, figs. 142, 143.

Pale grey to pale brown. Male genitalia (Fig. 58) very similar to those of *T. parvus* except that mesal lobe of inferior appendage is evenly convex to acute lateral corner.

Female genitalia (Fig. 87) similar to those of *T. parvus*, except sensilla-bearing processes usually more triangular, often with small mesal finger-like projection; secondary carina in pleural region of segment IX less pronounced. Spermathecal sclerite occasionally with posterior portion recurved ventrad. Both sexes usually with fork no. 1 in hindwing absent or S_1 represented only by short, vestigial stub, but exceptions exist.

Length of anterior wing: ♂ ♀ 10-12 mm.

Type material: Type ♂, Eidsvold, Qld., October, 1926, I. M. Mackerras (ANIC).

Other material examined: **Queensland**—2 ♂ 1 ♀, Upper Jardine River, 11°17'S 142°35'E, 17 Oct. 1979, M.S. & B.J. Moulds (NMV); 4 ♀, Iron Range, 2-9 June 1971, E. F. Riek (ANIC); 1 ♂, Annan River, 15°41'S 145°12'E, 27 Sept. 1980, J. C. Cardale (ANIC); 1 ♂ 2 ♀, Millstream Falls, W of Ravenshoe, 25 June 1971, E. F. Riek (ANIC); 1 ♂, Christmas Creek, Fairview via Laura, 26-27 June 1975, S. R. Monteith (ANIC); 1 ♂ 3 ♀, Granite Creek, Many Peaks, 1 Apr. 1972, S. R. Monteith (ANIC); 5 ♂ 1 ♀, Kenilworth, 7 Apr. 1967, N. Dobrotworsky (NMV); 2 ♂ 4 ♀, Upper Brookfield nr. Brisbane, 4 Apr. 1967, N. Dobrotworsky (NMV); 15 ♂ 9 ♀, Camp Mountain, 31 Mar. 1967, N. Dobrotworsky (specimen PT-850 ♂ and PT-867 ♀ figured)

NMV); 1 ♀, Manchester Dam, Ipswich, 1 Feb. 1973, M. H. Colbo (NMV); **New South Wales**—♂ ♀ (numerous), Upper Allyn River, Eccleston, 21 Feb. 1980, A. A. Calder (NMV); 2 ♂ 1 ♀, Serpentine River, 21 Feb. 1966, E. F. Riek (ANIC); 1 ♂, Orrarol River 40 km S of Canberra, 10 Apr. 1981, A. Neboiss (NMV); 1 ♂, Stroud, 13 Nov. 1953, A. Neboiss (NMV); 1 ♂, Neimer River, Wakool, 26 Dec. 1954, E. Matheson (NMV); 14 ♂, Upper Kangaroo Valley, 24 Nov. 1960, E. F. Riek (ANIC); **Victoria**—1 ♀, Irymple, 25 Nov. 1964, A. Neboiss (NMV); 1 ♂, Mitta Lagoon, 30 Nov. 1973, NMV Survey (NMV); 1 ♂, Gibbo River—Morass Creek Junctn., 1 Feb. 1974, A. Neboiss (NMV); 1 ♂, Rose River Whitfield, 11 Feb. 1963, A. Neboiss (NMV); 5 ♂ 6 ♀, Meredith, 12 Feb. 1959, A. Neboiss (NMV).

Distribution: Qld.; NSW; Vic.

Habitat: fast and slow streams, lagoons.

Proximus Group

Wing venation (Figs. 11-14) is similar to that in the Australis Group. The tibial spur formula is 2, 2, 4. Male genitalia are distinguishable by the narrow, parallel-sided superior appendages about as long as acute tergum X (see also Neboiss, 1977, fig. 704). The ventral edge of the harpago is serrate. The tip of the phallus is somewhat enlarged and the apical lips are recurved laterally. The mesal lobe of each inferior appendage has 2 distinct projections. Female genitalia exhibit a pair of short, spatulate dorsal setose lobes, flexible basally. No sensilla-bearing projections are evident. Lamellae are small, but well sclerotized and without conspicuous setae or striae. Antero-ventrad from each lamella is a distinct, semi-membranous projection. The fused gonopods are with (*T. bilobus*) or without (*T. proximus*) transverse striae. The spermathecal sclerite has an ovoid ring which traverses it obliquely, crossing above the anterior end of the sclerite, near its tip, and nearly, but not quite, closing near the postero-ventral end.

***Triplectides bilobus* Neboiss**

(Figs. 11, 12, 59, 88)

Triplectides bilobus Neboiss, 1977, p. 130, figs. 703-706.

Dark brown. Male genitalia (Fig. 59) dis-

tinguishable from those of *T. proximus* by smaller, less-flared apex of phallus; shorter, out-turned baso-ventral lobe of inferior appendage; and much smaller, acute mesal process of mesal lobe of inferior appendage.

Female genitalia (Fig. 88) with lamella narrow in lateral view, 2X as long as broad. Gonopod plate with transverse striae. Oblique ring of spermathecal sclerite crossing above anterior end of sclerite further from tip than in *T. proximus*.

Length of anterior wing: ♂ ♀ 15-18 mm.

Type material: Holotype ♂, Franklin River 20 km SW of Derwent Bridge, Tas., 11 Feb. 1971, A. Neboiss (NMV, T-5406), paratypes collected with holotype, specimens PT-309 ♂ and PT-860 ♀ figured.

Other material examined: **Tasmania**—(localities additional to those listed by Neboiss 1977); 2 ♂, Ropeway Creek—Gordon River junction, 2 Feb. 1977, D. Coleman (NMV); 2 ♂ Denison-Maxwell River junction, 10 Jan. 1977, A. Neboiss and R. Swain (NMV); 1 ♂ 2 ♀, Sir John Falls, Cataract Creek, 12 Dec. 1975, D. Coleman and W. Fulton (NMV); ♂ ♀ (numerous), Olga River 19 km above Gordon River junction, 13 Jan. 1977, D. Coleman, A. Neboiss, et al. (NMV).

Distribution: NW and SW Tas.

Habitat: rivers and larger creeks.

Triplectides proximus Neboiss (Figs. 13, 14, 60, 89)

Triplectides proximus Neboiss, 1977, p. 130-131, figs. 707-708.

Blackish-brown. Male genitalia (Fig. 60) with phallus enlarged and conspicuously flared apically. Straight, parallel-sided baso-ventral lobe of inferior appendage extends to base of harpago. Mesal lobe of inferior appendage with rounded mesal projection broader than lateral projection.

Female genitalia (Fig. 89) with lamella triangular in lateral view, as broad basally as long. Gonopod plate without conspicuous transverse striae. Oblique ring of spermathecal sclerite traversing dorsal side of sclerite very near anterior end.

Length of anterior wing: ♂ 13-16 mm; ♀ 14-16 mm.

Type material: Holotype ♂, Leven River nr. Heka, Tas., 17 Nov. 1972, A. Neboiss (NMV, T-5417); paratype ♂ collected with holotype, specimen PT-218 and paratype ♀, St Patricks River, Targa, PT-859 figured (NMV).

Other material examined: **New South Wales**—15 ♂ 2 ♀, Brown Mtn., 18 Jan. 1961, E. F. Riek (ANIC; NMV); 1 ♂ Sawpit Creek, Mt Kosciusko, 13 Feb. 1975, T. Petr (NMV); **Victoria**—numerous localities in Central, Eastern and North-eastern highlands, North-central Gippsland, East-Gippsland, dates ranging between October and March.

Distribution: N-Tas.; E-Vic; SE-NSW.

Habitat: medium sized rapid streams.

Australicus Group

Wing venation (Figs. 15-20) is similar to that in the Australis Group. The tibial spur formula is 2, 2, 2 (*T. ciuskus*) or 2, 2, 4 (*T. australicus*). Male genitalia are distinctive for their pair of thin, longitudinal plates on the ventral side of segment X, beneath its broadened and occasionally incised apex. The superior appendages are nearly as long as tergum X, but are broader basally than in the Similis, Elongatus, and Truncatus Groups. The harpago is long and with subapical teeth. The apico-dorsal lobe of the inferior appendage is scarcely longer than the harpago. The baso-ventral lobe extends to the base of the harpago. The mesal lobe of the inferior appendage is nearly truncate, either slightly convex (*T. australicus*) or slightly concave (*T. ciuskus*), with an acute lateral corner; its dorsal face has 1 or 2 longitudinal carinae. The phallus is angled near the base. Female genitalia are typical for the genus except that the lamellae lack conspicuous setae and the spermathecal sclerite is rectangular.

Triplectides australicus Banks (Figs. 15, 16, 61, 90)

Triplectides australica Banks, 1939, p. 486, figs. 47, 66.

Moderate to pale yellow. Spurs generally 2, 2, 4, but rarely 2, 2, 2 on one side, 2, 2, 4 on other! Male genitalia (Fig. 61) distinguishable from those of *T. ciuskus* by sinuate edge of ventral, longitudinal plates of segment X and by convex apex and blunt lateral corner of mesal lobe of inferior appendage. Sinuate edge of

ventral plates of tergum X varying from that seen in Fig. 61a nearly to that of Fig. 62a.

Setose dorsal lobe of female genitalia (Fig. 90) narrow, its dorsal edge straight in lateral view. Striae of lamellae and gonopod plate less conspicuous than in *T. ciuskus*.

Length of anterior wing: ♂ 11.5-13 mm; ♀ 12.5-14 mm.

Type material: Type ♂, Ravenshoe, Atherton Tableland, 27 Apr. (1932) Darlington, Harvard Expedition. MCZ type no. 22080 now in ANIC (specimen figured).

Other material examined: **Queensland**—1 ♂ 1 ♀, Cairns, May 1963. K. Korboot (NMV) (specimens PT-855 ♂ and PT-862 ♀ figured); 1 ♀ Broken River Camp. Eungella National Park, 9 May 1980, I. D. Naumann and J. C. Cardale (ANIC); 1 ♂ 36 km S of Miriam Vale, 25 May 1971, E. F. Riek (ANIC); 1 ♂ 8 ♀, Saddletree Creek via Maidenwell, 29 Mar. 1975, S. R. Monteith (ANIC); 5 ♂, same loc., 16 Oct. 1973, A. Neboiss (NMV); 3 ♂, Clintonvale, 14 Oct. 1973, A. Neboiss (NMV); 3 ♂ 2 ♀, Myall Creek 3 km N of Rangemore, 15 Oct. 1973, A. Neboiss (NMV); 4 ♂, Bulimba Creek, Brisbane, 23 Oct. 1979, Survey Group (NMV); 2 ♂, Goomburra, 14 Oct. 1973, A. Neboiss (NMV); 1 ♂ 8 ♀, Upper Brookfield, 4 Apr. 1967, N. Dobrotworsky (NMV); 8 ♂, Brisbane, 15 Aug. 1957 (no collector) (NMV); **New South Wales**—2 ♂ 3 ♀, Wallangarra, 31 Dec. 1956, J. Kerr (NMV); 3 ♀, Molong, 29 Dec. 1973, M. S. Moulds (NMV); 1 ♂, Limestone Creek, Lyndhurst, 21 Dec. 1977, A. Neboiss (NMV); 3 ♂, Kangaroo Valley, 22 Mar. 1961, E. F. Riek (ANIC); **Victoria**—3 ♂ 1 ♀, Hopkins River, 19 Jan. 1953, A. Neboiss (NMV); 1 ♂, same loc., 28 Oct. 1955, A. Neboiss (NMV); 1 ♂, Avenel, 9 Dec. 1954, A. Neboiss (NMV); 1 ♂, Campaspie River, Woodend, 19 Jan. 1956, A. Neboiss (NMV); 3 ♂, Sunbury, 18 Dec. 1953, A. Neboiss (NMV); 15 ♂ 1 ♀, Reedy Creek, Orbost, 6 Feb. 1961, N. Dobrotworsky (NMV); **Western Australia**—1 ♂, Deep Reach, Fortescue River, 3 Dec. 1974, K. F. Walker (NMV); 2 ♀, Crossing Pool, Millstream, 21 Oct. 1970, J. C. Cardale (ANIC); 1 ♂ 20 ♀, same loc., 2 Apr. 1971, E. F. Riek (ANIC).

Distribution: Qld.; NSW; Vic; N-WA.

Habitat: larger, slow flowing rivers; slow flowing sections of creeks.

***Triplectides ciuskus* Mosely** (Figs. 17, 18, 62, 91)

Triplectides ciuska Mosely in Mosely and Kimmins 1953, pp. 209-210, fig. 141.

Triplectides ciuskus, Neboiss, 1977, pp. 127-128, figs. 690-693.

Triplectides ciuskus, Neboiss, 1978, p. 836, fig. 27.

Light to dark brown. Spurs 2, 2, 2. Edge of ventral, longitudinal plates of segment X varying from blunt or acute angle (Fig. 62a) to projecting point (Mosely & Kimmins 1953, Fig. 140b) in lateral view. Mesal lobe of inferior appendage usually slightly concave apically, with acute lateral corner.

Setose dorsal lobe of female genitalia broad, its dorsal edge evenly convex in lateral view. Striae of lamellae and gonopod plate conspicuous.

Length of anterior wing: ♂ 12-14.5 mm; ♀ 12.5-15 mm.

Type material: Type ♂, Mt. Kosciusko, 3000 ft., NSW, 20 Jan. 1914 (ANIC).

Other material examined: extensive number of specimens were examined from numerous localities in the Eastern States, and Northern Territory; Tasmanian localities are listed in detail by Neboiss (1977). The species is known from Western Australia by a subspecies in the Kimberley area; it is absent from Central Australia. Specimen PT-856 ♂, Dartmouth, Vic. and PT-863 ♀, Orroral River, ACT., figured (NMV).

Distribution: N.T.; Qld.; NSW; Vic; Tas.

Habitat: usually associated with sluggishly flowing sections of moderately large permanent streams.

***Triplectides ciuskus seductus*, n. subsp.** (Figs. 19, 20, 63)

Body and wings light to dark brown. Spurs 2, 2, 2. Male genitalia (Fig. 63) as for nominal subspecies except edge of ventral, longitudinal plates of segment X evenly convex in lateral view. Apex of segment X sometimes deeply incised. Female genitalia indistinguishable from those of nominal subspecies.

Despite the clear distinction in at least one character, we are reluctant to assign full species

status to this form in light of the small number of specimens seen and in light of the variability in that character throughout the broad range of the nominal subspecies.

Etymology: *seductus*—(Latin) remote.

Length of anterior wing: ♂ 10.5-11.5 mm; ♀ 11-12.5 mm.

Type material: Holotype ♂, Camp Creek, Mitchell Plateau, NWA., 13 Jul. 1978, P. Suter (NMV, T-7541); paratypes 1 ♂, same loc., 14 Feb. 1979, J. E. Bishop (specimen PT-857 ♂ figured) (NMV); 1 ♂ 1 ♀, Camp Creek at Crusher site, Mitchell Plateau, NWA., 21 Jul. 1978, P. Suter (NMV); 3 ♂ 1 ♀, Carson escarpment, 14°49'S 126°49'E, NWA., 9-15 Aug. 1975, I. F. B. Common and M. S. Upton (ANIC); 2 ♂ 1 ♀, Morgan Falls, 15°02'S 126°40'E, NWA., 16-17 Aug. 1975, I. F. B. Common and M. S. Upton (ANIC); 1 ♂ 2 ♀, Drysdale River, 14°39'S 126°57'E, NWA., 19-21 Aug. 1975, I. F. B. Common and M. S. Upton (ANIC).

Other material examined: **Northern Territory**—1 ♀, King River, 17 Aug. 1960 (no collector) (NMV); 2 ♂, Butterfly Gorge, 27 Jan. 1977, M. S. Moulds (NMV).

Distribution: NW Australia (Kimberley area); NT.

Habitat: small, shallow creeks.

Enthesis Group

The single distinctive species in this group shows some relationship to members of the Australicus Group, as evidenced by a pair of ventral, longitudinal plates on segment X, a harpago with subapical teeth, and an angled phallus. The female resembles species in the Truncatus Group with its somewhat rectangular gonopod plate and short dorsal setose lobes. On the other hand, the unmodified form of segment IX is unlike that of any of the preceding groups and the nearly-straight closing crossvein of the forewing discoidal cell (Fig. 24) is unique in *Triplectides*.

Triplectides entthesis Neboiss

(Figs. 24, 64, 92)

Triplectides entthesis Neboiss, 1982, p. 305, figs. 82-84.

Dark brown body; wings dark brown with small, scattered lighter irrorations, especially basally. Spurs 2, 2, 4.

Superior appendages of male genitalia slender, $\frac{2}{3}$ as long as tergum X. Sclerotic lobes of segment X nearly completely separate, joined by membranes almost to deep apical incision dorsally and to sclerotic bridge above anal opening on underside of segment. Basal portion and baso-ventral lobe of each inferior appendage nearly as long as segment X. Mesal lobes of inferior appendages subtruncate with blunt angles.

Female genitalia (Fig. 92) with dorsal setose lobes short, triangular, each with tiny sensilla-bearing process on inside ventral margin. Lamellae with short setae, nearly rectangular in lateral view. Striae of lamellae and gonopod plate inconspicuous. Spermathecal sclerite rounded anteriorly. Vertical crescentic carina on upper lateral surface of segment IX relatively closer to anterior edge of segment than in other known *Triplectides* species.

Length of anterior wing: ♂ 13.5 mm; ♀ 13-14 mm.

Type material: Holotype ♂, Beedelup Falls, W.A., 13 Nov. 1971, E. F. Riek (ANIC) (holotype figured); paratypes 4 ♀, collected with holotype (ANIC; NMV), specimen PT-878 ♀ figured.

Distribution: SW-Australia.

Habitat: rapidly flowing section of a creek.

Similis Group

In the long, slender superior appendages and apico-dorsal lobes of the male genitalia and the short, oblique dorsal setose lobes and triangular spermathecal sclerite of the female genitalia, the single species in this group resembles those of the Truncatus and Elongatus Groups. However, the 2, 2, 2 spur formula, the angled posterior apex of the male forewing discoidal cell (Fig. 22), and the short, simple mesal lobe of the male inferior appendages make the group distinctive.

Triplectides similis Mosely

(Figs. 21, 22, 65, 66, 93)

Triplectides similis Mosely in Mosely and Kimmins, 1953, p. 210, fig. 141.

Triplectides similis, Neboiss, 1977, p. 129, figs. 697, 698.

Dark brown body with hoary appearance given by whitish setae. Forewings distinctively marked with light and dark brown hairs. Apical

forks of $S_4 + M$ veins in male hindwing unusual for *Triplectides* with MA (or M_2) continuing in straight line from base of M , S_4 (or $S_4 + M_1$) and MP diverging from it at acute angles. Spurs 2, 2, 2. Eye size of males variable; ratio of greatest eye width in dorsal view to narrowest distance between them either 0.50-0.62 or 1.2-1.6. Small-eyed forms generally have shorter forewings. Female eyes normal small size as other *Triplectides* species. Male genitalia (Figs. 65, 66) somewhat variable, yet variations not restricted to particular eye forms. Tergum X tapered or rounded in lateral view with pair of dorsal, longitudinal ridges. Harpago without supabical teeth. Baso-ventral lobe of inferior appendages short or long, extending no more than mesal lobes or to beyond base of harpago. Mesal lobe rounded apically, with variable breadth.

Females (Fig. 93) with short, oblique dorsal setose lobes. Broad lamellae and gonopod plate with conspicuous striations. Distinct carina extending anteriorly from ventral edge of each lamella.

Although the range of this species extends over most of eastern Australia, we have seen no large-eyed forms from Queensland nor small-eyed forms from Tasmania. In Victoria and New South Wales the two forms are often captured in the same light-trap collection. Females from throughout the range of the species are indistinguishable. These data suggest that the distinctive eye forms represent variation at a single, sex-linked gene locus. Breeding experiments and rearing from single egg masses will be needed to corroborate this interesting observation.

Length of anterior wing: ♂ ♀ 14-18 mm.

Type material: Type ♂, Deloraine, Tas., 27 Dec. 1884, MacLachlan Collection (BMNH).

Other material examined: **Queensland**—Carnarvon Range, Conondale Range, Mt Mee; **New South Wales**—Dorrigo, Upper Allyn River, Gloucester River, Singleton, Canberra, Colo, Rosebank, Brown Mtn., Khancoban (dates range through from November to Mid-April); **Victoria**—numerous localities mainly in southern districts, dates ranging from late-October to mid-April (specimen PT-818 ♂, Cowwarr weir, Vic., figured); **Tasmania**—

various localities between late-November till early February (specimen PT-868 ♀, Evandale, Tas., figured); **South Australia**—National Park, Dec.

Distribution: SE-Qld.; E-NSW; Vic.; Tas.; SA.

Habitat: medium size streams with slowly flowing pools.

Niveipennis Group

Although the single species of this group has a sharply angled posterior apex in the forewing discoidal cell and a harpago with subapical teeth like most of the preceding species and a superanal sclerotic bridge and long basal segment of inferior appendage like *T. enthesis*, several peculiar features of the male set this species apart from other known groups. The short, broad superior appendages, the divergent apical lobes of tergum X (Mosely and Kimmins, 1953, fig. 145), the short baso-ventral lobe of the inferior appendages, the very long mesal lobe of the inferior appendages, and especially the unusually broad hindwings, each with 2 additional veins in the anal field (Fig. 23) all complicate attempts for more refined taxonomic placement. Surely the discovery of the female for this species will shed light on its historical relationships.

Triplectides niveipennis Mosely (Figs. 23, 67)

Triplectides niveipennis Mosely in Mosely and Kimmins, 1953, p. 217, fig. 145.

Triplectides niveipennis, Neboiss, 1982, p. 305, figs. 79-81.

Body and forewings light brown with white and light brown hairs interspersed. Hindwings white. Spurs 2, 2, 4. Compound eyes black and thus quite conspicuous, but, contrary to Mosely's (1953) remark, not unusually large (ratio of greatest eye width from above to narrowest distance between them = 0.65). Male genitalia as in Fig. 67. Female unknown.

Length of anterior wing: ♂ 12-14 mm.

Type material: Type ♂, Yanchep, N of Perth, WA., 13-23 Nov. 1935, R. E. Turner (BMNH), paratype ♂ collected with holotype, PT-714 figured (NMV).

Other material examined: **Western Australia**—Yanchep, Margaret River (November) (ANIC, NMV).

Distribution: SW-Australia.

Habitat: lakes and slowly flowing pools in creeks.

Elongatus Group

In this and the following group, the posterior apex of the discoidal cell in the male forewing projects toward the median vein in an evenly curved line. In this group the discoidal cell is connected with the median vein by a short base of vein S_4 , obscured or absent in the *Truncatus* Group. The apex of the male forewing thyridial cell in both species groups narrowed, especially in the *Truncatus* Group, the basal end of the narrowed portion marked by an accessory m-cu crossvein beyond the fork of cubitus vein (fork no. 5). Spurs are 2, 2, 4 in both groups. In males of both groups, the apical membranes and phallosclerite are more nearly enclosed by the sclerotized apex of the phallobase; the synsclerotized segment IX is narrow, broadest dorsally; and a row of 1 or more straight setae arise about mid-length on each ventral edge of segment X. The spermathecal sclerite in females of both groups is more nearly triangular than in the preceding species except *T. similis*. The gonopod plate of the 2 species in this group whose females are known is nearly triangular, with lateral ridges (and the pockets above them) converging toward the posterior apex.

Triplectides prolatus, n. sp.

(Figs. 25, 26, 68)

Body and wings light yellowish brown. Male forewing (Figs. 25, 26) with rounded posterior apex of discoidal cell as in other *Elongatus* Group species, clearly connected with M vein by basal section of S_4 as long as m-cu crossvein. Position of crossvein variable, sometimes more distal than shown.

Male genitalia (Fig. 68) with long, slender superior appendages. Tergum X long, narrow in lateral view, with divergent, acute apices in dorsal view. Inferior appendages long basally; apico-dorsal lobe 1.5X as long as harpago; baso-ventral lobe very long, extending to apex of tergum X; mesal lobe divided into long blunt mesal projection and acute, triangular lateral projection. Harpago with obtuse angle at mid-length on dorsal and ventral edges. Phallus

abruptly curved basally, then nearly straight to rounded apex, deeply incised in ventral view.

This species is probably most closely related to the following two species but can be distinguished from them readily by the much longer baso-ventral lobe and shorter mesal lobe of the inferior appendage, the simpler harpago, and the lack of sharp carinae on the dorsum of tergum X. Female unknown.

Etymology: *prolatus*—(Latin) extended, elongated.

Length of anterior wing: ♂ 10-11 mm.

Type material: Holotype ♂, Davies Creek Road, Mareeba, N-Qld., 21 Feb. 1976, A. Walford-Huggins (NMV, T-7501); paratypes 1 ♂, Crystal Cascades nr. Cairns, 10 June 1971, E. F. Riek (specimen PT-841 ♂ figured) (NMV); 1 ♂, Julatten, N-Qld., 21 Dec. 1975, A. Walford-Huggins (NMV); 1 ♂, Tinaroo Dam, Kairi Creek, N-Qld., 22 June 1971, E. F. Riek (ANIC); 1 ♂, Kuranda, N-Qld., 23 Jan. 1975, N. Quick (NMV); 1 ♂, Kirrama Range via Kennedy, N-Qld., 12 May 1975, Storey and Hancock (QM); 1 ♂, Moses Creek, 4 km N by E of Mt Finnigan, N-Qld., 14-16 Oct. 1980, J. C. Cardale (ANIC); 1 ♂, 14 km W by N Hope Vale Mission, 15°16'S 144°59'E, N-Qld., 8-10 Oct. 1980, J. C. Cardale (ANIC); 2 ♂, Bellenden Ker Range, Cableway Base Stn. 100 m, 17-31 Oct. 1981, Earthwatch survey (QM).

Distribution: N-Qld.

Habitat: small, fast flowing creeks.

Triplectides liratus, n. sp.

(Figs. 27, 28, 69, 94)

Wings and venter of body pale yellowish brown; dorsum of body medium brown; distinctive brown triangular mark at stigma of forewing with darker brown marginal streak beyond it. Male forewing venation (Figs. 27, 28) very similar to that of *T. prolatus* except base of S_4 vein and m-cu crossvein slightly shorter.

Male genitalia (Fig. 69) with slender superior appendages slightly more than half as long as segment X. Segment X long, narrow, acute in lateral view, with pair of prominent, longitudinal dorsal ridges. Basal segment of inferior appendages shorter than in following species, 1.5X as long as harpago; apico-dorsal lobe and

baso-ventral lobe longer, with apico-dorsal lobe 2X as long as harpago and baso-ventral lobe extending beyond base of harpago. Shape of harpago distinctive with 2 small teeth apically and 2 or 3 additional small teeth on short, broadened portion of ventral flange set off by more narrow portion about mid-length. Mesal lobe of each inferior appendage very long triangle with blunt apex extending past base of harpago to tip of baso-ventral lobe; tiny acute projection basally. Lateral view of phallus similar to that of *T. prolatus*; in ventral view apex not as deeply incised, apices of lateral arms of phallotremal sclerite apparently fused with apex of phallobase.

Female genitalia (Fig. 94) with long, slender dorsal setose lobes apparently lacking sensilla-bearing processes. Lamellae nearly rectangular in lateral view.

This species is most closely related to the following one, but the male is easily diagnosed by the more pronounced dorsal lobes of tergum X, the longer apico-dorsal and baso-ventral lobes of the inferior appendages, and especially by the different shapes of the harpago and mesal lobe of each inferior appendage.

Etymology: *liratus*—(Latin) plowed ridge or furrow.

Length of anterior wing: ♂ ♀ 9-10 mm.

Type material: Holotype ♂, Windsor Tableland, NW of Mossman, N-Qld., 27 Dec. 1976, M. S. and B. J. Moulds (NMV, T-7497); paratypes 2 ♀, collected with holotype (specimen PT-874 ♀ figured) (NMV); 3 ♂ 1 ♀, Moses Creek, 4 km N by E of Mt Finnigan, N-Qld., 14-16 Oct. 1980, J. C. Cardale (specimen PT-837 ♂ figured) (ANIC; NMV); 1 ♂, Lock-Davies Creek Road, Lamb Range Mareeba district, N-Qld., 10 Nov. 1974, M. S. Moulds (NMV); 1 ♂, Kuranda N-Qld., 13 Mar. 1956, J. L. Gressitt (BPBM); 1 ♂, Upper Mulgrave River via Gordonvale, N-Qld., 29-30 Apr. 1970, S. R. Curtis (ANIC); 4 ♂, Bellenden Ker Range, Cableway Base Stn. 100 m, 17-24 Oct. 1981, Earthwatch Survey (NMV; QM).

Other material examined: **North Queensland**—1 ♀, 3 km NE of Mt Webb, 2 Oct. 1980, D. H. Colless (ANIC); 1 ♀, Lacey's Creek, Mission Beach, 14 May 1980, I. D. Naumann and

J. C. Cardale (ANIC); 1 ♀, Kairi Creek, Tinaroo Dam, Atherton Tableland, 24 Apr. 1970, S. R. Curtis (ANIC).

Distribution: N-Qld.

Habitat: small to medium size fast flowing creeks.

***Tripletides liratellus*, n. sp.**

(Figs. 29, 30, 70)

Colour of body and wings as in *T. liratus* except 2 additional darker brown triangular markings equally spaced near anterior edge of forewing basad of stigmal triangle. Male forewing venation (Figs. 29, 30) very similar to that of *T. liratus* except that basal section of S_4 vein and m-cu crossvein even shorter; accessory m-cu crossvein weak posteriorly.

Male genitalia (Fig. 70) similar to those of *T. liratus* except dorsal ridges of tergum X not as pronounced, basal segment of inferior appendages 1.8X as long as harpago, apico-dorsal lobe of inferior appendage only 1.6X as long as harpago, baso-ventral lobe of inferior appendage more slender and not extending to base of harpago. Harpago with 2 prominent apical teeth; subapical region narrow, strongly curved mesad; basal $\frac{2}{3}$ of ventral flange uniformly broad. Mesal lobe of each inferior appendage similar to that of *T. liratus* except baso-lateral projection broad, half as long as mesal projection. Phallus essentially as for *T. liratus*. Female unknown.

Etymology: *liratellus*—(Latin) little plowed ridge or furrow.

Length of anterior wing: ♂ 9-9.5 mm.

Type material: Holotype ♂, Shiptons Flat, 15°47'S 145°14'E, N-Qld., 17-19 Oct. 1980, J. C. Cardale (ANIC); paratype 1 ♂, The Boulders, W of Babinda, N-Qld., 29 June 1971, E. F. Riek (specimen PT-839 ♂ figured) (NMV).

Distribution: N-Qld.

Habitat: moderately fast flowing shallow creeks with deep pools.

***Tripletides varius* Kimmins**

(Figs. 31, 32, 71)

Tripletides varius Kimmins, 1953, in Mosely and Kimmins, 1953, pp. 221-223, figs. 145, 149.

Body and forewings dark brown with white and brown hairs. Hindwings paler. Male fore-

wing venation (Figs. 31, 32) with apex of thyridial cell very narrow, accessory m-cu crossvein shorter than more distal m-cu crossvein. Base of S_4 vein between discoidal cell and thyridial cell weak.

Male genitalia with slender superior appendages half as long as segment X. Segment X long, narrow, sinuate in lateral view, with out-turned ventral flanges and tiny midline excision apically (Mosely and Kimmins, 1953, fig. 149). Basal portion of inferior appendage 1.5X as long as harpago; apico-dorsal lobe 2.25-3.0X as long as harpago; baso-ventral lobe extending nearly to, or beyond, apex of harpago (Fig. 71). Harpago without accessory teeth, nearly straight to curved tip, narrow in ventral view. Mesal lobe of inferior appendage truncate with blunt mesal and lateral corners; lateral corner darker with minute reticulation. Phallus short, broadened and rounded apically in ventral view. Female unknown.

Length of anterior wing: ♂ 15-16 mm.

Type material: Type ♂, Mt Kosciusko, 5000 ft., NSW, 6 Dec. 1921 (BMNH).

Other material examined: **New South Wales**—4 ♂, Mt Kosciusko, 5500 ft., 17 Feb. 1968, M. S. Upton (specimen PT-846 ♂ figured) (ANIC; NMV); **Victoria**—1 ♂, Upper Macalister River above Howitt Plains, 25 Feb. 1979, A. A. Calder (NMV).

Distribution: SE-NSW; Vic.

Habitat: mountain creeks.

***Triplectides dolabratus*, n. sp.**

(Figs. 33, 34, 72)

Colour uniformly light to moderate brown. Male forewing venation (Figs. 33, 34) as in *T. varius* except veins of thyridial cell fused for short distance at usual position of accessory m-cu crossvein. Base of S_4 vein and m-cu crossvein distinct but very short.

Male genitalia (Fig. 72) with slender superior appendages half as long as segment X. Segment X long, narrow, apically rounded in lateral view, apex slightly concave, but not incised, in dorsal view. Inferior appendages similar to those of *T. varius* except baso-ventral lobe extends only to mid-length of harpago; mesal lobe with prominent, acute mesal projection, convex reticulate apical region, and blunt or acute

lateral corner. Phallus very long, rounded apically in lateral view, with slightly broadened apex. Female unknown.

This species appears most closely related to *T. varius* but can be distinguished by the different shape of the mesal lobe of the inferior appendage.

Etymology: *dolabratus*—(Latin) shaped like an axe.

Length of anterior wing: ♂ 11.5-13 mm.

Type material: Holotype ♂, Kirrama State Forest, 24 km WNW of Kennedy, N-Qld., 28 Jan. 1981, M. S. and B. J. Moulds (NMV, T-7505); paratypes 1 ♂, 1 km N of Tully Falls, N-Qld., 8 Jan. 1976, A. Walford-Huggins (specimen PT-843 figured) (NMV); 1 ♂, 25 km along Mt Lewis Road SW of Mossman, N-Qld., 16 Jan. 1977, M. S. and B. J. Moulds (NMV); 2 ♂, Bellenden Ker Range, Cableway Base Stn, 100 m, 17-31 Oct. 1981, Earthwatch survey (QM); 2 ♂, Mt Bartle Frere, ½ km N of South Peak, 1500 m, 6-8 Nov. 1981, Earthwatch survey (QM).

Distribution: N-Qld.

Habitat: small, fast flowing creeks.

***Triplectides elongatus* Banks**

(Figs. 35, 36, 73, 95)

Triplectides elongatus Banks, 1939, p. 486, pl. 4, fig. 39.
Triplectides dubius Mosely, in Mosely and Kimmins, 1953, p. 219, fig. 147.

Triplectides dubius var. *subalbidus* Kimmins, in Mosely and Kimmins, 1953, p. 219 (new synonym).

Triplectides elongatus, Neboiss, 1977, pp. 131-132, figs. 709-711.

Colour uniformly dark brown except sides of abdomen pale. Male forewing venation (Figs. 35, 36) without accessory m-cu crossvein and virtually without basal section of S_4 vein; discoidal cell and thyridial cell gradually convergent, nearly touching.

Although Neboiss (1977) synonymized *T. dubius* Mosely with *T. elongatus*, the subspecies *T. dubius subalbidus* Kimmins technically was still recognized. As it occurs within the range of *T. elongatus*, its genitalia and vestiture does not deviate noticeably from the typical form, it is here reduced to a synonym.

Male genitalia with superior appendages slender and half as long as segment X which is

rounded and deeply, but narrowly, incised apically in dorsal or ventral view (Mosely and Kimmins, 1953, Fig. 147; Neboiss, 1977, Fig. 711). Inferior appendages similar to those of *T. varius* except apico-dorsal lobe more than 3X as long as harpago (Fig. 73). Mesal lobe triangular, without lateral corner, or tiny lateral corner evident in some specimens. Phallus of moderate length, slightly broadened subapically in ventral view.

Female genitalia (Fig. 95) with short, rounded, dorsal setose lobe about as long as sensilla-bearing process or only slightly longer. Lamella in lateral view obliquely truncate or concave. Transverse striations of gonopod plate confined to small apical region.

Length of anterior wing: ♂ 12-15 mm; ♀ 14-16 mm.

Type material: Type ♂, Blackheath, Blue Mts. 3000 ft., NSW, 21 Jan. (1932) Darlington, Harvard Expedition, MCZ type no. 22079 now in ANIC.

Type ♂ of *Triplectides dubius* Mosely, Cradle Mts. Tas., 18 Jan. 1917, R. J. Tillyard (BMNH).

Type ♂ of *Triplectides dubius subalbidus* Kimmins, Hampton, NSW, Jan. 1918 (BMNH).

Other material examined: **New South Wales**—Styx River nr. Ebor, Barrington Tops (specimen PT-853 ♂ figured), Kyeamba, Kananora—Boyd National Park, Mt Kosciusko National Park, Kiandra (specimen PT-871 ♀ figured) (dates between mid-October to mid-January); **Victoria**—Mt Buffalo, Cobungra, Dartmouth, Mt Buller area (dates between mid-October to late-February); **Tasmania**—Cradle Mtn, Wilmot, Great Lake, Andover, Olga River (dates from early December to early-February). Specimens from the collection of ANIC; AM; NMV.

Distribution: E-NSW; NE-Vic; Tas.

Habitat: small to medium size creeks in high country, or fast flowing streams at lower altitude.

Truncatus Group

This group is quite similar to the preceding one. However, the male forewing in these species is more highly modified: the posterior

apical portion of the discoidal cell with its vein swollen and closely parallel to the apex of the thyridial cell; the basal section of S₄ vein is usually indiscernible; the apex of the thyridial cell is very narrow or at least the anterior and posterior veins are close together; the accessory m-cu crossvein often is not evident; there are rows or patches of long, stiff bristles on veins and/or membranes behind the modified apex of the thyridial cell; and in most species the apical thyridial cell membrane forms a small fold above the median vein, sometimes with a pile of many short setae in the resulting pocket.

The male genitalic lobes are all typically long and slender in this group (*T. rossi* an exception) and the harpago is simple, without subapical teeth. The female dorsal setose lobe is broad in lateral view, usually with a small sensilla-bearing process. The gonopod plate is more or less rectangular, the apical ridges (and the pockets above them) transverse.

Triplectides truncatus Neboiss (Figs. 37, 38, 39, 74, 75, 96)

Triplectides truncatus Neboiss, 1977, pp. 129-130, Figs. 699-702.

Body and wings dark brown. Male forewing with swollen posterior apical portion of discoidal cell parallel with narrowed thyridial cell apex; pile-bearing membranous fold of thyridial cell apex overlapping median vein; bristles along Cu₁ vein at thyridial cell apex; base of S₄ vein and accessory m-cu crossvein apparently absent.

Male genitalia (Figs. 74, 75) with superior appendages half as long as segment X, somewhat paddle-shaped in dorsal view. Mesal lobe of each inferior appendage slightly concave apically, corner acute. Some variation from more common form (Fig. 74) noted in this lobe such that mesal process broader and more rounded (Fig. 75b). Phallus gently curved over entire length.

Female genitalia (Fig. 96) generally resembling those of other known species in this group except lamellae nearly triangular in lateral view.

Length of anterior wing: ♂ 10-12 mm; ♀ 11.5-13.5 mm.

Type material: Holotype ♂, Bluff Hill Creek 12 km S of Marrawah, Tas., 30 Nov. 1974, A. Neboiss (NMV); paratypes collected with holotype (specimens PT-495 ♂ and PT-496 ♀ figured).

Other material examined: **Victoria**—Grampians, Warrnambool, Latrobe River, Wilsons Promontory, Meeniyan, Lake Mountain, Kinglake West, Toolangi, Myrtleford, Merrigig, Gibbo River, Mitta Mitta River, dates ranging between end of October and early April; **Tasmania**—all localities situated on the western half of the state—dates between November and February (figured variety—specimen PT-851 ♂ from Olga River, SW-Tas.).

Distribution: Vic.; Tas.

Habitat: fast flowing creeks and rivers.

***Triplectides tambina* Mosely**
(Figs. 40-43, 76, 77, 98)

Triplectides tambina Mosely in Mosely and Kimmins, 1953, pp. 217-219, fig. 146.

Body and wings reddish fuscous with brown hairs. Male forewing venation (Figs. 40-43) similar to that of *T. truncatus*, but discoidal cell shorter, broader subapically, more closely parallel to thyridial cell along modified portion. Few bristles present along Cu_1 vein at modified portion. Base of S_4 vein and accessory m-cu crossvein evident (Fig. 43) or not (Fig. 41).

Male genitalia (Figs. 76, 77) with patch of setae sometimes present on lateral portion of segment IX. Superior appendages slender, little more than half as long as segment X. Tergum X rounded apically and with (Mosely and Kimmins, 1953, Fig. 146) or without (Fig. 77d) apical incision in dorsal view. Apico-dorsal lobe of inferior appendages only 2.5X as long as harpago. Baso-ventral lobe extending beyond apex of harpago. Mesal lobe of inferior appendage narrow, short, truncate and acute (Fig. 76b) or hooked (Fig. 77b) laterally.

Female genitalia (Fig. 98) with sensilla-bearing projections each on a distinct rounded portion below its short, straight dorsal setose lobe. Lamellae rather rectangular in lateral view.

Length of anterior wing: ♂ 11-12 mm; ♀ 12-17 mm.

Type material: Type ♂, Tambourine Mts., Qld., 11-18 Apr. 1935. R. E. Turner (BMNH).

Other material examined: **SE-Queensland**—1 ♂, Cunningham Gap, 21 Sept. 1955, J. Kerr (specimen PT-824 ♂ figured) (NMV); 1 ♂ 3 ♀, Maleny, rainforest, 6 Apr. 1967, N. Dobrotworsky (NMV); 5 ♀, Kenilworth, 7 Apr. 1967, N. Dobrotworsky (NMV); 2 ♂, Bunya Mts., 9 Apr. 1966, I. Burgess (QU) 4 ♂ 1 ♀, same loc., 15 Oct. 1973, A. Neboiss (specimen PT-877 ♀ figured) (NMV); 2 ♂, Saddletree Creek via Maidenwell, 29 Mar. 1975, S. R. Monteith, (specimen PT-845 ♂ figured) (ANIC); **New South Wales**—2 ♀, Wiangaree State Forest via Kyogle, 18 Nov. 1974, S. R. Monteith (ANIC); 1 ♂ 4 ♀, Kangaroo Valley, 22 Mar. 1961, E. F. Riek (ANIC).

Distribution: SE-Qld.; E-NSW.

Habitat: moderately fast flowing creeks.

***Triplectides gonetalus*, n. sp.**
(Figs. 44, 45, 78, 97)

Body and wings generally rufous with brown hairs. Apices of tarsi on forelegs and midlegs and their tarsal segments conspicuously dark brown. Forewings with dark streak along S vein from near wing base to stigma. Patches of light hairs causing irrorate appearance. Male forewing venation (Figs. 44, 45) with very short base of S_4 vein just visible between discoidal and thyridial cells. Accessory m-cu crossvein and fold of apical thyridial cell membrane apparently absent. Stiff bristles along bases of both branches of Cu vein, along apex of P vein and cell behind it just before arculus.

Male genitalia (Fig. 78) resembling those of other species in this group. Apico-dorsal lobe of inferior appendage 3.5X as long as harpago. Baso-ventral lobe extending to middle of harpago. Mesal lobe sometimes visible in lateral view; long, broad, slightly widened apically; apex obliquely subtruncate, slightly convex. Phallus long, straight beyond basal turn.

Female genitalia (Fig. 97) similar to those of *T. tambina*. Dorsal setose lobe short, blunt, its sensilla-bearing process long, situated directly on ridge below lobe. Lamella vaguely trapezoidal in lateral view.

The large size and distinctive colour pattern of this species help make it readily identifiable. The mesal lobe of the inferior appendages resembles those of *T. insperatus* and *T.*

altenogus, but their differing forms are consistent.

Etymology: *gonetalus*—anagram of *elongatus*, after the enjoyable tradition of M. E. Mosely for coining new scientific names.

Length of anterior wing: ♂ 16.5-17.5 mm ♀ 17-18 mm.

Type material: Holotype ♂, Zarda Creek nr. Mt Misery, W of Mossman, 350 m, N-Qld., 23 Dec. 1974, M. S. Moulds (NMV, T-7483); paratypes 2 ♂ 3 ♀, collected with holotype (specimen PT-873 ♀ figured) (NMV); 2 ♂ 1 ♀, 3 km N by E Mt Tiptree (17°02'S 145°37'E), N-Qld., 20 Oct. 1980, J. C. Cardale (specimen PT-836 ♂ figured) (ANIC; NMV); 4 ♂, The Crater nr. Herberton, N-Qld., 18 Dec. 1974, M. S. Moulds (NMV); 2 ♂ 1 ♀, Mt Fisher 8 km SW of Millaa Millaa, N-Qld., 21 Nov. 1979, M. S. and B. J. Moulds (NMV); 4 ♂ 1 ♀, Birthday Creek, 6 km NW by W Paluma, N-Qld., 25 Sept. 1980, J. C. Cardale (ANIC); 2 ♂, Mt Spurgeon, NW of Mossman (near summit, N-Qld., 28 Dec. 1976, M. S. Moulds (NMV); 3 ♂, 25 km along Mt Lewis Road, SW of Mossman, N-Qld., 16 Jan. 1977, M. S. and B. J. Moulds (NMV).

Other material examined: **North Queensland**—1 ♂, Windsor Tableland, NW of Mossman, 6 Jan. 1981, M. S. Moulds (NMV); 1 ♂, Tully Falls, 11 Jan. 1977, M. S. Moulds (NMV); 5 ♂, 1 km N of Tully Falls, 8 Jan. 1976, A. Walford-Huggins (NMV); 1 ♂, Lock-Davis, Ck. road, Lamb Range, Mareeba distr., 10 Nov. 1974, M. S. Moulds (NMV); 2 ♂ 1 ♀, same loc., 25 Dec. 1976, M. S. and B. J. Moulds (NMV); 2 ♂ 2 ♀, Kirama Range via Kennedy, 12 May 1975, Storey and Hancock (NMV). 1 ♂ 1 ♀, Bellenden Ker Range, Summit TV Stn. 1560 m, 1-7 Nov. 1981, Earthwatch survey (QM).

Distribution: N-Qld.

Habitat: moderately fast flowing creeks with calm water pools.

***Triplectides insperatus*, n. sp.**

(Figs. 46, 47, 79)

Body pale yellow. Wings whitish, translucent. Male forewing venation (Figs. 46, 47) with discoidal and thyridial cell veins very closely parallel in modified region. Base of S₄ vein and

accessory m-cu crossvein both absent. Thyridial cell membrane folded over median vein. Nygma elongate. Stiff bristles basally on branches of Cu vein and on veins, and membranes just basad of arculus.

Male genitalia (Fig. 79) with slender superior appendages. Tergum X with pair of low, dorsal carinae; deeply incised apically in dorsal view, but incision joined by thin strip distally in holotype. Base of inferior appendage longer than in *T. gonetalus*, 1.5X as long as harpago; apico-dorsal lobe 2.5X as long as hapago; baso-ventral lobe extending to middle of harpago. Mesal lobe of inferior appendage shorter and straighter than in *T. gonetalus*; apex obliquely truncate with blunt lateral corner. Phallus moderately long, straight beyond base. Female unknown.

This species closely resembles *T. gonetalus*, but is most distinctive in its smaller size, much lighter colour and shorter apico-dorsal and mesal lobes of the inferior appendage.

Etymology: *insperatus*—(Latin) surprise.

Length of anterior wing: ♂ 10 mm.

Type material: Holotype ♂, Cooloola area, open forest, Qld., 28 Aug. 1979, 'K.L.' (NMV, T-7500) (Holotype figured).

Distribution: SE-Qld.

Habitat: slowly flowing coastal creek.

***Triplectides hamatus*, n. sp.**

(Figs. 50, 51, 80)

Body and wings uniformly moderate to dark brown. Male forewing venation (Figs. 50, 51) similar to that of *T. insperatus* except that nygma oblong, accessory m-cu crossvein present but indistinct, and stiff bristles absent.

Male genitalia (Fig. 80) with rounded apex of tergum X narrowly, but deeply incised. Apico-dorsal lobe of inferior appendage 3X as long as harpago; baso-ventral lobe extending to tip of harpago. Mesal lobe of inferior appendage sometimes visible in lateral view; long, divided into 2 equally long processes apically, mesal one rounded, lateral one hooked. Phallus abruptly widened subapically in ventral view, obtusely angled beyond the base in lateral view. Female unknown.

The distinctive mesal lobe of the inferior appendage and the broadened apex of the phallus

of this species are most useful for distinguishing it from others in this group.

Etymology: *hamatus*—(Latin) hooked.

Length of anterior wing: ♂ 12 mm.

Type material: Holotype ♂, Upper Manning River, 20 km NNW of Rawdon Vale, NSW, 31°52'S 151°34'E, 19 Feb. 1980, A. A. Calder (NMV, T-7509) (holotype figured); paratype 1 ♂, Styx River, 12 km S of Ebor, NSW, 17 Oct. 1973, A. Neboiss (NMV).

Distribution: E-NSW.

Habitat: mountain streams.

Triplectides altenogus, n. sp.

(Figs. 48, 49, 81, 99)

Colour of body and wings similar to that of *T. gonetalus*, but paler brown. Male forewing venation (Figs. 48, 49) with modified veins at apex of discal and thyridial cells very closely parallel, together slightly convex anteriorly. Base of S₄ vein and accessory m-cu crossvein apparently absent. Folded thyridial cell membrane with dense pile. Nygma round. Stiff bristles on veins and membrane just basad on arculus.

Male genitalia with slender superior appendages $\frac{3}{4}$ as long as segment X. Segment X slightly incised apically in dorsal view. Apico-dorsal lobe of inferior appendage 3X as long as harpago; baso-ventral lobe reaching just beyond base of harpago. Mesal lobe of inferior appendage long, curved laterally, convex apically; lateral half of apex dark with minute reticulation; dorsal surface with high ridge, phallus moderately long, nearly straight beyond slight basal curve, slightly widened apically in ventral view.

Female genitalia (Fig. 99) with straight, blunt dorsal setose lobes each shorter than its sensilla-bearing process. Lamella subrectangular, rounded apically in lateral view. Spermathecal sclerite apparently highly deformed in only known female specimen.

The mesal lobe of the inferior appendage in this species resembles that of *T. gonetalus*, but its shape is clearly and consistently different.

Etymology: *altenogus*—anagram of *elongatus*.

Length of anterior wing: ♂ 15.5-16 mm; ♀ 15.5-16.5 mm.

Type material: Holotype ♂, Peter's Creek, (26°41'S 152°36'E) Conondale Range via Bellthorpe, Qld., 29 Nov. 1974, S. R. Monteith (ANIC); paratypes 5 ♂ (specimen PT-835 ♂ figured), collected with holotype (ANIC; NMV); 1 ♂, Mt Mee, Qld., 9 Jan. 1971, S. R. Monteith (ANIC); 1 ♂ 1 ♀, Saddletree Creek via Maidenwell, Qld., 29 Mar. 1975, S. R. Monteith (specimen PT-872 ♀ figured) (ANIC); 2 ♂, Flaggy Creek, Mistake Mtn. via Laidley, Qld., 11 Feb. 1973, S. R. Monteith (ANIC).

Other material examined: **New South Wales**—2 ♂, Kangaroo Valley, 22 Mar. 1961, E. F. Riek (ANIC); 1 ♂, Tenterfield, 20 Feb. 1975, (collector unknown) (NMV); **Victoria**—1 ♂, Back Creek above Cann River junction, 9 Feb. 1980, A. Wells (NMV).

Distribution: SE-Qld.; E-NSW; E-Vic.

Habitat: small, fast flowing creeks.

Triplectides rossi, n. sp.

(Figs. 52, 53, 82, 100)

Body and wings pale brown, stigma darker. Male forewing venation (Figs. 52, 53) most highly modified of *Truncatus* Group. Base of S₄ vein apparently absent; accessory m-cu vein indistinct. Pile-laden membranous fold broad, touching discoidal cell vein. Stiff bristles possibly along several veins in middle of wing, but apparently rubbed off specimen illustrated.

Male genitalia (Fig. 82) with short, somewhat spatulate superior appendages. Segment X short, truncate in both dorsal and lateral views. Apico-dorsal lobe of inferior appendage only 2.25X as long as harpago; baso-ventral lobe just reaching base of harpago. Mesal lobe of inferior appendage broad basally, tapering to 2 distally pointing rounded projections. Phallus gradually widening to apex in both lateral and ventral views.

Female genitalia (Fig. 100) with very short dorsal setose lobe apparently without sensilla-bearing projection. Lamella with ventral edge semicircular, margined.

The shorter genital appendages in the 2 sexes and the distinctive male forewing venation and mesal lobe of each inferior appendage clearly distinguish this species from other members of the *Truncatus* Group.

Etymology: *rossi*—for the late Prof. Herbert H. Ross whose interest in the Australian cad-disflies and their transantarctic relationships provided the initial impetus to undertake this study.

Length of anterior wing: ♂ 10-12 mm; ♀ 12-13.5 mm.

Type material: Holotype ♂, Mt Fisher, 8 km SW of Millaa Millaa, N-Qld., 21 Nov. 1979, M. S. and B. J. Moulds (NMV, T-7491); paratypes 2 ♀, collected with holotype (specimen PT-875 ♀ figured) (NMV); 2 ♂, Kirrama State Forest, (Western fall), N-Qld., 30 May 1971, E. F. Riek (specimen PT-838 ♂ figured) (ANIC; NMV); 1 ♂, Moses Creek, 4 km N by E of Mt Finnigan, N-Qld., 14-16 Oct. 1980, J. C. Cardale (ANIC); 1 ♂, Lock-Davies Creek Road, Lamb Range, Mareeba district, N-Qld., 10 Nov. 1974, M. S. Moulds (NMV); 1 ♂, same loc., 25 Dec. 1976, M. S. and B. J. Moulds (NMV); 1 ♀, Kirrama State Forest, 24 km WNW of Kennedy, N-Qld., 28 Jan. 1981, M. S. and B. J. Moulds (NMV); 1 ♂, Bellenden Ker Range, ½ km S Cable Tower No 7, 500 m, 25-31 Oct. 1981, Earthwatch survey (QM); 2 ♂, Bellenden Ker Range, Summit TV Stn. 1560 m, 1-7 Nov. 1981, Earthwatch survey (QM; NMV).

Distribution: N-Qld.

Habitat: small, fast flowing creeks.

KEY TO MALES OF AUSTRALIAN
TRIPLECTIDES SPECIES

1. Spurs 2, 2, 2 2
- Spurs 2, 2, 4 (at least on one side) 9
2. Segment X with only rounded latero-ventral margins *Australis* Group, 2
- Segment X with pair of longitudinal dorsal or ventral carinae 7
3. Apex of phallus tapered in ventral view 4
- Apex of phallus parallel-sided or gradually widening in ventral view 5
4. Harpago with subapical tooth on dorsal and ventral edges; mesal lobe of inferior appendage broad (Fig. 54b); Australia except Tasmania *australis* Navás
- Harpago without subapical teeth; mesal lobe of inferior appendage narrow (Fig. 55b); transcontinental northern Australia *helvolus*, n. sp.
5. Large dark species, forewing 15-18 mm long; mesal lobe of inferior appendage very broad, blunt lateral corner clearly projecting beyond rest of lobe (Fig. 56b); S-Tas., S-Vic. *magnus* (Walker)
- Smaller, pale grey to pale brown, forewing 10-13 mm long; apex of mesal lobe of inferior appendage rounded or truncate (Fig. 58b) or concave (Fig. 57b) with acute lateral corner 6
6. Apex of mesal lobe of inferior appendage concave (Figs. 57b', 57) or sinuous (Fig. 57g), lateral corner usually small; hindwing S₁ vein usually present; Qld., northern NT *parvus* (Banks)
- Apex of mesal lobe of inferior appendage rounded or truncate, lateral corner prominent (Fig. 58b); hindwing S₁ vein usually reduced or absent; Qld., NSW, Vic. *volda* Mosely
7. Segment X with pair of ventral carinae (Figs. 62a 63a); apex of mesal lobe of inferior appendage subtruncate with prominent lateral corner (Fig. 62b); wings uniformly brown; eyes always small 8
- Segment X with pair of dorsal carinae (Figs. 65a, 66a); mesal lobe of inferior appendage triangular with blunt apex (Figs. 65b, 66b) wings patterned with light and dark brown; eyes often large; SE Qld. to SA, Tas *similis* Mosely
8. Ventral carinae of segment X sinuate, angled or projecting in lateral view (Fig. 62a); Australia except W.A. *ciuskus ciuskus* Mosely
- Ventral carinae of segment X evenly convex (Fig. 63a); NW Australia, NT *ciuskus seductus*, n. subsp.
9. Harpago serrate on ventral edge subapically (Figs. 59b, 60b) Proximus Group 10
- Harpago with single tooth (Fig. 61b) or with abruptly broad region (Fig. 89b) subapically 11

- 10. Mesal lobe of inferior appendage with mesal projection much narrower than lateral projection (Fig. 59b); baso-ventral lobe short, out-turned; W. Tas. *bilobus* Neboiss
 - Mesal lobe of inferior appendage with mesal projection broader than lateral projection (Fig. 60b); baso-ventral lobe long, straight; N. Tas., E. Vic., SE NSW *proximus* Neboiss
- 11. Segment X with longitudinal pair of sinuate ventral carinae (Figs. 61a, 64a; mesal lobe of inferior appendage truncate (Figs. 61b', 64b) 12
 - Segment X without pair of ventral carinae 13
- 12. Superior appendages broad basally in dorsal view (Fig. 61d), acute apex as long as base and baso-ventral lobe of inferior appendage; Qld., NSW, Vic., N WA *australicus* Banks
 - Superior appendages slender, shorter than base and baso-ventral process of inferior appendage (Fig. 64a), SW Australia *enthesis* Neboiss
- 13. Baso-ventral lobe of inferior appendage extending only half the distance to the base of the harpago (Fig. 67b); superior appendages short, broad (Fig. 67a); SW Australia *niveipennis* Mosely
 - Baso-ventral lobe of inferior appendage extending at least most of the distance to the base of the harpago (Fig. 70b); superior appendages slender at least basally (Fig. 82d) 14
- 14. Posterior apical portion of discoidal cell with vein of uniform thickness and pigmentation (Fig. 26); basal section of S₄ vein between discoidal and thyridial cells present, though short; apical thyridial cell membrane not folded over M vein .. *Elongatus* Group, 15
 - Posterior apical portion of discoidal cell with vein swollen, darker or less translucent (Fig. 38); basal section of S₄ vein usually absent; apical thyridial cell membrane usually folded over M-vein *Truncatus* Group, 20
- 15. Ventral edge of harpago conspicuously broadened in middle (Figs. 68b, 69b, 70b) 16
 - Ventral edge of harpago straight or slightly curved (Fig. 71b) 18
- 16. Harpago without apical teeth (Fig. 68b); baso-ventral process of inferior appendage long, extending to middle of harpago; mesal lobe of inferior appendage with large lateral process triangular, acute apically; tergum X without sharp longitudinal carinae (Figs. 68a, 68d); N Qld. ... *prolatus*, n. sp.
 - Harpago with 2 apical teeth (Figs. 69b, 70b); baso-ventral process of inferior appendage at most reaching base of harpago; mesal lobe of inferior appendage with lateral process tiny (Fig. 69b) or blunt (Fig. 70b); tergum X with longitudinal carinae 17
- 17. Mesal lobe of inferior appendage with tiny baso-lateral process (Fig. 69b); ventral edge of harpago narrowed below broad middle; N Qld. *liratus*, n. sp.
 - Mesal lobe of inferior appendage with large, blunt baso-lateral process (Fig. 70b); ventral edge of harpago uniformly broad along basal 2/3; N Qld. *liratellus*, n. sp.
- 18. Mesal lobe of inferior appendage truncate (Fig. 71b); harpago slightly sinuous; SE NSW, Vic. ... *varius* Kimmins
 - Mesal lobe of inferior appendage triangular (Fig. 73b) or with conspicuous mesal and lateral projections (Fig. 72b); harpago gradually and evenly curved to apex 19
- 19. Mesal lobe of inferior appendage with conspicuous mesal and lateral projections (Fig. 72b); N Qld. *dolabratus*, n. sp.
 - Mesal lobe of inferior appendage triangular (Fig. 73b); E NSW NE Vic., Tas. *elongatus* Banks
- 20. Mesal lobe of inferior appendage with mesal portion of apex as large as, or larger than, lateral projection (Figs. 74b, 75b, 80b, 82b) 21

- Mesal lobe with mesal portion small (Figs. 77b, 81b) or not evident in ventral view (Figs. 76b, 78b, 79b) 23
- 21. Apex of mesal lobe subtruncate, slightly concave, without a clearly differentiated mesal projection in ventral view (Figs. 74b, 75b); Vic., Tas. *truncatus* Neboiss
 - Apex of mesal lobe clearly differentiated from lateral projection by deep excision (Figs. 80b, 82b) 22
 - 22. Lateral projection of mesal process of inferior appendage hooked laterally (Fig. 80b); baso-ventral process of inferior appendage extending to tip of harpago; E NSW *hamatus*, n. sp.
 - Lateral projection of mesal process of inferior appendage bluntly pointed posteriorly (Fig. 82b); baso-ventral process of inferior appendage just reaching base of harpago; N Qld *rossi*, n. sp.
 - 23. Mesal lobe of inferior appendage small, apically truncate (Figs. 76b, 77b); baso-ventral lobe extending beyond tip of harpago; SE Qld, E NSW *tambina* Mosely
 - Mesal lobe of inferior appendage nearly as broad as base of inferior appendage, mesal corner much more distal than lateral corner (Figs. 78b, 79b, 81b); baso-ventral lobe of inferior appendage reaching only to middle of harpago 24
 - 24. Large brown species, forewing more than 15 mm long; Mesal lobe of inferior appendage at least as long as its obliquely convex apex (Figs. 78b, 81b) 25
 - Smaller, pale yellow species, forewing 10 mm long; mesal lobe of inferior appendage with outer lateral margin shorter than obliquely straight apex (Fig. 79b); SE Qld. *insperatus*, n. sp.
 - 25. Forewing 17.5 mm; mesal lobe of inferior appendage with only small apico-lateral corner dark, rugous (Fig. 78b); N Qld. *gonetalus*, n. sp.
- Forewing 15.5 mm; mesal lobe of inferior appendage with lateral half of apex dark, rugous (Fig. 81b); SE Qld., E NSW, E Vic. *altenogus*, n. sp.

KEY TO FEMALES OF AUSTRALIAN
TRIPLECTIDES SPECIES

- (Females of *T. niveipennis*; Elongatus Group—*T. prolatus*, *T. liratellus*, *T. varius* and *T. dolabratus*; and Truncatus Group—*T. insperatus* and *T. hamatus* are unknown.)
1. Spurs 2, 2, 2 2
 - Spurs 2, 2, 4 (at least on one side) 8
 2. Dorsal setose lobe longer than weakly sclerotized lamella (Fig. 83a), sensilla-bearing process often forming sclerotized plate below dorsal setose lobe (Fig. 86b); viviparous Australis Group, 3
 - Dorsal setose lobe shorter than strongly sclerotized lamella (Fig. 90a); sensilla-bearing process a small, slender projection; oviparous 7
 3. Sensilla-bearing process slender, acute, semimembraneous, longer than dorsal setose lobe (Figs. 83a, 83b); Australia except Tas. *australis* Navás
 - Sensilla-bearing process broader, blunt, truncate, or plate-like, well sclerotized, shorter than dorsal setose lobe (Figs. 84-87) 4
 4. Sensilla-bearing process truncate, with short apical setae (Fig. 84); transcontinental northern Australia *helvolus*, n. sp.
 - Sensilla-bearing process blunt (Fig. 85b) or plate-like (Figs. 86b, 87b) 5
 5. Large, dark species, forewing 17-18 mm long; sensilla-bearing process triangular, with blunt apex (Fig. 85b); S Tas., S Vic. *magnus* (Walker)
 - Small, pale species, forewing 10-13 mm long; sensilla-bearing process plate-like (Figs. 86b, 87b) 6
 6. Sensilla-bearing plate more or less rectangular in ventral view (Fig. 86b); lateral portion of segment IX with 2 well-marked carinae (Fig.

- 86a); hindwing S₁ vein usually present; Qld., northern NT . . . *parvus* (Banks)
- Sensilla-bearing plate more or less triangular, often with small projection near mesal base (Fig. 87b); lateral portion of segment IX with caudal carina weak or absent (Fig. 87a) hindwing S₁ vein usually absent; Qld., NSW, Vic. *volda* Mosely
7. Dorsal setose lobe with upper margin convex in lateral view (Fig. 91a); lamella without setae; wings uniformly brown; Australia except SW Australia *ciuskus* Mosely
- Dorsal setose lobe with upper margin straight in lateral view (Fig. 93a); lamella setose; forewings patterned with light and dark brown hairs; SE Qld. to SA, Tas. *similis* Mosely
8. Sensilla-bearing process absent (Figs. 88a, 89a, 94a, 100a) 9
- Sensilla-bearing process present (e.g. Fig. 90a) 12
9. Dorsal setose lobe very short; lamella with ventral edge semicircular and margined (Fig. 100a); N Qld. . . *rossi*, n. sp.
- Dorsal setose lobe long, slender or paddle-shaped (Figs. 88, 89, 94); lamella finger-like (Fig. 88a), triangular (Fig. 89a), or rectangular (Fig. 94a) in lateral view 10
10. Lamella finger-like or triangular, lacking conspicuous setae (Figs. 88, 89); a distinct semimembranous lobe projecting below ventral edge of lamella. Proximus Group, 11
- Lamella rectangular (Fig. 94a) in lateral view, with fine setae, and without semimembranous lobe ventrally; N Qld. *liratus*, n. sp.
11. Lamella finger-like in lateral view (Fig. 88a), twice as long as broad basally; gonopod plate with evident transverse striae (Fig. 88b); W Tas. *bilobus* Neboiss
- Lamella triangular in lateral view (Fig. 89a) as long as broad basally; gonopod plate without striae (Fig. 89b); N Tas., E Vic., SE NSW *proximus* Neboiss
12. Dorsal setose lobe straight, narrow (Fig. 90a); lamella without setae; spermathecal sclerite rectangular (Fig. 90b); Qld., NSW, Vic., N WA *australicus* Banks
- Dorsal setose lobe with convex upper margin in lateral view or broader (Fig. 96a); if straight and narrow, lamella setose (Fig. 92a; spermathecal sclerite more triangular 13
13. Sensilla-bearing process tiny, situated on lower mesal surface of dorsal setose process (Fig. 92a); SW Australia *enthesi* Neboiss
- Sensilla-bearing process conspicuous, usually situated on ridge below dorsal setose lobe (Fig. 96a) 14
14. Gonopod plate triangular, the apicolateral ridges and the pockets above them converging posteriorly (Fig. 95b); E NSW, NE Vic., Tas.
- *elongatus* Banks
 - Gonopod plate rectangular, the apical ridges and the pockets above them forming a more nearly straight transverse line 15
15. Lamella nearly triangular in lateral view (Fig. 96a); Vic., Tas.
- *truncatus* Neboiss
 - Lamella rectangular (Fig. 98a) or trapezoidal (Fig. 97a) in lateral view 16
16. Sensilla-bearing process situated on distinct rounded ridge below dorsal setose lobe (Fig. 98a); SE Qld., E NSW *tambina* Mosely
- Sensilla-bearing process situated directly on ridge below dorsal setose lobe (Fig. 97a); lamella somewhat trapezoidal; N Qld *gonetalus*, n. sp.
 - Sensilla-bearing process situated mesad of ridge below dorsal setose lobe (Fig. 99a); lamella subrectangular, rounded apically in lateral view; SE Qld., E NSW, E Vic. *altenogus*, n. sp.

Acknowledgements

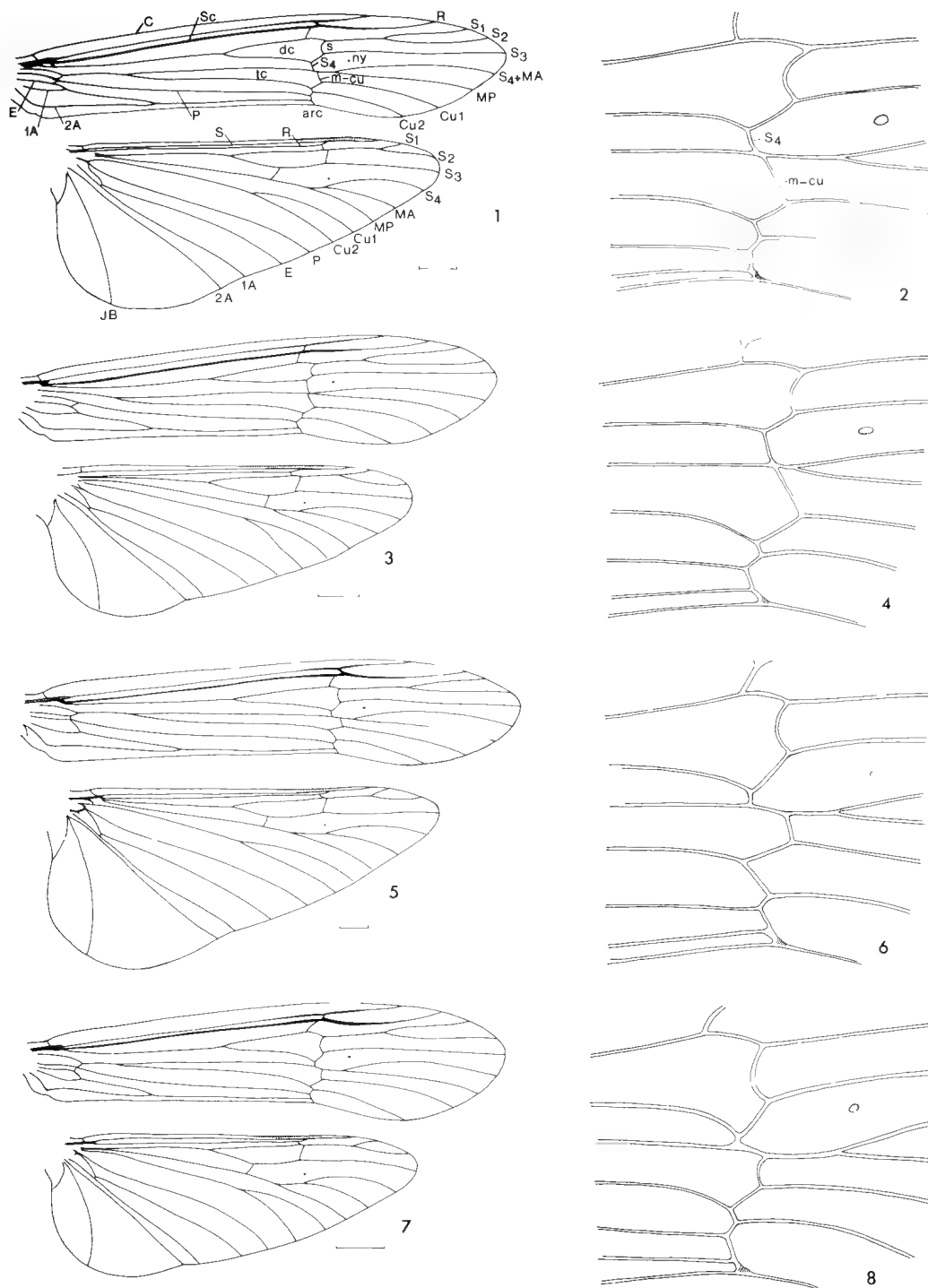
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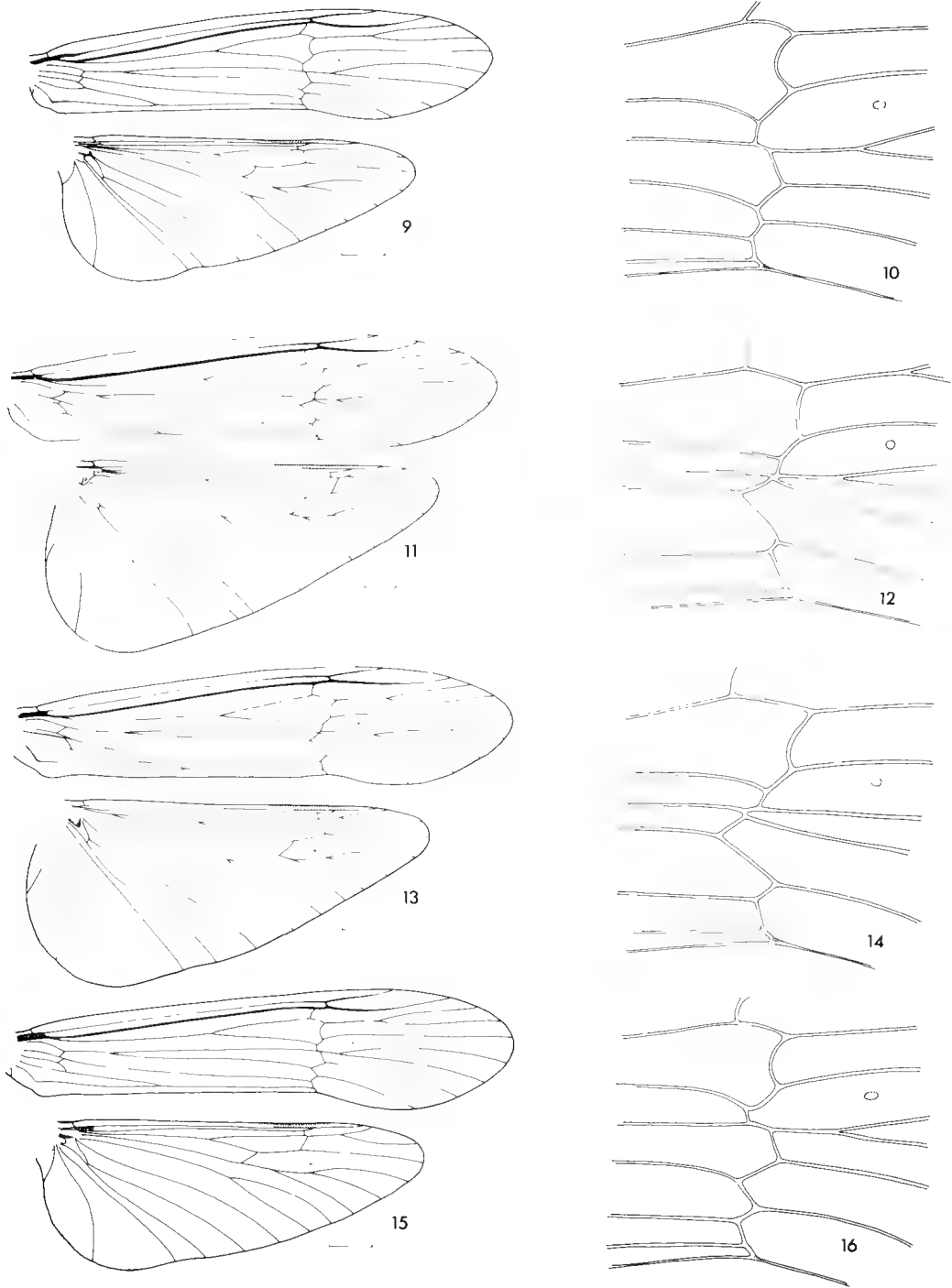
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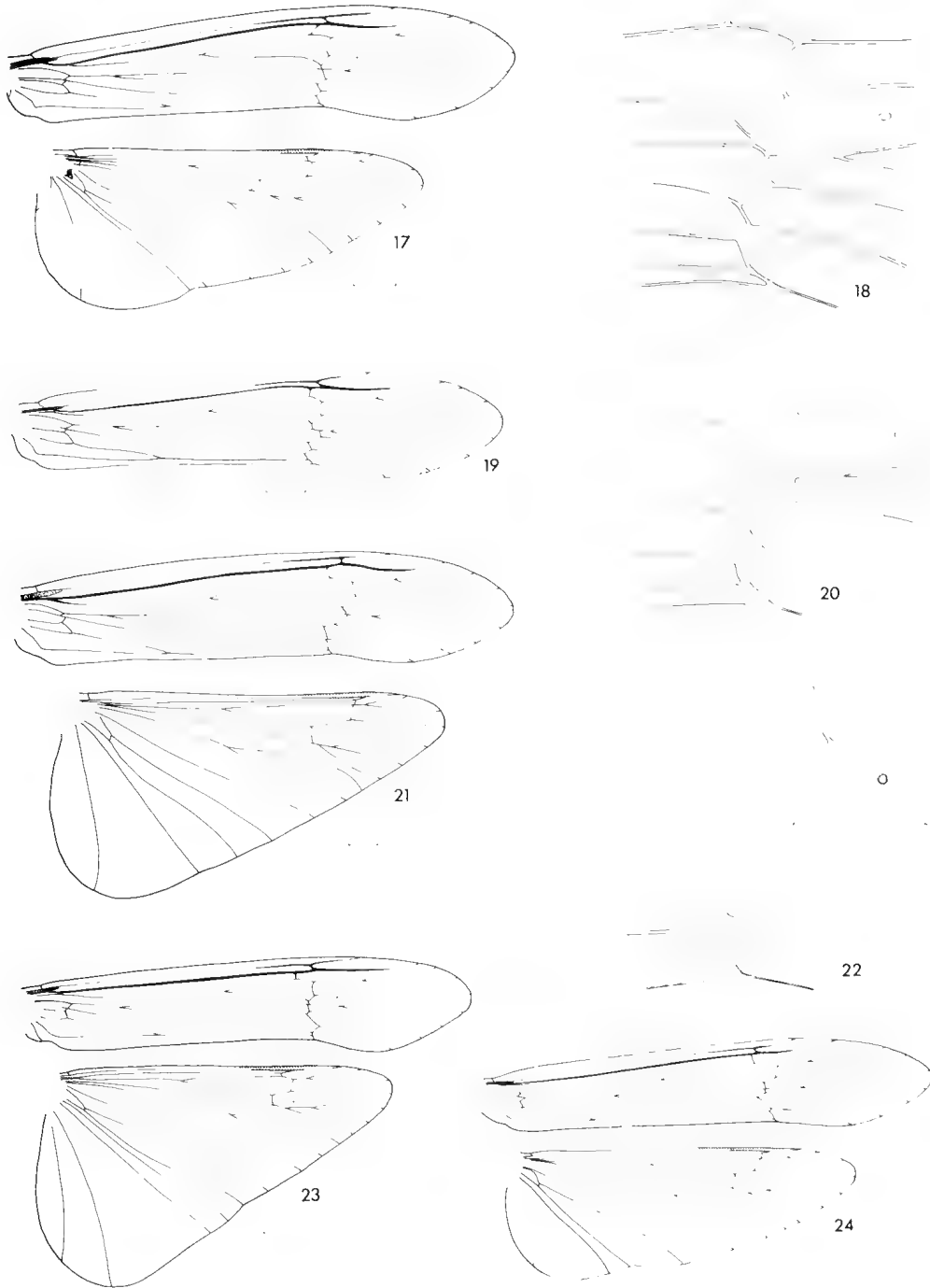
Figs. 1-8. male wing venation: Figs. 1-2 *Triplectides australis* Navás, Lake Hindmarsh, Vic. (PT-830); Figs. 3-4 *Triplectides helvolus* Morse and Neboiss, paratype, East Alligator

River, N.T. (PT-842); Figs. 5-6 *Triplectides magnus* (Walker), Lake Pedder, Tas. (PT-314); Figs. 7-8 *Triplectides parvus* (Banks), Upper Freshwater Creek, N-Qld.



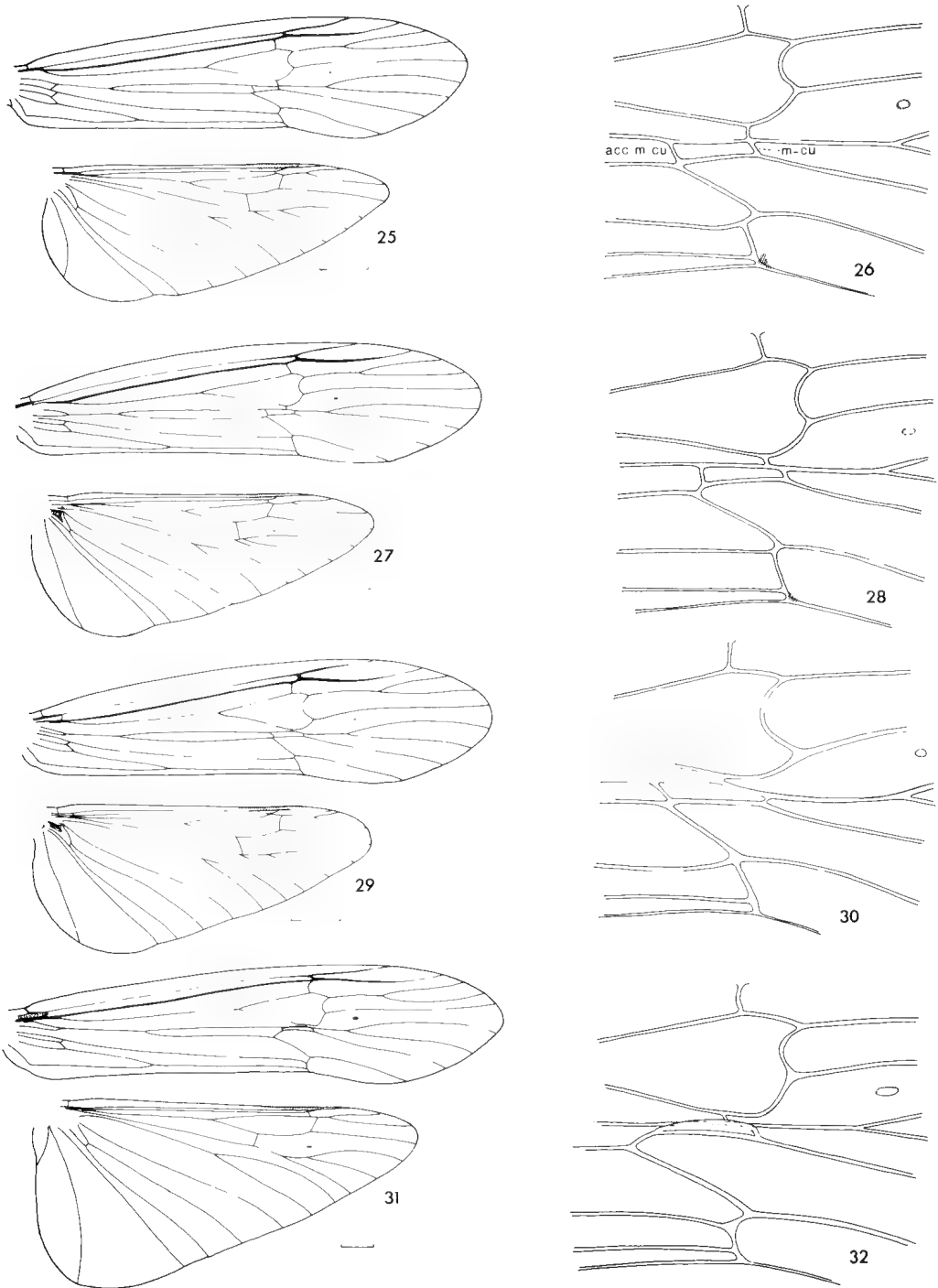
Figs. 9-16. male wing venation: Figs. 9-10 *Triplectides volda* Mosely, Camp Mountain, Qld.; Figs. 11-12 *Triplectides bilobus* Neboiss, paratype, Franklin River, Tas. (PT-309); Figs. 13-14

Triplectides proximus Neboiss, paratype, Leven River, Tas. (PT-218); Figs. 15-16 *Triplectides australicus* Banks, Cairns, Qld. (PT-855).



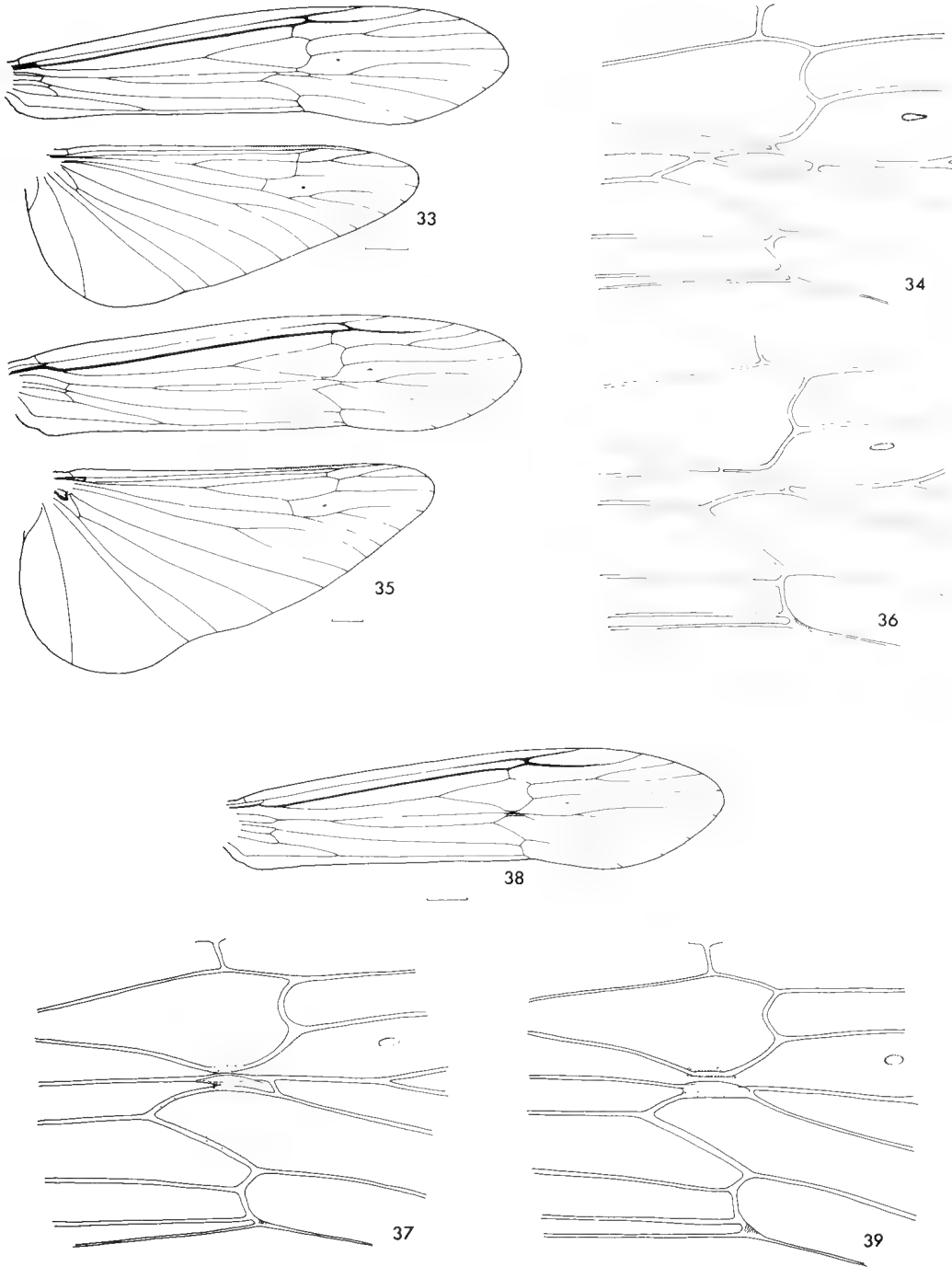
Figs. 17-24. male wing venation: Figs. 17-18 *Triplectides ciuskus* Mosely, Dart-Mitta River junction, Vic. (PT-856); Figs. 19-20 *Triplectides ciuskus seductus* Morse and Neboiss, paratype, Mitchell Plateau, NWA (PT-857); Figs. 21-22 *Triplectides similis* Mosely (large eyed form), Sundown Creek, Marrawah,

Tas.; Fig. 23 *Triplectides niveipennis* Mosely, paratype, Yanchep, W.A. (redrawn from Mosely and Kimmins 1953); Fig. 24 *Triplectides enthesis* Neboiss, holotype, Beedelup Falls, W.A. (from dry, only partly denuded wing).



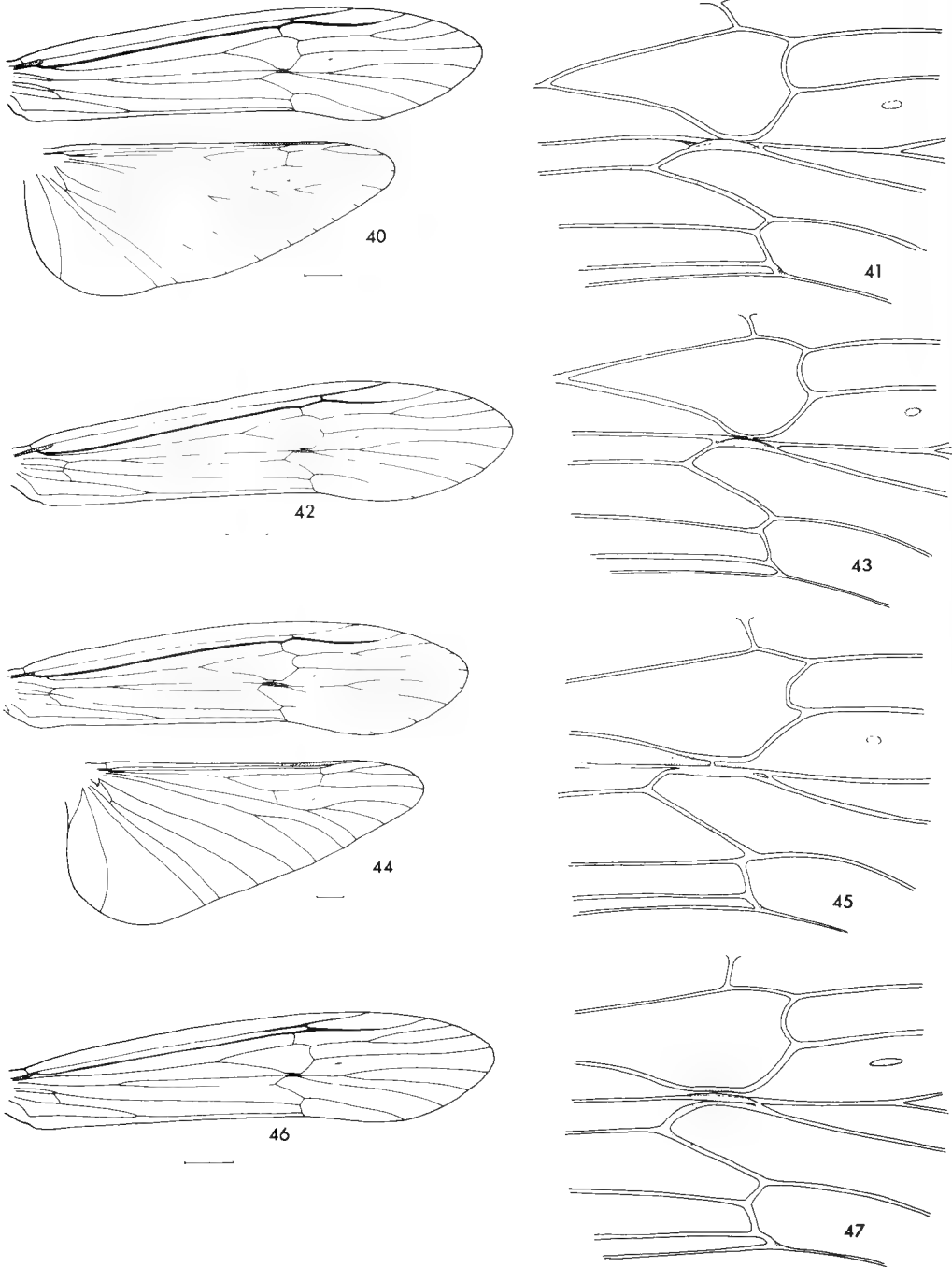
Figs. 25-32. male wing venation: Figs. 25-26 *Triplectides prolatus* Morse and Neboiss, paratype, Crystal Cascades, Cairns N-Qld., (PT-841); Figs. 27-28, *Triplectides liratus* Morse and Neboiss, paratype, Moses Creek, N-Qld.

(PT-837); Figs. 29-30 *Triplectides lirattellus* Morse and Neboiss, paratype, Babinda, N-Qld. (PT-839); Figs. 31-32, *Triplectides varius* Kimmins, Mt. Kosciusko, NSW. (PT-846).



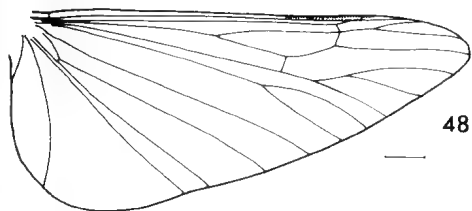
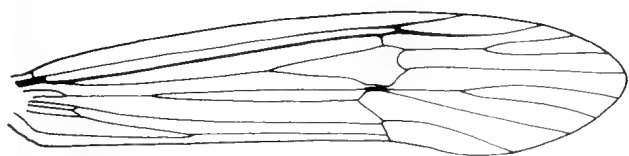
Figs. 33-39. male wing venation: Figs. 33-34, *Triplectides dolabratus* Morse and Neboiss, paratype, Tully Falls, N-Qld. (PT-843); Figs. 35-36, *Triplectides elongatus* Banks, Barrington

Tops, NSW (PT-853); Fig. 37, *Triplectides truncatus* Neboiss, paratype, Bluff Hill Creek, Tas. (PT-495); Figs. 38-39, *Triplectides truncatus* var. Toolangi, Vic. (PT-852).

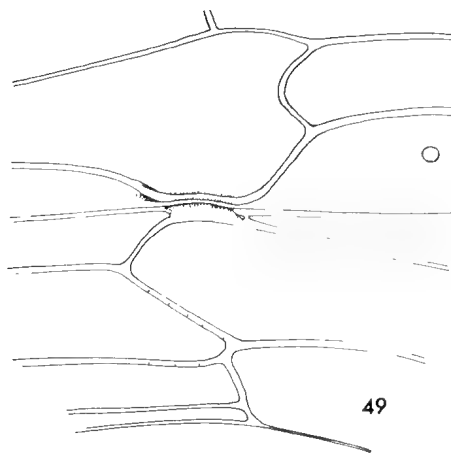


Figs. 40-47. male wing venation: Figs. 40-41, *Tripectides tambina* Mosely, Cunningham Gap, Qld. (PT-824); Figs. 42-43, *Tripectides tambina* var. Saddletree Creek, Maidenwell, Qld. (PT-845); Figs. 44-45, *Tripectides gonetalus*

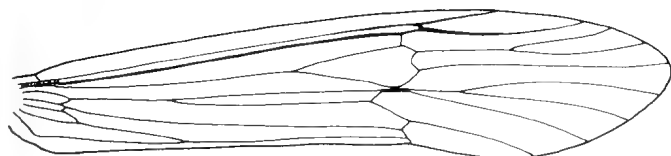
Morse and Neboiss, paratype, Mt. Tiptree, N-Qld (PT-836); Figs. 46-47, *Tripectides insperatus* Morse and Neboiss, holotype, Cooloola, Qld. (PT-840).



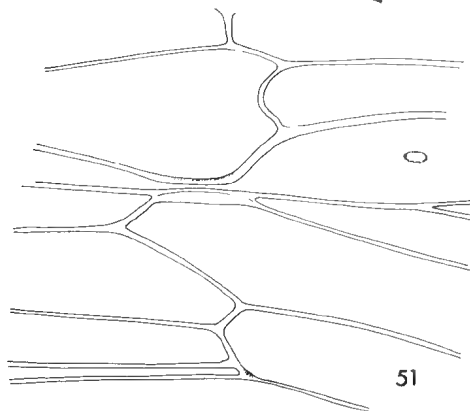
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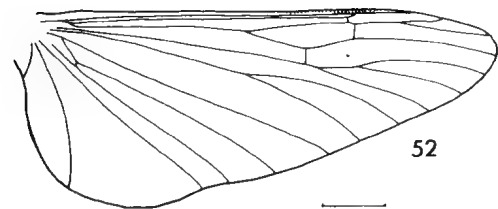
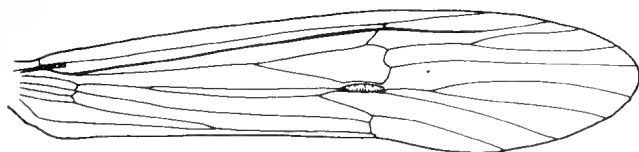
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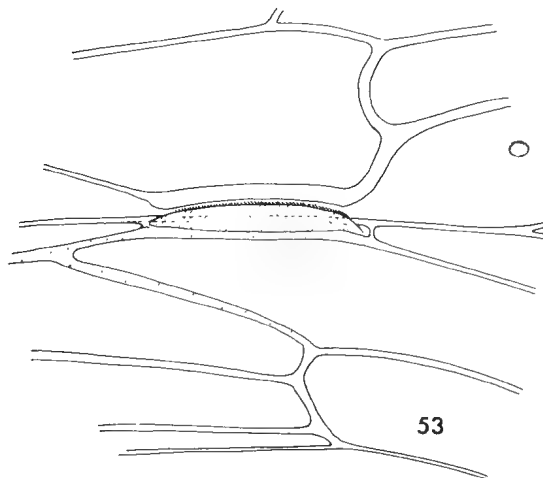
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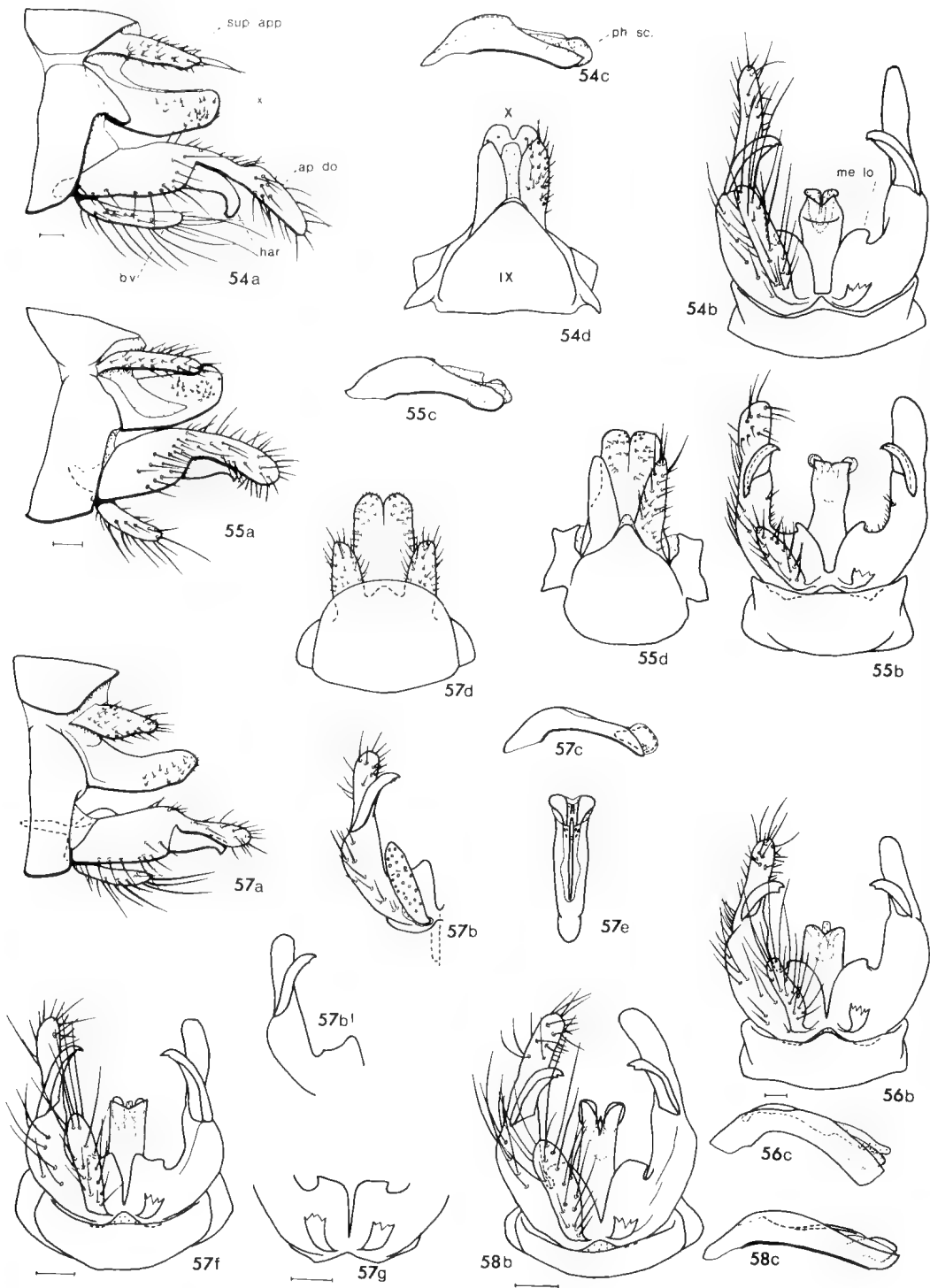
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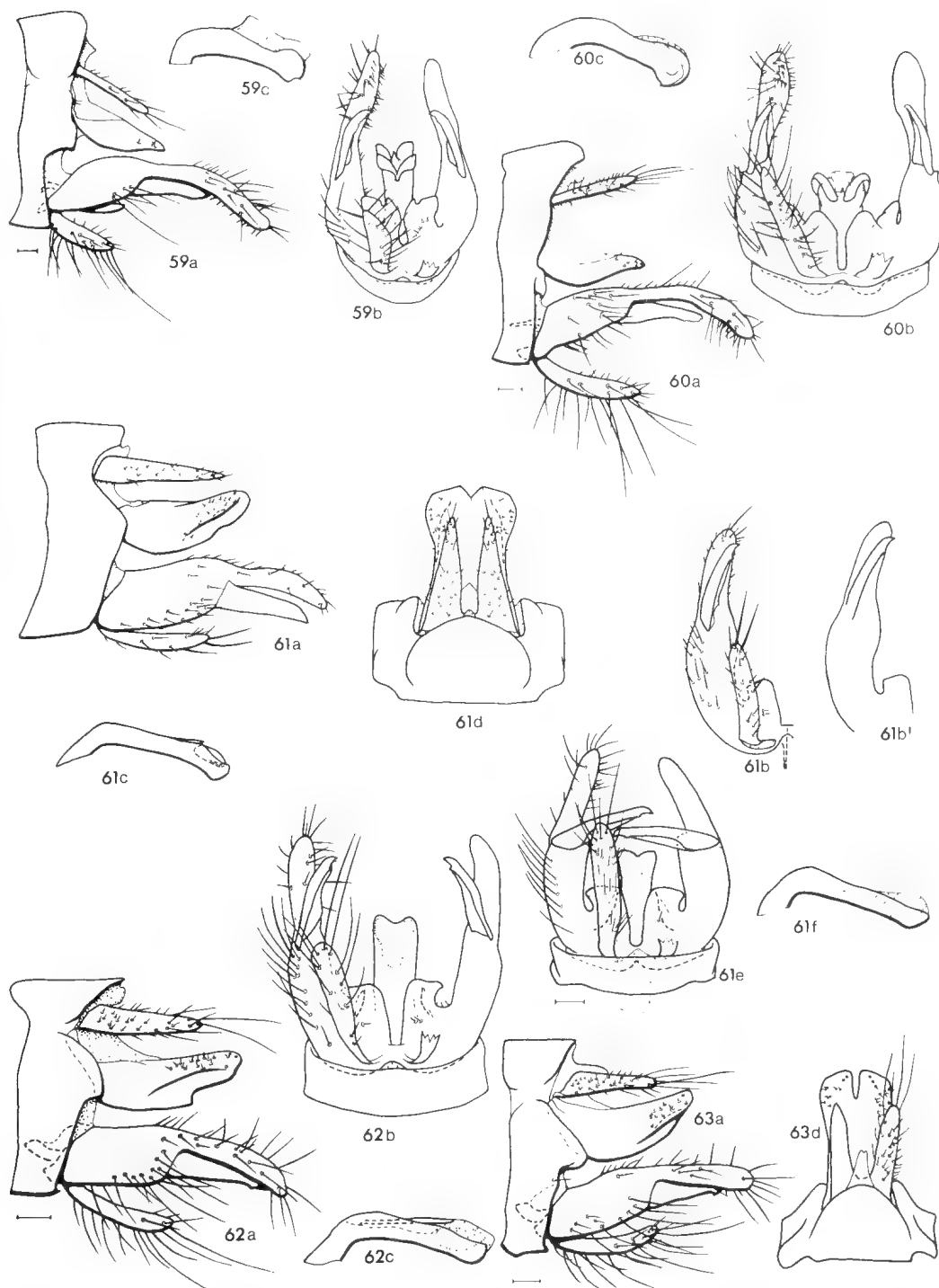
Figs. 48-53. male wing venation: Figs. 48-49, *Triplectides altenogus* Morse and Neboiss, paratype, Conondale Range, SE-Qld. (PT-835); Figs. 50-51, *Triplectides hamatus* Morse and Neboiss,

holotype, Upper Manning River, NSW (PT-844); Figs. 52-53, *Triplectides rossi* Morse and Neboiss, paratype, Kirrama State Forest, N-Qld. (PT-838).



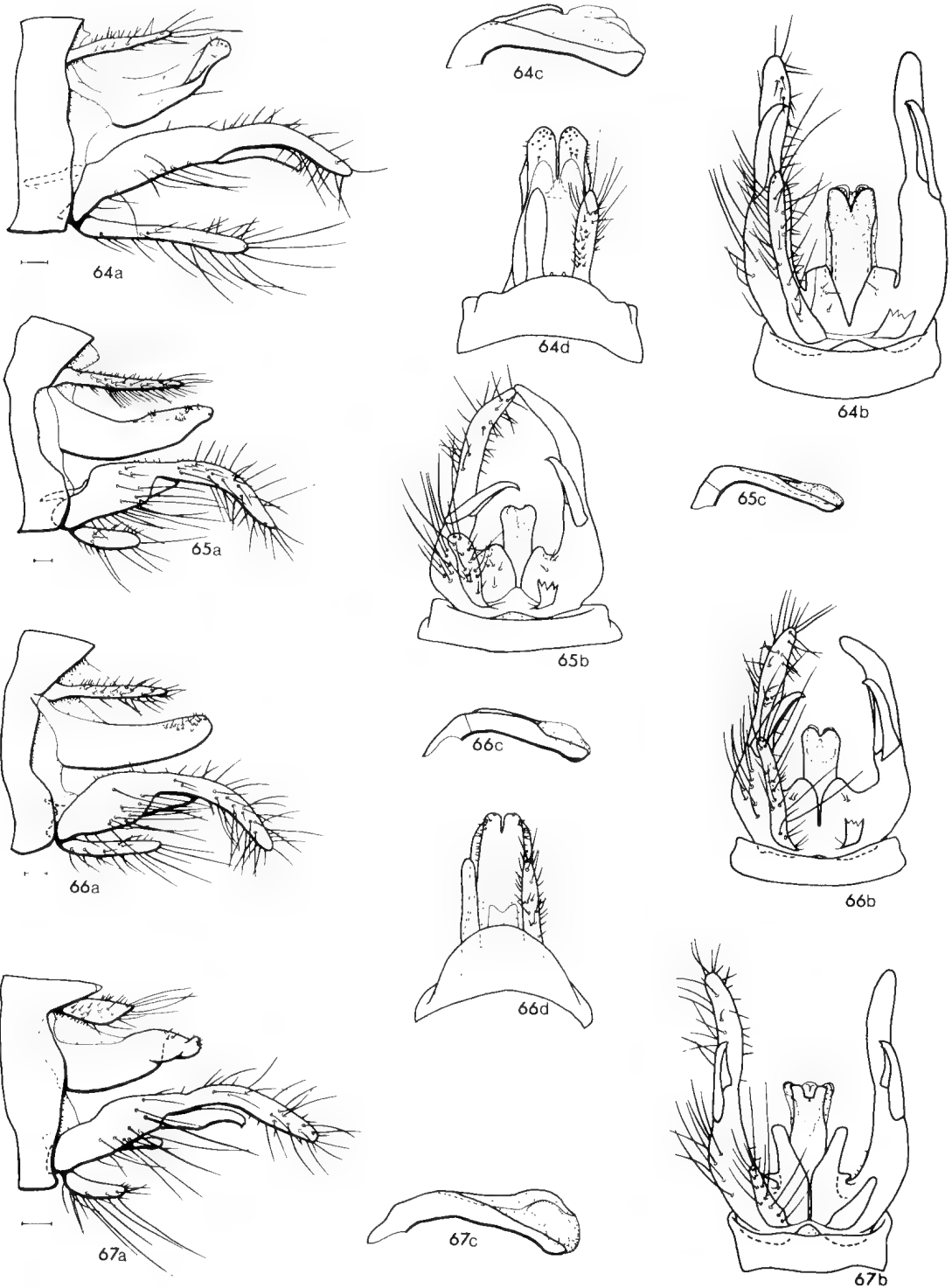
Figs. 54-58. male genitalia: Fig. 54 a, b, c, d, *Triplectides australis* Navás, Jindabyne, NSW. (PT-849); Fig. 55 a, b, c, d, *Triplectides helvolus* Morse and Neboiss, paratype, East Alligator River, NT. (PT-842); Fig. 56 b, c, *Triplectides magnus* (Walker), Lake Pedder, SW-Tas. (PT-314); Fig. 57 a, b, c, d, e, *Triplectides*

parvus (Banks), holotype, Ravenshoe, N-Qld., f-male from Kenilworth, SE-Qld. (PT-823) ventral, g-male from Holmes Jungle, Darwin, NT. ventral; Fig. 58 b, c, *Triplectides voldai* Mosely, Camp Mountain SE-Qld. (PT-850).



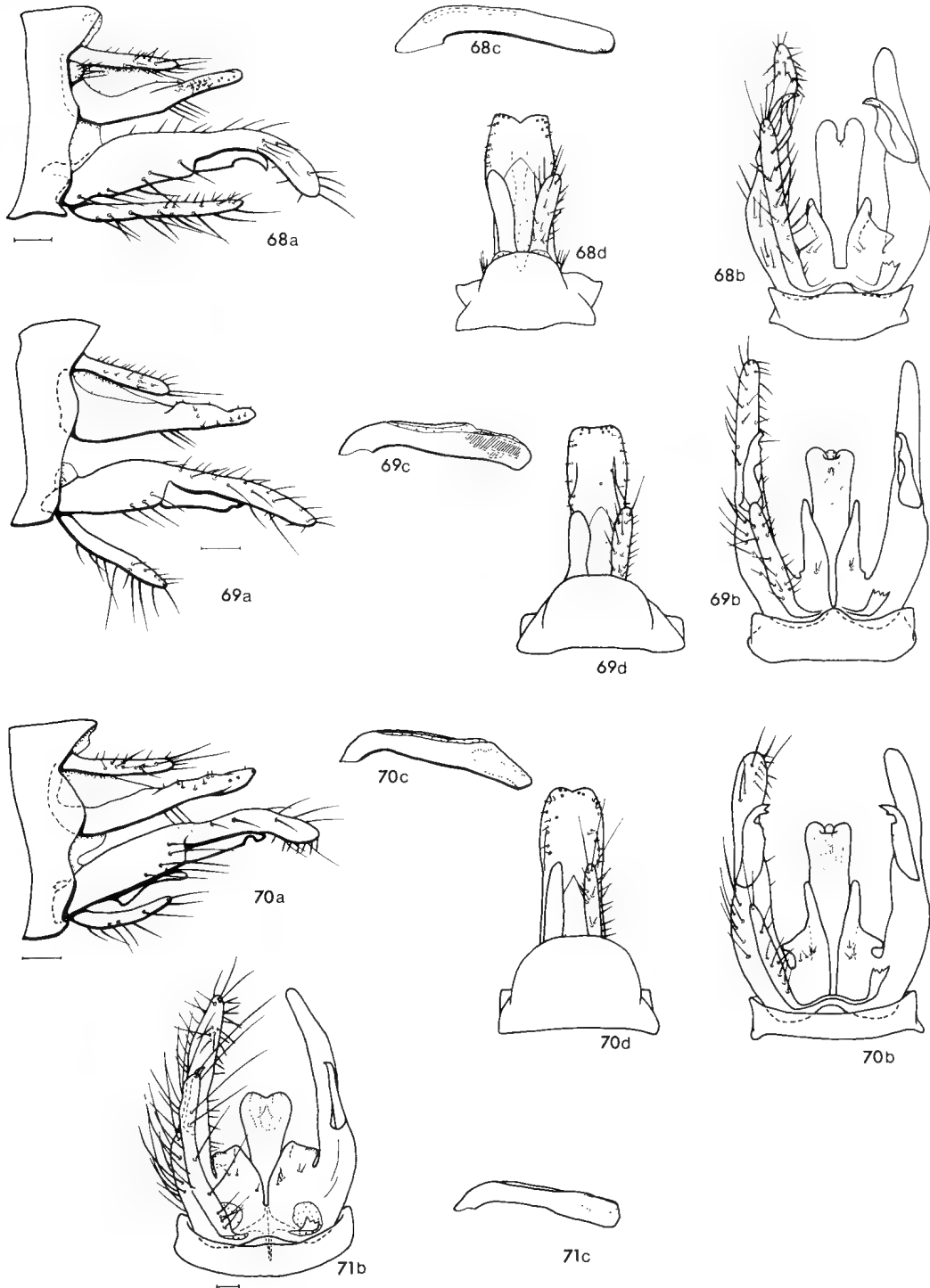
Figs. 59-63. male genitalia: Fig. 59 a, b, c, *Triplectides bilobus* Neboiss, paratype, Franklin River, SW-Tas. (PT-309); Fig. 60 a, b, c, *Triplectides proximus* Neboiss, paratype, Leven River, Heka, Tas. (PT-218); Fig. 61 a, b, b', c, d, *Triplectides australicus* Banks, holotype, Ravenshoe, N-Qld., e-male from Cairns

(PT-855) ventral, f-phallos lateral; Fig. 62 a, b, c, *Triplectides ciuskus* Mosely, Dartmouth, Vic. (PT-856); Fig. 63 a, d, *Triplectides ciuskus seductus* Morse and Neboiss, paratype, Camp Creek, Mitchell Plateau, NWA (PT-858).



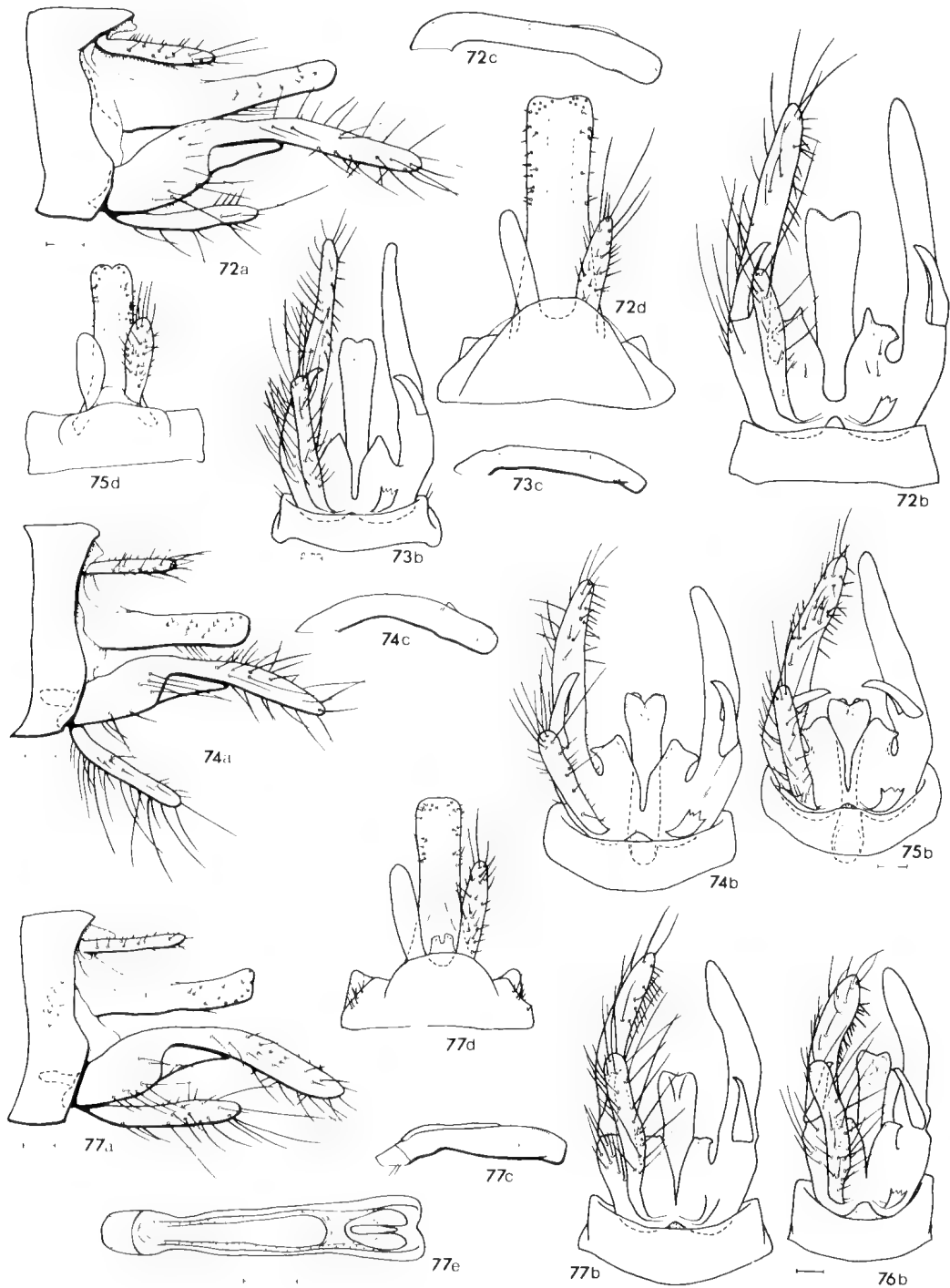
Figs. 64-67. male genitalia: Fig. 64 a, b, c, d, *Triplectides enthesis* Neboiss, holotype, Beedelup Falls, WA; Fig. 65 a, b, c, *Triplectides similis* Mosely large-eyed form, Cowwarr weir, Thomson River, Vic. (PT-818); Fig. 66 a, b,

c, d, *Triplectides similis* Mosely small-eyed form, Porepunkah, Vic. (PT-817); Fig. 67 a, b, c, *Triplectides niveipennis* Mosely, paratype, Yanhep, WA (PT-714).



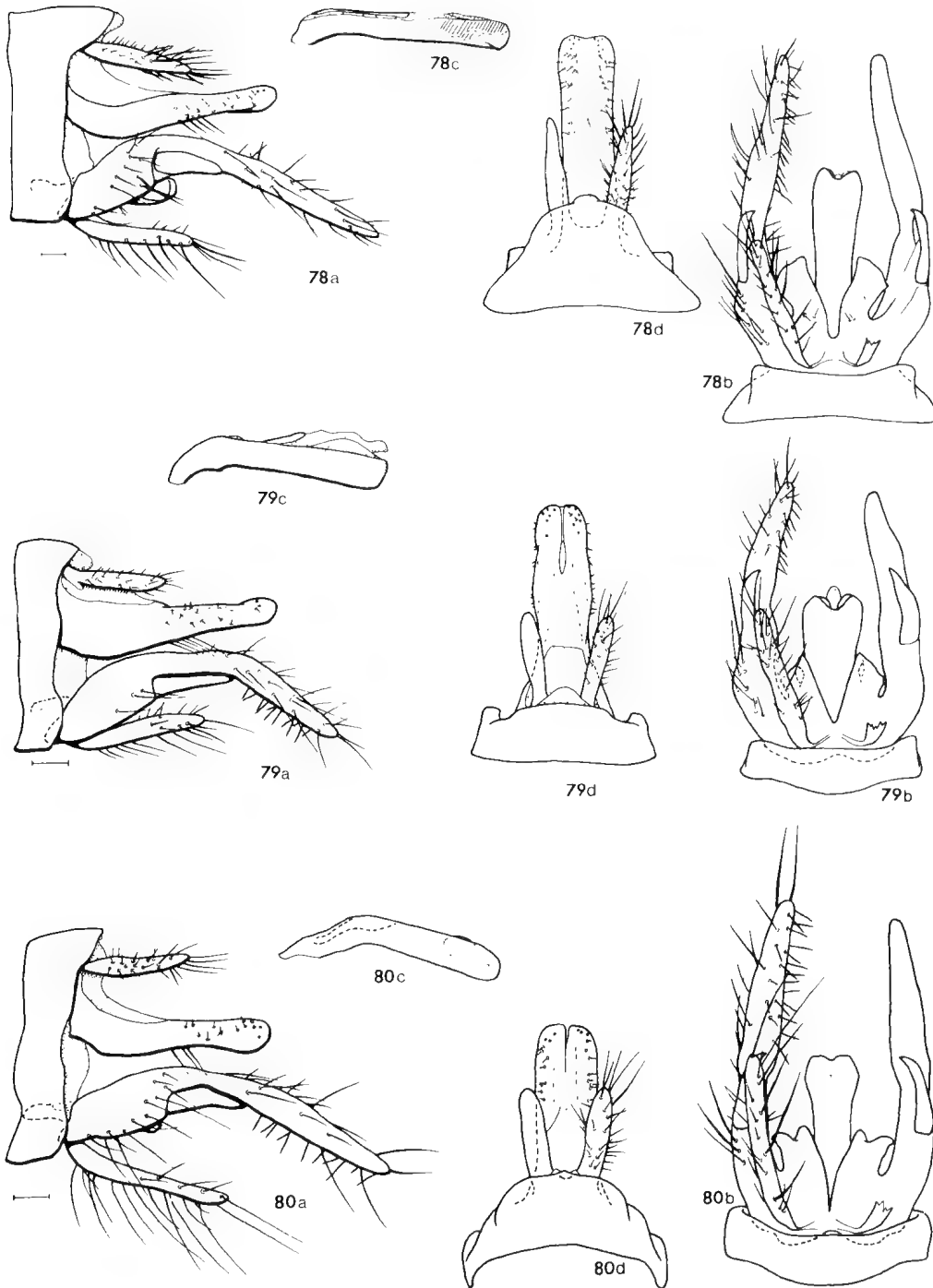
Figs. 68-71. male genitalia: Fig. 68 a, b, c, d, *Triplectides prolatus* Morse and Neboiss, paratype, Crystal Cascades, Cairns, N-Qld. (PT-841); Fig. 69 a, b, c, d, *Triplectides liratus* Morse and Neboiss, paratype, Moses Creek, nr. Mt.

Finnigan, N-Qld. (PT-837); Fig. 70 a, b, c, d, *Triplectides liratellus* Morse and Neboiss, paratype, Babinda, N-Qld. (PT-839); Fig. 71 b, c, *Triplectides varius* Kimmins, Mt. Kosciusko, NSW (PT-846).



Figs. 72-77. male genitalia: Fig. 72 a, b, c, d, *Triplectides dolabratus* Morse and Neboiss, paratype, Tully Falls, N-Qld. (PT-843); Fig. 73 b, c, *Triplectides elongatus* Banks, Barrington Tops, NSW (PT-853); Fig. 74 a, b, c, *Triplectides truncatus* Neboiss, paratype, Bluff Hill Creek, Marrawah, Tas. (PT-495); Fig. 75 b,

d, *Triplectides truncatus* Neboiss (variety), Olga River, SW-Tas. (PT-851); Fig. 76 b, *Triplectides tambina* Mosely (typical form), Cunningham Gap, SE-Qld. (PT-824); Fig. 77 a, b, c, d, *Triplectides tambina* Mosely variety, Maidenwell, SE-Qld. (PT-845), e-phallus ventral, more enlarged.



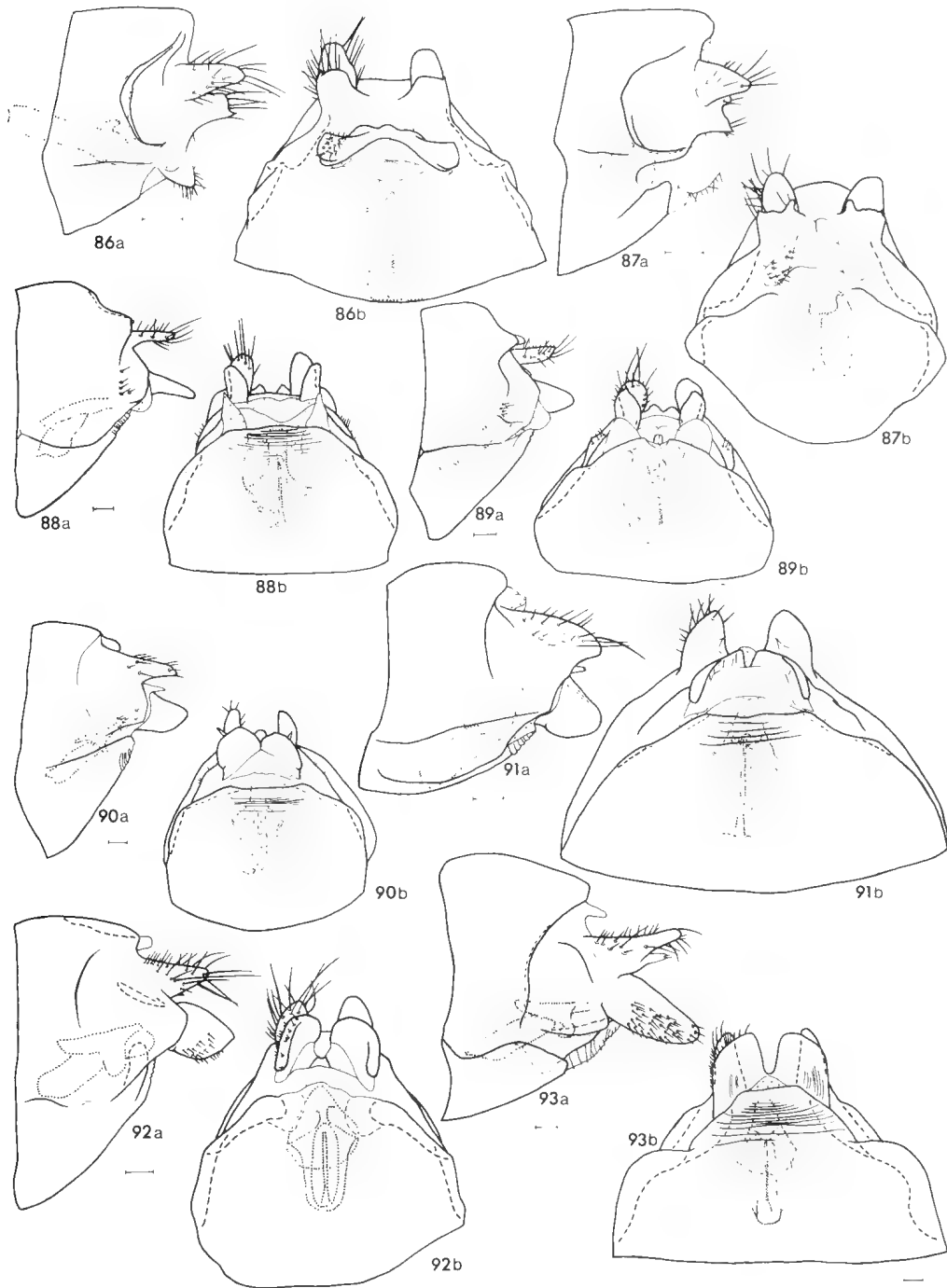
Figs. 78-80. male genitalia: Fig. 78 a, b, c, d, *Triplectides gonetalus* Morse and Neboiss, paratype, Mt. Tiptree, N-Qld. (PT-836); Fig. 79 a, b, c, d, *Triplectides insperatus* Morse and Neboiss,

holotype, Cooloola, SE-Qld. (PT-840); Fig. 80 a, b, c, d, *Triplectides hamatus* Morse and Neboiss, holotype, Upper Manning River, NSW (PT-844).



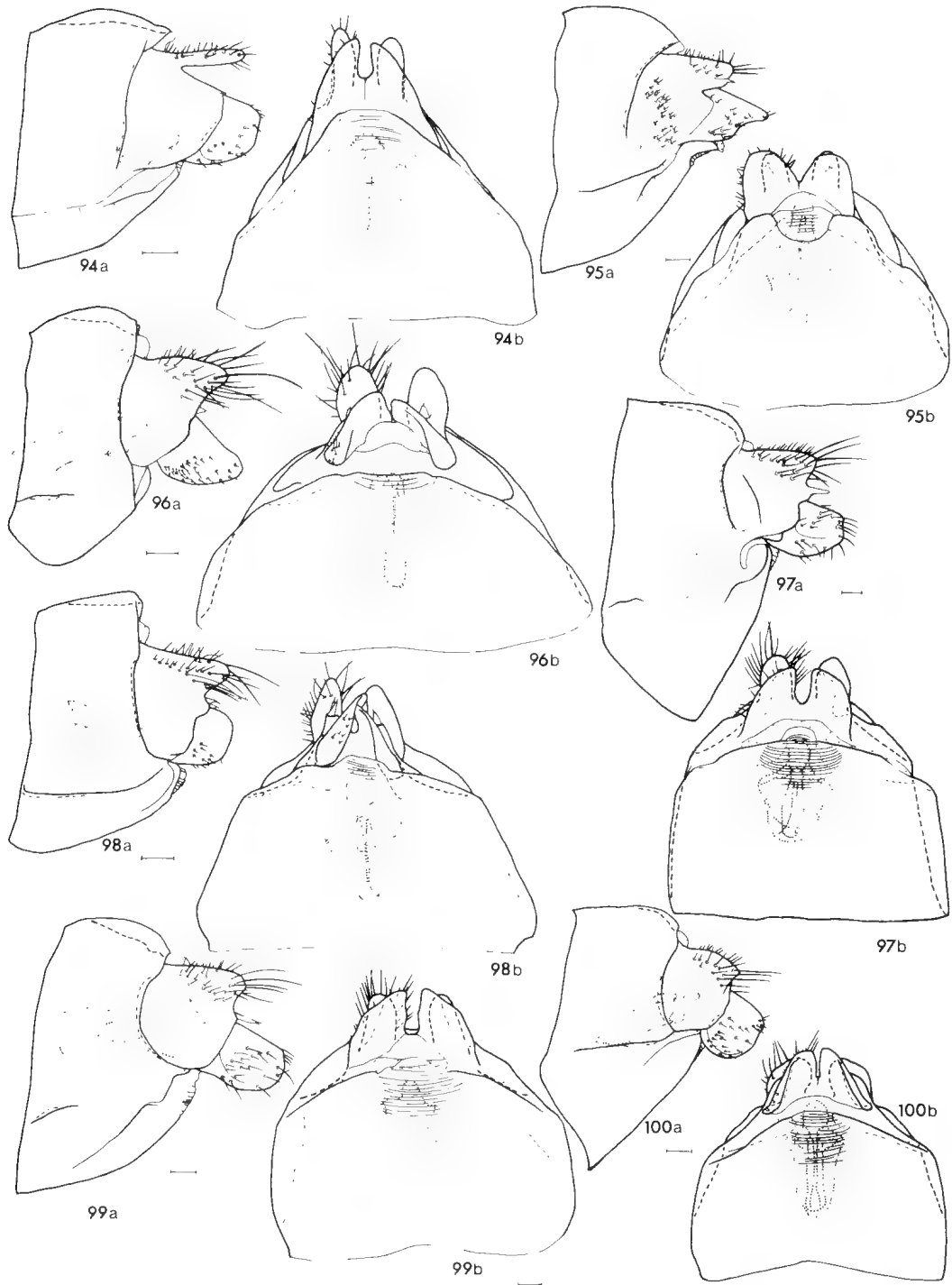
Figs. 81-85. male and female genitalia: Fig. 81 a, b, c, d, *Triplectides altenogus* Morse and Neboiss, paratype, Conondale Range, SE-Qld. (PT-835); Fig. 82 a, b, c, d, *Triplectides rossi* Morse and Neboiss, paratype, Kirrama State Forest, N-Qld. (PT-838); Fig. 83 a, b, *Triplectides australis* Navás, Molong, NSW

(PT-864) female genitalia, c-left lateral view of abdominal segments VII-X; Fig. 84 a, b, *Triplectides helvolus* Morse and Neboiss, paratype, Lambells Lagoon, NT. (PT-866); Fig. 85 a, b, *Triplectides magnus* (Walker), Lake Pedder, SW-Tas. (PT-825).



Figs. 86-93. female genitalia: Fig. 86 a, b, *Triplectides parvus* (Banks), Mt. Webb, N-Qld. (PT-832); Fig. 87 a, b, *Triplectides volda* Mosely, Camp Mountain, SE-Qld. (PT-867); Fig. 88 a, b, *Triplectides bilobus* Neboiss, paratype, Franklin River, SW-Tas. (PT-860); Fig. 89 a, b, *Triplectides proximus* Neboiss, paratype, St. Patricks River, Targa, Tas.

(PT-859); Fig. 90 a, b, *Triplectides australicus* Banks, Cairns, N-Qld. (PT-862); Fig. 91 a, b, *Triplectides ciuskus* Mosely, Orroral River, ACT. (PT-863); Fig. 92 a, b, *Triplectides enthesis* Neboiss, Beedelup Falls, SWA. (PT-878); Fig. 93 a, b, *Triplectides similis* Mosely, Evandale, Tas. (PT-868).



Figs. 94-100. female genitalia: Fig. 94 a, b, *Triplectides liratus* Morse and Neboiss, paratype, Windsor Tableland, N-Qld. (PT-874); Fig. 95 a, b, *Triplectides elongatus* Banks, Kiandra, NSW. (PT-871); Fig. 96 a, b, *Triplectides truncatus* Neboiss, paratype, Bluff Hill Creek, Marrawah, NW-Tas. (PT-496); Fig. 97 a, b, *Triplectides gonetalus* Morse and Neboiss,

paratype, Mt. Misery, W. of Mossman N-Qld. (PT-873); Fig. 98 a, b, *Triplectides tambina* Mosely, Bunya Mts.; Fig. 99 a, b, *Triplectides attenogus* Morse and Neboiss, paratype, Maidenwell, SE-Qld. (PT-872); Fig. 100 a, b, *Triplectides rossi* Morse and Neboiss, paratype, Mt. Fisher, Millaa Millaa, N-Qld. (PT-875).

A REDESCRIPTION OF *ASTROSCLERA WILLEYANA* LISTER, 1900
(CERATOPORELLIDA, DEMOSPONGIAE), A NEW RECORD FROM THE
GREAT BARRIER REEF

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Abstract

A large number of specimens of *Astrosclera willeyana* Lister 1900 were collected from amongst coral rubble and from caves and underhangs in depths of 4-53 m from Escape reef (15°50'S 145°49'E), one of the northerly reefs on the outer rampart of the Great Barrier Reef. This collection extends the known geographic distribution of the species and includes specimens far larger than those previously recorded. The characteristics of these large specimens are described. Examination of the spicule content in a wide range of different sizes of *A. willeyana* revealed that spicules were only present in small individuals. This variation in spicule content has led some authors to believe that two species may be involved rather than one. The present collection shows that *A. willeyana* cannot be split into two species and has enabled an unambiguous new description of the species.

Introduction

Astrosclera willeyana Lister 1900, was first found off the Loyalty and Tuvalu Islands (Lister, 1900) and has since been discovered off Madagascar (Vacelet and Vasseur, 1965, 1971; Vacelet et al., 1976), L'île Europa (Vacelet, 1967), Christmas Island (Kirkpatrick, 1910), New Caledonia (Vacelet, 1981), La Réunion and French Polynesia (Vacelet, 1977) and Guam (Hartman pers. comm.). The sponge lives in depths of 4-183 m, in small crevices and caves within the coral in front reef and lagoon habitats. All specimens reported have maximum head diameters of less than 25 mm but the largest specimens collected by Hartman reached 135 x 105 mm (Hartman pers. comm.). The spicule quantity and characteristics of reported specimens varies markedly. Vacelet (1977, 1981) suggests that this may be linked with geographic location. Described specimens from the Indian Ocean have numerous acanthostyli, often with regular spining, while those from New Caledonia have no spicules or a few fine spicules with irregular spining. No spicules were found in specimens from the Central Pacific (Stearn, 1972; Vacelet, 1977). The possibility has been raised that *A. willeyana* as hitherto understood may comprise two species, one with spicules and one without (Vacelet, 1981). The

present collection, which includes a good size range of specimens, has enabled a resolution of the seeming spicular differences reported previously. Using the present specimens a redescription of the sponge is given along with notes on habitat and ecology.

Methods

Specimens in caves could be picked off the substratum by hand while those living in coral rubble were collected with the aid of a crowbar to lever the rubble apart. Specimens were preserved initially in 90% alcohol and then three days later in 70% alcohol. Spicule mounts were made using 5.25% sodium hypochlorite (commercial bleach). Thin sections of the skeleton were prepared after impregnation with araldite. Histological sections were made from decalcified sections stained in Mallory's Triple Stain.

Description of the Species

Sub-class	Ceractinomorpha Lévi
Order	Ceratoporellida Hartman and Goreau
Family	Astroscleridae Lister
	<i>Astrosclera willeyana</i> Lister

Figure 1

- Astrosclera willeyana* Lister, 1900; 459, pls. 45-48, figs. A, B, C.
Astrosclera willeyana Kirkpatrick, 1910a: 380, pl. 11.
Astrosclera willeyana Kirkpatrick, 1910b: 83.
Astrosclera willeyana Vacelet and Vasseur, 1965: 115, pl. X, fig. 37.
Astrosclera willeyana Vacelet, 1967: 127, figs. 3, 6, 7, 8.
Astrosclera willeyana Vacelet and Vasseur, 1971: 116.
Astrosclera willeyana Vacelet, 1977: 346, pl. 1a, c.
Astrosclera willeyana Vacelet, 1981: figs. 1a, b, c.

Material: Specimens are deposited in the Australian Museum (A.M.), National Museum of Victoria (N.M.V) and the British Museum (B.M.).

- A.M. Z3894, diameter 95 mm, back reef, Escape Reef, 6 m, A. L. Ayling, 19.12.80;
 A.M. Z3893, diameter 105 mm, front reef, Escape Reef, 53 m, A. M. Ayling, 14.12.80;
 N.M.V. G3298, diameter 40 mm, front reef, Escape Reef, 12 m, A.L.A., 15.12.80;
 A.M. Z3891, diameter 60 mm, front reef, Escape Reef, 11 m, A.M.A., 15.12.80 (includes one 6 mm in diameter specimen and the tabulate sponge *Acanthochaetetes wellsii* Hartman and Goreau, A.M. Z3892);
 N.M.V. G3297, diameter 130 mm, outer reef, Escape Reef, 53 m, W. A. Starck, 13.12.80; (includes five specimens 6-15 mm in diameter);
 A.M. Z3890, diameter 4 mm, back reef under rubble, Escape Reef, 10 m, A.L.A., 22.12.80;
 B.M.N.H. 1982: 3:9:1-26: twenty-six specimens ranging in size from 7 to 50 mm in diameter, front reef cave, 12 m, A.L.A., 2.10.81;
 B.M.N.H. 1982: 3:9:27: diameter 130 mm, front reef cave, Escape Reef, 12 m, A.L.A., 2.10.81;
 B.M.N.H. 1982: 3:9:28-47: twenty specimens ranging in size from 1.5 to 14 mm in diameter, back reef under rubble, Escape Reef, 17 m, A.L.A., 27.10.81.

Colour: Very small specimens were pale pink in life while specimens above 5 mm maximum head diameter were salmon orange. Very large

sponges were orange sometimes shaded with a tinge of pink. The central mass of the sponge was white. Specimens turned a dark orange in preservative.

Growth form and dimensions: The specimens in the present collection range from 1.5 to 130 mm maximum head diameter and 1 to 55 mm in height. The largest specimen observed in the field was 165 x 115 mm in diameter but this was not collected. The smallest individuals are thinly encrusting and sometimes have finger-like processes spreading out over the substratum. With increase in size the sponge grows upwards into a cylindrical structure with the pedicel no wider than the head. The head is flattened in these young specimens, then gradually becomes rounded and larger than the pedicel until in the largest specimens the margin of the head has curved down to the substratum. In all specimens growth rings are visible. The surface of the sponges is usually smooth except in some large individuals where it becomes irregularly mammillate. Sponges were occasionally found with surfaces pitted by 0.8 mm wide holes of unknown origin.

Oscules: The oscules always occur on the mammillae where these are present but are otherwise regularly scattered over the surface at 2 to 5 per square centimetre. Oscules have 3 to 6 astrorhizae extending from them and are deeply etched into the skeleton of the sponge covering an area of the surface of the sponge from 2 to 12 mm in diameter. The diameter of these oscular areas is independent of the size of the sponge. The structure of the astrorhizae is discussed in Stearn (1975).

Mineral skeleton: The main skeleton of the sponge is formed of spherules of aragonite, 10 to 60 μm in diameter (mineralogy confirmed by Dr. W. Birch, NMV) which are loose at the surface but coalesce further down in the sponge to form short columns 100-550 μm in diameter (see Lister, 1900, for figures of the internal structure). These columns are quite distinct in larger specimens but in the smaller specimens they often join in a more lamellar pattern. In individuals less than 5 mm in maximum head diameter, the columns of spherules are so close together that they form an almost continuous

surface. Toward the interior of the sponge the columns gradually coalesce and become more distorted. The living tissues extend down to a depth of 8 mm.

Spicules: In living specimens up to 6 mm in maximum head diameter, some spicules could always be found although the number of spicules varied markedly. The range in spicule size from 80 measurements taken from a number of specimens is 29.2 to $98.1 \mu\text{m} \times 1.1$ to $5.3 \mu\text{m}$ and the mean and standard deviation is $56.4 \mu\text{m}$ ($12.2 \mu\text{m}$) \times $3.0 \mu\text{m}$ ($0.8 \mu\text{m}$). Most spicules have narrow heads followed by a swelling which tapers to a point (Fig. 1a). However, a few spicules have little or no narrowing of the head and lack the distinctive swelling (Fig. 1b).

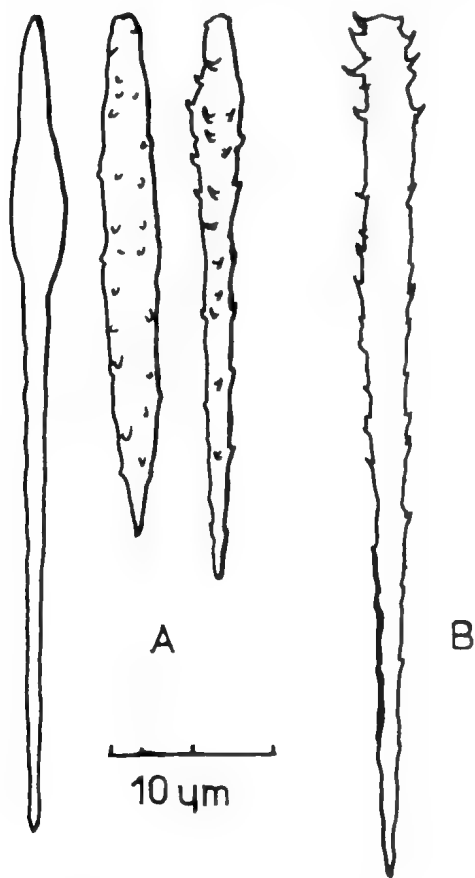


Fig. 1. Spicules from *Astrosclera willeyana*.
(a) common form,
(b) rarer form.

Most acanthostyli have barely perceptible spines or irregular short spines. However, in some specimens, especially those with spicules without narrowing of the head, spines are pronounced. These spicule forms and sizes are similar to previously described material.

In specimens from 7 to 18 mm in maximum head diameter, spicules are normally rare and sometimes absent. Above this size no spicules were found in the present collection. It is worth noting that spicules could rarely be found in dead or even roughly handled specimens.

Remarks: The discovery of *Astrosclera willeyana* on the Great Barrier Reef extends the known range of this species. The species is abundant at Escape Reef in shaded situations in caves and chimneys on the front reef (3.32 (SD 3.67) per quarter metre square) and under coral rubble (0.7 (SD 1.1) per quarter metre square). Small specimens were found on the undersurfaces of coral pieces up to 30 cm deep in coral rubble, under small ledges along the front reef and outer reefs, and deep within caves. These habitats were clear of silt and algae. The larger specimens were found in large open tunnels along the front reef where water movement from both currents and surge was constant and often strong. This suggests that this species grows to a large size only in certain situations. The size-frequency of the populations is shown in Fig. 2. Individuals between 5 and 20 mm in maximum head diameter on the front reef form 87.1% of the population while on the back reef 50% of the population are between 1 and 4 mm in maximum head diameter.

Apart from *Astrosclera willeyana*, two other coralline sponges were found to be common in the caves of Escape Reef; the tabulate sponge *Acanthochaetetes wellsi* Hartman and Goreau, and a living sphinctozoan species *Neocoelia crypta* Vacelet. In the coral rubble sclerospices were found associated with the brachiopod *Frenulina sanguinolenta* (Gmelin).

Oocytes were found in several specimens from 8 to 105 mm in maximum head diameter collected during the period November-December 1980/81. Oocytes measured up to $105 \mu\text{m}$ in maximum diameter.

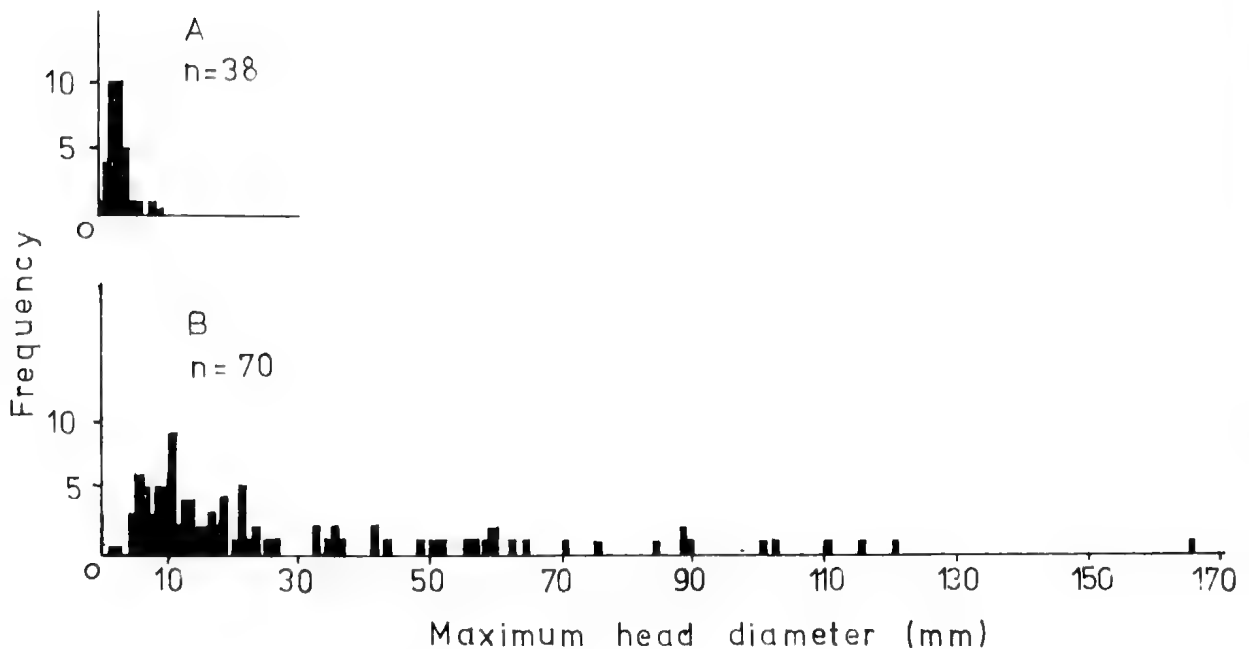


Fig. 2. Size-frequency of two populations of *Astrosclera willeyana* from Escape Reef.
(a) back reef coral rubble,
(b) front reef caves.

Conclusions

The large populations and range in size of the specimens of *Astrosclera willeyana* from the Great Barrier Reef allow the species to be more fully described and also provide useful information on the variability in spicule content of the sponge body. The variability in spicule content found in the present sponges due to size, individual variation and state of preservation of the specimens could account for the seeming geographic variation in this character reported by previous authors (see summary Vacelet, 1981), especially as these previously described specimens were all below a head diameter of 25 mm. In the present collection the only individuals found to have spicules consistently were those with a head diameter of less than 6 mm. After a head diameter of 18 mm is reached, the sponge either no longer produced spicules or the spicules may erode (Hartman and Goreau, 1970). Large *A. willeyana* appear only to develop in situations of strong water movement. These individuals, unlike the smaller sponges, have no visible pedicel as the head reaches down to the substratum and the surface is sometimes produced into mammillae.

Acknowledgements

I gratefully acknowledge Dr. Walter Starck who found the first specimen of *Astrosclera willeyana* at Escape Reef and for use of his research vessel 'El Torito'. Dr. Jean Vacelet, Dr. Willard D. Hartman and Dr. Felix Wiedenmayer gave invaluable comments. Dr. Tony Ayling assisted in collections. This work was made possible by a private grant from the Englehart Foundation and support from the Australian Biological Resources Survey. I also wish to thank Dr. Barry Wilson for use of the facilities of the National Museum of Victoria, Dr. W. D. Birch for making thin sections, and Mr Max Campbell (Royal Melbourne Institute of Technology) for histological preparations of the sponges.

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GENUS *SETODES* (RAMBUR) NEW TO AUSTRALIAN FAUNA
(TRICHOPTERA: LEPTOCERIDAE)

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Abstract

The genus *Setodes* Rambur is recorded from Australia for the first time, and a new species—*Setodes bracteatus* is described from North-Queensland.

Introduction

The genus *Setodes* Rambur constitutes a group of small, delicate insects with a wing span 10-15 mm, with almost a world wide distribution (Schmid, 1980). The differences between *Setodes* and *Leptocerus* Leach were established and their respective type species formally designated by Milne (1934). However, placement of many species is still in doubt (Fischer 1966 & 1972). The presently described Australian species closely resembles *Setodes niveolineata* Kimmins (1962) from Kokoda, New Guinea. If at any future date the present-day generic concept of *Setodes* is revised and generic separation takes place, these two species undoubtedly will remain together in one generic group.

Setodes bracteatus described in this paper, together with a group of other species shown by Neboiss (1981) is restricted to the rainforest areas of North Queensland as delineated by Kikkawa et al. (1981) and does not extend further south than the estimated south-eastern boundary of Torresian province near Townsville (Neboiss, 1981).

The present study is based on material now deposited in the institutions indicated in the text by the following abbreviations:

ANIC—Australian National Insect Collection, Canberra.

BM— British Museum (Natural History), London.

NMV— National Museum of Victoria, Melbourne.

QM— Queensland Museum, Brisbane.

Genus *Setodes* Rambur, 1842

Setodes Rambur, 1842, p. 515; Ulmer, 1907 p. 145; 1951 p. 421. Marlier, 1962 p. 194.

Type species: *Setodes punctella* Rambur 1842 = *Phryganea viridis* Fourcroy, 1785. Subsequent designation by Milne, 1934.

Generic diagnosis:

Head and thorax clearly marked with silvery-white, longitudinal lines which extend onto the wings in closed position. Antennae long, about twice the length of wings, in males slightly longer than in females, segment 1 enlarged, ovoid; segment 2, short, globular; segment 3 and subsequent segments slender with fuscous annulations. Maxillary palpi (Fig. 2) slender, 5-segmented, segments 4 and 5 granular in appearance, flexible. Spurs 0:2:2.

Wing venation similar in both sexes. Anterior wings long, narrow, lanceolate, apex acute, apical forks 1 and 5 present, discoidal cell short, thyridial cell long and narrow; posterior wing narrower than anterior, acute apically, costal margin obtusely angled, Rs incomplete at base, discoidal cell absent.

***Setodes bracteatus* sp. n. (Figs. 1-9)**

This Australian species is characterized by having four silvery stripes on thorax. All other diagnostic features are found in the male and female genitalia.

Male genitalia (Figs. 4-6)

Dorsal section of segment 9 very short, ventral section long, posterior margin broadly triangular in ventral view; superior appendages short, dorso-ventrally flattened; tergite 10 with lateral margins gradually curved to bluntly

pointed apex, slightly down-turned distally. Phallus in lateral view (Fig. 3) broad at base, apex bluntly pointed and arched downward, a pair of transparent hook-like processes on dorsal margin; a pair of strong downwardly-directed parameres arises dorso-basally, apices of which are curved and pointed; a pair of slender processes arise on the inner surface, their length varies between individuals. Inferior appendages short, three-branched; upper basal branch laterally flattened, inner surface covered with long bristles, the postero-ventral angle produced into a digitiform process; the two lower branches curved, apices pointed, directed mesally.

Female abdomen (Figs. 7-9) with segment 9 short, laterally with a row of sparse marginal bristles dorsally a pair of short lobes, bearing a few short setae; segment 10 extended distally to a slender digitiform process; lateral lobes rather large, elongate, apically incised, lower lobe being the smallest with several long bristles at apex. Ventral plate broad, apically rounded, mesally produced to a short central projection and covered with stout scattered spicules.

Length of anterior wing: ♂ ♀ 4.5-5.5 mm.

Type material: Holotype ♂ Gordon Creek, Iron Range, Cape York Peninsula, North Queensland, 18 Apr.-18 June 1975, M. S. and B. J. Moulds (NMV, T-7479); paratypes 50 ♂ 20 ♀, collected with holotype (ANIC, BM, NMV; QM); 10 ♂ 3 ♀, same loc., 2-9 June 1971, E. F. Riek (ANIC, NMV) (specimen PT-1156 ♀ figured); 9 ♂ 2 ♀, same loc., 27 Apr.-4 May 1973, S. R. Monteith (ANIC); 4 ♂ 1 ♀, Upper Daintree, 11 June 1971, E. F. Riek (ANIC, NMV) (specimen PT-1139 ♂ figured).

Other material examined: **North Queensland**—1 ♀, Gordon Creek, Iron Range, 16 Oct. 1974, M. S. Moulds (NMV); 1 ♀, Middle Claudie River, Iron Range, 2-9 Oct. 1974, M. S. Moulds (NMV); 1 ♂, Mossman, 12 June 1971, E. F. Riek (ANIC); 2 ♂, Lacey's Creek, Mission Beach, 13 May 1980, I. D. Naumann and J. C. Cardale (ANIC); 2 ♂ 1 ♀, Downfall Creek, Tinaroo Falls Dam, 22 May 1980, I. D. Naumann and J. C. Cardale (ANIC); 1 ♂, Little Mulgrave River, 28 June 1971, E. F. Riek (ANIC); 1 ♂, 40 km W of Tully, 31 May 1971, E. F. Riek (ANIC); 1 ♀, Rocky Creek, Tully, 1

May 1979, A. Wells (NMV); ♂ ♀ (numerous), Alice River, Hervey Range Road, 25 km W of Townsville, 9 May 1979, A. Wells (NMV).

Distribution: North Queensland.

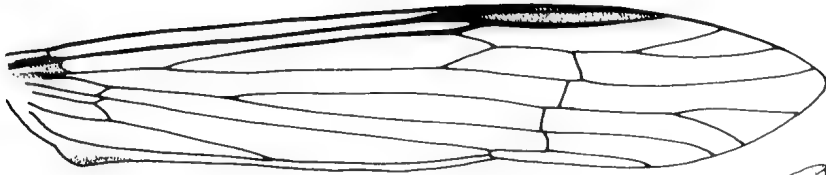
Acknowledgements

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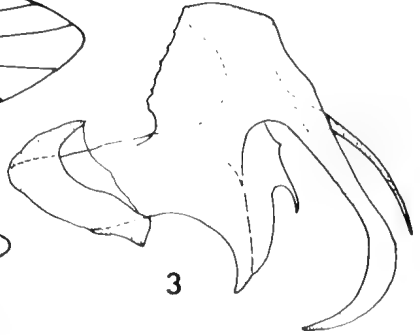
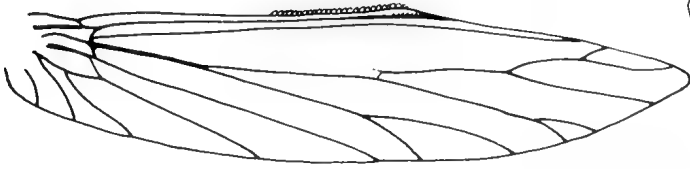
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Fig. 1-9. *Setodes bracteatus*, sp. nov., male, 1-6, 1, wings; 2, maxillary palp; 3, phallus, lateral; 4, 5, 6, genitalia, lateral, dorsal, ventral; 7, 8, 9, female genitalia, lateral, dorsal, ventral.



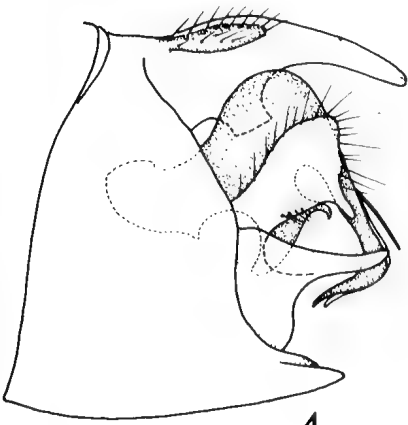
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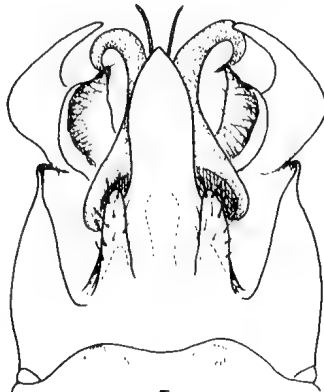
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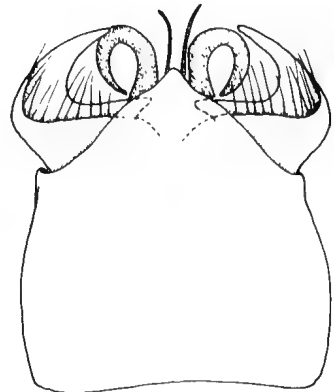
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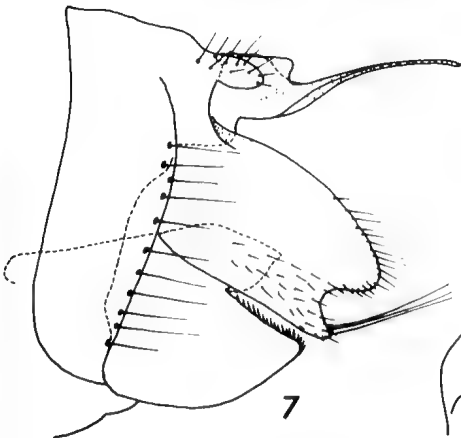
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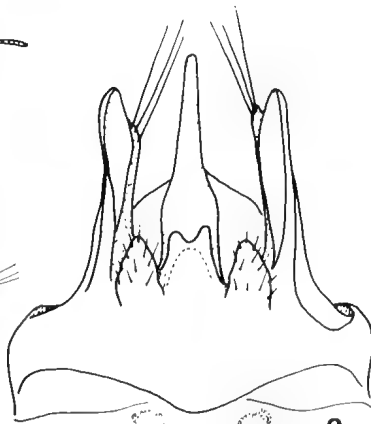
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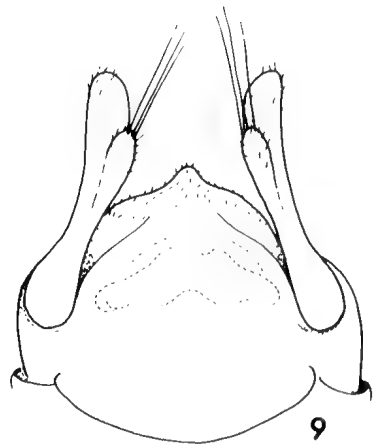
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**WARENDJA WAKEFIELDI, A NEW GENUS OF WOMBAT
(MARSUPIALIA, VOMBATIDAE) FROM PLEISTOCENE SEDIMENTS IN
McEACHERNS CAVE, WESTERN VICTORIA**

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Abstract

Two mandibles and six isolated teeth recovered from Pleistocene sediments in McEacherns Cave, western Victoria, represent a new genus and species of a morphologically primitive wombat. It combines unrooted, slightly bilobed molars showing little curvature, with a slender ramus, unfused symphysis, weak development of the masseteric and pterygoid fossae, a low set articular condyle, and a broad coronoid process. The associated faunal assemblage includes typical later Pleistocene taxa, such as *Zygomaturus trilobus*, *Sthenurus gilli*, *S. cf. occidentalis* and *Thylacoleo carnifex*. Modern taxa, dominated by *Rattus fuscipes*, *Antechinus stuartii* and *Perameles nasuta*, indicate wet sclerophyll forest conditions.

Introduction

McEacherns Cave lies about 550 m south of the Glenelg River, in the Lower Glenelg National Park, southwestern Victoria. In 1963, A. C. Beaglehole and F. Davies discovered fossil mammal bones in the cave and commenced preliminary excavations in the floor sediments. This work was continued in 1964 and 1965 by the late N. A. Wakefield, who carried out extensive excavations. In 1967, Wakefield published a preliminary report describing the cave and its sediments, and listing the faunal remains from the initial excavations in 1963 and 1964. The bulk of the material, only partly sorted, was deposited in the National Museum of Victoria in 1972, after Wakefield's death. In 1975, J. H. Hope commenced sorting the Wakefield Collection, and followed this by further excavations at McEacherns Cave in November-December 1977. In May 1978, the remains of a previously undescribed genus of wombat were found in the material from the 1964-5 excavation. The specimens have been registered in the palaeontological collection of the National Museum of Victoria.

Terminology and Measurements

Mandibular terminology follows Stirton (1967), and dental morphology Archer (1978). In this latter system, the permanent cheek teeth of vombatids are P3, M2, M3, M4 and M5. Measurements were made with a Mitutoyo dial caliper, to 0.1 mm.

Systematics

The following diagnoses are not intended to be exhaustive at each taxonomic level, but rather are restricted to those features which can be observed on the type and referred specimens of *Warendja wakefieldi*.

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTA Owen, 1866
Family VOMBATIDAE Burnett, 1830

Diagnosis: Distinguished from all other Marsupialia by the presence of four bilobed, hyposodont, labially curved and open-rooted molars and open-rooted I1 and P3.

Warendja gen. nov.

Type species: *Warendja wakefieldi* sp. nov.

Known distribution: Pleistocene, western Victoria.

Diagnosis: Distinguished from all other vombatids by small, sub-rectangular, minimally bilobed molars, which show little longitudinal curvature; smooth, unfused mandibular symphysis; the combination of a broad ascending ramus and well developed coronoid process with poorly-developed masseteric and pterygoid fossae; and the close approximation of the articular condyle to the plane of the mandibular tooth row.

Etymology: In the language of the Woiwuro people of the Melbourne district, *warendj* means wombat (Hercus, 1969).

Warendja wakefieldi sp. nov.

Plate 3, Figure 2

Holotype: NMV P48980, right mandibular fragment with P₃, M₂₋₅, and alveolus for I₁. The articular condyle is present but the upper portion of the coronoid process is broken away.

Referred specimens: NMV P48982, right mandibular fragment with P₃, M₂₋₅ and the basal portion of I₁. The articular condyle and part of the coronoid process are not preserved. NMV P48981, isolated right M₅. NMV P165428, isolated left I₁. NMV P165429, isolated left P₃. NMV P165430, isolated left M₄. NMV P165431, isolated right M₄. NMV P165432, isolated left M₃.

Type locality: McEacherns Cave, Lower Glenelg National Park, western Victoria. The specimens were among material in the National Museum of Victoria derived from the sediments identified as Pleistocene by Wakefield (1967). P48980 was collected 21 December 1964, from level 'R', by N. A. Wakefield. P48982 was collected 4-5 September 1964, from a section 24 to 27 feet northwest of the cave entrance, 0 to 1 inch below 'ML', by N. A. Wakefield. P48981 was collected 22nd May 1964, from level 'B2' in a section 18 to 21 feet northwest of the cave entrance, by N. A. Wakefield. P165428-32 were collected from level 'Q', by N. A. Wakefield.

Diagnosis: That of the genus until other species are described.

Etymology: Named in honour of the late Norman Arthur Wakefield.

Description

Mandible: (Table 1): The mandible is remarkably smaller and more delicately built than in all other known vombatids. In P48980 especially, and to only a slightly lesser degree in P48982, this is emphasised by the swept-back appearance of the ascending ramus, the anterior border of which is inclined at a lesser angle than in any other described species. The lightly built appearance of the mandible is due to the presence of very shallow masseteric and pterygoid fossae, again a feature not found in any other wombat species.

When viewed laterally, the ventral border of the mandible forms a very shallow curve with a

TABLE I
Measurements (mm) of the mandible of
Warendja wakefieldi

	P48980	P48982
Length of mandible	92.5	est. 100
Greatest width of mandible	21.5	21.2
Depth of ramus below mid M ₄	20.3	24.2
Length of diastema	16.8	16.9
Length from alveolus of incisor to posterior alveolar margin of M ₅	51.2	57.6
Width of ascending ramus	33.0	
Condyle—transverse width in vertical orientation	12.9	
maximum transverse width	14.1	
maximum length in antero-posterior direction	7.8	
Height from ventral border of ascending ramus to sigmoid notch	33.1	

concavity beneath the anterior root of the ascending ramus and a convexity beneath M₄. In both mandibles the symphysis is elliptical in shape. Its major axis is about 34 mm long in P48982 (the posterior end is broken in P48980), and in both specimens dips posteriorly at an angle of 30° with respect to the dorsal edge of the horizontal ramus. The length of the minor axis is 9.4 mm in P48980 and 10.8 mm in P48982. The surface of the symphysis is only slightly roughened in both specimens, and there is no indication of symphyseal fusion between left and right mandibles.

This condition could be taken as evidence that both mandibles were juvenile, but P48980 is certainly fully adult. A fortuitous break between P₃ and M₂ allowed inspection of the full length of these teeth, which have almost identical top and bottom dimensions. In juvenile wombats, all teeth are distinctly conical, with proximal dimensions greater than distal (wear surface). The disparity reduces progressively until adulthood is reached. P48982 is an older adult specimen, showing a greater amount of tooth wear. Therefore the lack of symphyseal fusion is a valid diagnostic character.

The diastema is simple in morphology and relatively short. In P48980 the diastemal margin is a sharp crest, folded inwards slightly, above a longitudinal groove on the labial surface of the ramus. P48982 is similar, but is not as well preserved. The mental foramen in P48982 is large, and lies below the anterior

alveolar edge of P_3 . In P48980 the mental foramen lies anterior to P_3 , below the diastema. A second, smaller foramen lies posterior to this, below the posterior half of P_3 .

In both mandibles the anterior root of the ascending ramus is opposite the posterior lobe of M_5 . Its anterior border sweeps back in a gentle convex curve. Although the top of the coronoid process is not preserved in either specimen, it is clear that it, and the ascending ramus, are larger relative to the postero-ventral width of the ramus than in any other wombat.

Angle a as defined in Figure 1 is 56° in P48980, and 59° in P48982. The condyle is preserved only in P48980. It is small and ovoid, its transverse width about twice its length antero-posteriorly. It is set very low, close to the plane of the tooth row, as indicated by a measurement of 18° for angle b as defined in Figure 1. The articular surface of the condyle is on the lingual side, approaching the line of the tooth row.

The masseteric fossa is well-preserved in both mandibles. It is very shallow in P48980, deeper in P48982. The deepest area of the concavity lies immediately behind the anterior border of the ascending ramus, indicating that the main area of insertion of the masseteric muscle was higher and more anterior than in other wombats. The posterior masseteric eminence is well developed in P48982, with a sharp up-turned edge; in P48980 this outer flange is smooth and weakly developed. There are two foramina within the masseteric fossa in P48982, but only one in P48980.

The pterygoid fossa is also very shallow for a vombatid. In P48980 it forms a shallow lateral concavity with no ventral floor, due to the lack of development of the lingual flange of the fossa. In P48982, this flange is better developed, and the fossa is deeper with a flat floor ventrally. The height of the ventral rim of the mandibular foramen above the ventral border of the horizontal ramus is 9.8 mm in P48980, and 10.1 mm in P48982. In P48980 this foramen is simple and rounded; in P48982 it is part of a large depression in the centre of the pterygoid fossa, and the bone posterior to it is fenestrated. In both mandibles the angular process is broken but in the better preserved

P48980 it probably did not extend as far as the most posterior point on the condyle.

There is no digastric fossa present on either mandible. Instead, the lingual surface of the horizontal ramus forms a smooth convexity, with its highest point immediately behind the posterior limit of the symphysis. This bulge is caused by the large open root of the lower incisor, which in P48982 can be seen through a break in the bone.

Dentition (Tables 2, 3): The total length of the molar row in the holotype P48980 is 32.5 mm (occlusal measurement), and the corresponding figure for the referred specimen P48982 is 37.8 mm. These figures are significantly smaller than for any other wombat currently accepted as a valid species. All the teeth are open rooted. As in *Vombatus* and *Lasiiorhinus* there is no distinct cemento-enamel junction. The cementum continues over the enamel up the column of the tooth to the occlusal surface, so in most cases enamel is visible only as a rim at the occlusal surface. With isolated teeth, the distribution of enamel can be determined not only by its appearance at the occlusal surface, but by the presence of brown and white transverse markings, indicating zones of enamel formation, on the columns of the tooth, towards the root.

I_1 : The incisor is represented by a broken basal portion in P48982, and by an almost complete alveolus in P48980. In P48982 it is a simple, ovate tooth, much deeper than wide at its broken end. The alveolus in P48980 is similar in shape. The enamel is restricted to the ventral and lower labial surfaces. The open root extends back to beneath the mid-point of M_3 .

P_3 : The premolar is sub-triangular in occlusal outline, weakly bilobate, and has its long axis parallel to the antero-posterior axis of the mandible. It is slightly offset lingually to the molar row, and the posterior apex of the triangular occlusal outline is adpressed against the antero-lingual corner of M_2 . In P48980 the tooth is nearly vertical, but in P48982 it is curved antero-posteriorly. Enamel is restricted to the anterior rim of the anterior lobe of P_3 in P48980; in P48982, enamel occurs only on the anterior labial surfaces of both the lobes. There

TABLE 2

Measurements (mm) of lower teeth of *Warendja wakefieldi* (occlusal, unless otherwise stated)

	P48980	P48982
Total length P ₃ -M ₅	32.3	37.8
Total length P ₃ -M ₅ †	35.5	40.8
P ₃ length	5.3	6.6
width of anterior lobe	2.4	2.9
width of posterior lobe	3.1	3.7
height above alveolar margin of posterior crest	4.0	6.1*
height above alveolar margin of notch	2.2	5.3
difference in elevation between notch and posterior crest	1.8	0.8
M ₂ length	7.4	8.2
width of anterior lobe	3.9	4.7
width of constriction	3.5	4.6
width of posterior lobe	5.1	5.6
height above alveolar margin of crest of anterior lobe	4.4	9.3
height above alveolar margin of posterior lobe	2.5	6.2
difference in elevation between upwards projection of anterior lobe, and occlusal surface of the posterior lobe	2.3	3.1
M ₃ length	7.4	8.6
width of anterior lobe	4.4	5.5
width of constriction	4.2	5.2
width of posterior lobe	5.5	6.2
M ₄ length	6.8	8.7
width of anterior lobe	5.0	5.8
width of constriction	4.0	5.0
width of posterior lobe	4.8	6.0
M ₅ length	6.0	7.4
width of anterior lobe	4.2	5.1
width of constriction	3.7	4.8
width of posterior lobe	4.0	4.8
I ₁ width	5.2†	5.5
depth	8.3†	8.0

* Not strictly comparable to P48980 because alveolar margin appears to be more broken away.

† Alveolar measurements.

is a distinctive pattern of wear on both premolars. In P48980 this has resulted in a deep notch on the occlusal surface running diagonally from antero-lingual to postero-labial, leaving the anterior and posterior rims of the tooth standing as sharp crests. In P48982, at a later stage of tooth-wear, the occlusal surface is saddle-shaped, with the enamel-less posterior rim left as a sharp point.

M₂₋₅: The occlusal outline of all the molars is sub-rectangular, with slightly developed, but

TABLE 3

Measurements (mm) of isolated teeth of *Warendja wakefieldi* (occlusal, unless otherwise stated)

I ¹ (P165428)	
depth at proximal end of wear facet	5.9
width at proximal end of wear facet	4.0
depth at open root	5.4
width at open root	3.7
length of wear facet	9.2
width of wear facet	3.9
P ³ (P165429) length	6.4
width of anterior lobe	4.0
width of posterior lobe	4.5
M ⁴ (P165430) length	7.7
width of anterior lobe	6.5
width of constriction	5.2
width of posterior lobe	6.2
M ⁴ (P165431)	
width of anterior lobe	6.5
M ³ (P165432) length	7.8
M ₅ (P48981) length	5.6
width of anterior lobe	4.3
width of constriction	4.1
width of posterior lobe	4.9

distinct bilobation. The lobes are almost quadrangular in cross-section, with rounded corners. A thin rim of enamel extends around the lingual and labial edges of the occlusal surface of the teeth. It is absent anteriorly and posteriorly on each tooth. The anterior lobe of M₂ is narrower than the posterior, which is the most nearly cylindrical of any lobe of the four molars. The anterior lobe of M₂ is distinctly smaller in both length and width. It is also distinguished by a peculiar wear pattern, related to that of the premolar. Whereas the occlusal surfaces of M₃₋₅, and of the posterior lobe of M₂, are nearly horizontal, the occlusal surface of the anterior lobe of M₂ rises anteriorly at a sharp angle. When viewed laterally, the anterior lobe of M₂ in P48982 protrudes as a sharp, high crest from the nearly horizontal occlusal surface of the tooth row. In P48980 the equivalent high crest is made up of both the anterior lobe of M₂ and the posterior lobe of P₃.

In common with other vombatids, M₃ is the widest molar, its posterior lobe being the widest part of the molar row. The lobes are more nearly equi-dimensional than those of M₂, and the occlusal outline is almost subrectangular.

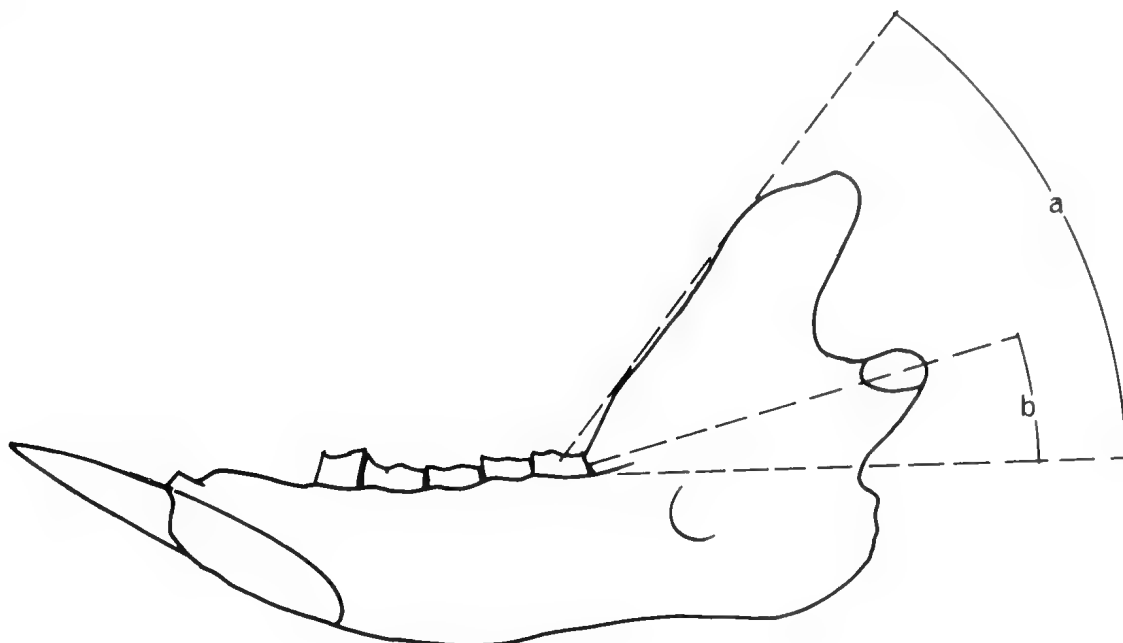


Fig. 1. Schematic diagram of the mandible of *Warendja wakefieldi* illustrating the method of measuring inclination of anterior border of ascending ramus (angle a) and elevation of condyle (angle b).

The anterior lobe in both specimens retains a trace of a transverse loph on the lingual side, and this is also visible on the anterior lobes of M_4 and M_5 in P48982. In M_4 the two lobes are nearly equal in size and the tooth is the most nearly rectangular of all the molars. The last molar, M_5 , is the smallest, and tapers markedly posteriorly. The isolated tooth, P48981, appears to be a right M_5 , in showing the bilobed form characteristic of the molars, but with one lobe clearly smaller than the other. It is most similar to M_5 of P48980. Wear on M_{3-5} is transverse and has left the lingual rim of the molars standing higher than the labial rim.

The remaining five isolated teeth are interpreted as representing elements of the upper dentition.

I^1 : A left upper incisor, P165428, is attributed to *Warendja* because of its open root, but smaller size and different morphology from any other wombat. The tooth is longitudinally curved, laterally compressed and ovate in cross-section. It tapers slightly from the distal to the proximal end. Enamel occurs on the anterior

(dorsal) and labial faces. There is an elongate, ovate wear surface on the posterior face of the tooth. The occlusal surface is slightly asymmetrical, being flattened on the lingual side, where it abuts the right incisor.

P^3 : A single tooth, P165429, is tentatively identified as a left upper premolar. It is similar to the lower premolars in being longitudinally, rather than laterally curved (as the molars are), and in having an extensive exposure of enamel on the convex (anterior) face. It is, however, larger and more ovate than the lower premolars. It is bilobed, with the labial groove deeper than that on the lingual face. The depth of enamel on the anterior face is 5.5 mm below the occlusal surface. Enamel extends onto the labial and lingual faces of the anterior lobe, and also occurs on the antero-labial face of the posterior lobe.

The upper premolar should occlude with both P_3 and the anterior lobe of M_2 . In both lower dentitions available, differential wear has occurred on the anterior teeth, leaving the anterior lobe of M_2 standing as a high crest. This suggests that the upper premolar occludes mainly with the lower, and that there is minimal wear on the anterior lobe of M_2 , except at the posterior of this lobe, where it meets M^2 . The

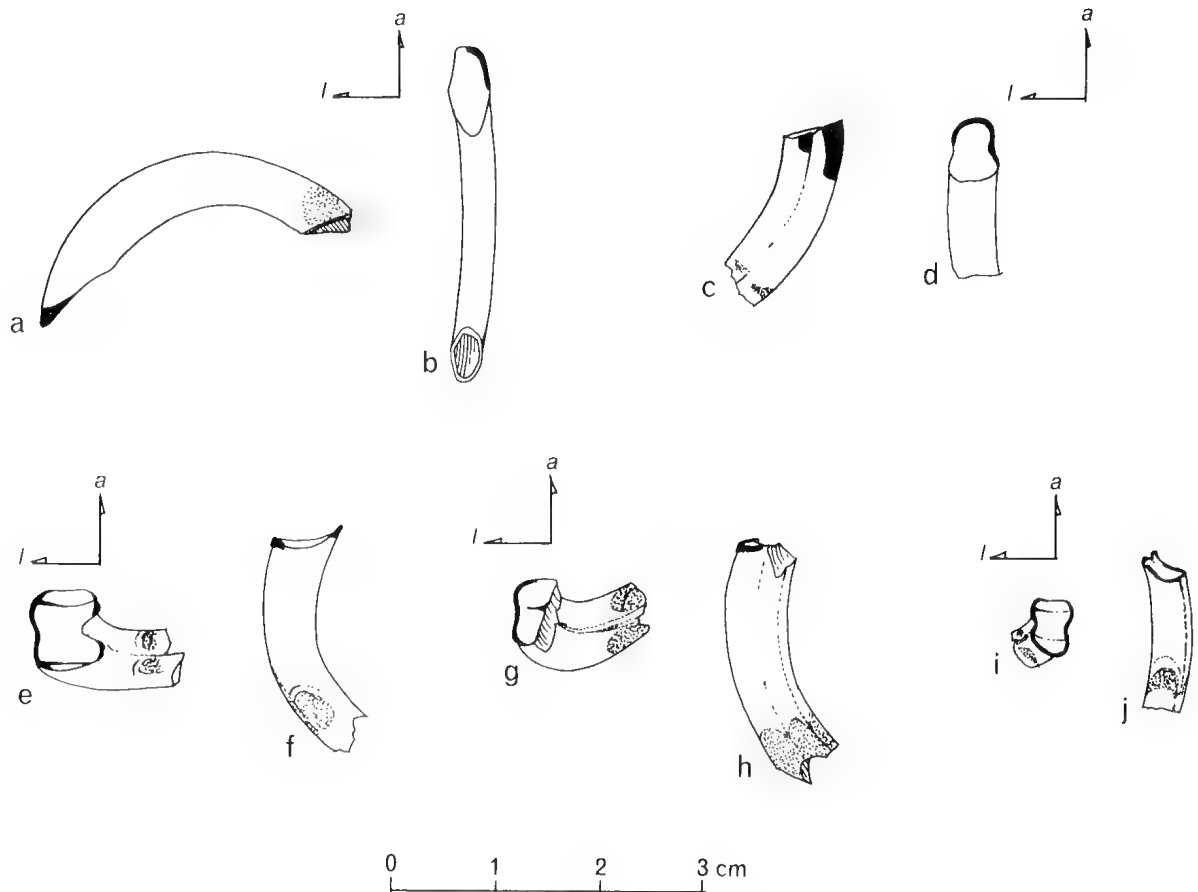


Fig. 2. Isolated teeth of *Warendja wakefieldi*. NMV P165428, left I^1 , a, labial view; b, occlusal view. NMV P165429, ? left P^3 , c, labial view; d, occlusal view. NMV P165430, ? left M^4 , e, occlusal view; f, posterior view. NMV P165432, ? left M^3 , g, occlusal view; h, posterior view. NMV P48181, right M_5 , i, occlusal view; j, posterior view. Orientation of occlusal views; a-anterior, l-lingual.

occlusal surface of P165429 shows a saddle-shaped wear pattern similar to that of the lower premolars, but less extreme. The wear is consistent with the argument that P^3 occludes mainly, or only, with P_3 , but a complete maxillary tooth row, with associated mandible, would be needed to verify this.

Upper molars: Three isolated molars are attributed to *Warendja* on the basis of size, and their minimal degree of bilobation and curvature. They are larger than the lower molars, have an asymmetric occlusal outline, and are more strongly curved, so are interpreted as upper molars.

On the assumption that the concave face of

each upper molar is labial, as in other vombatids, then the labial and lingual orientations are easily determined. The allocation of each tooth to left or right, or to specific positions in the tooth row, is tentative, and has been based on the direction of curvature of the roots, by comparison with *Vombatus* and *Lasiorhinus*.

These molars are distinguished by the asymmetry of their medial constriction. The lingual (convex) face is barely constricted, with a shallow indentation running the length of the root. The lingual enamel surface is virtually uninflected. In contrast, the labial (concave) surface is more deeply constricted, to the degree found on both labial and lingual faces of the lower molars.

As in the lower molars, enamel is restricted to the labial and lingual surfaces of the teeth. In the only unbroken specimen, P165430, the labial edges of the anterior and posterior lobes form sharp points, although this is more the result of wear than of the structure of the tooth.

Wear has left the labial rim of the tooth standing higher than the lingual rim. In P165430 traces of transverse lophs can be seen on the occlusal surface of the anterior and posterior lobes.

Discussion

The taxonomy of wombats at the generic level has been in a state of flux for many years. One of us (HEW) presented a phylogeny of the family at the 1971 Brisbane ANZAAS, but circumstances have so far prevented publication of this work, which was based on a comprehensive study of virtually all fossil wombat material available in Australia at that time. The most recent published consideration of wombat phylogeny is that of Dawson (1981), who recognised the following Pleistocene and modern taxa: *Vombatus ursinus*, *Phascolonus gigas*, *Ramsayia magna*, *Lasiorhinus medius*, and *Lasiorhinus latifrons*, and suggested that the recently described *Phascolonus lemleyi* Archer & Wade 1976 should be referred to *Ramsayia*. In addition to the above, Wilkinson (in prep) recognises *Vombatus hacketti*, *Lasiorhinus krefftii* and *Phascolonus angustidens* as valid species of true wombats, and regards the generic status of *medius* as problematical. *Rhizophascolonus crowcrofti* is the only described vombatid genus restricted to the Tertiary (Stirton et al. 1967), but this differs from all other vombatids in having a rooted premolar.

Dawson's phylogenetic scheme is at considerable variance with that put forward by Wilkinson (1971, in prep), on which the discussion below is largely based. However, the alternative views put forward by Dawson are also referred to.

Generic status for *Warendja wakefieldi* is justified by the so far unique combination of the open-rooted, hypsodont teeth, with the gracile mandibular morphology. The teeth, clearly vombatid in form, differ from all known vombatids in their minimal curvature, and their weakly bilobed morphology. The lower premolar shows some similarity to those of *Phascolonus* and *Ramsayia*, particularly in the antero-posterior orientation, incipient bilobation and size, relative to the molars, but differs

in being sub-triangular in occlusal outline rather than ovoid to sub-rectangular. There is little affinity with the ovoid, more or less obliquely set lower premolars of *Lasiorhinus* and *Vombatus*.

The sub-rectangular, sub-bilobate molars differ from all other wombats in their distinctive occlusal outline and small degree of longitudinal curvature, but are closest to *Phascolonus* and *Ramsayia* in general appearance. The most noticeable differences between *Phascolonus* and *Warendja* are the relatively small degree of medial constriction and the less rounded angles of the molars in the latter. It is easy to envisage an evolutionary trend from the *Warendja* molar type to that of *Phascolonus* by an increase in medial constriction, and an increase in rounding of the lobes to give a more cylindrical appearance. There is no close affinity to the rounded triangular lobes of *Lasiorhinus* molars, and even less to the sharply angled lobes of *Vombatus* molars.

The single tooth, considered to be a P₃, representing the Miocene genus *Rhizophascolonus*, differs from all known wombats, including *Warendja*, in having closed roots. Although not directly comparable with *Warendja*, as illustrated in Stirton et al. (1967), it does show some similarity to the molars of *Warendja* in the rounded cylindrical form of the lobes. The simple cylindrical lower incisor of ovoid cross-section is very similar to that of *Phascolonus angustidens* (Wilkinson, in prep.), and is also similar in both shape and the extent of surface enamel to *Phascolonus gigas*, and especially to *Ramsayia* (Dawson 1981, Wilkinson in prep.). The upper incisor is also simple and is quite distinct from the broad flattened upper incisor of *Phascolonus gigas*.

The larger of the two mandibles (P48982) is fully adult, so *Warendja wakefieldi* is considerably smaller than any of the described wombat species. The nearest in size is the small Bass Strait Islands wombat, *Vombatus ursinus*, but this is a scaled down version of the common wombat of southeastern Australia, *Vombatus hirsutus*, which is regarded by some authorities (e.g. Dawson 1981) as a sub-species of *ursinus*. Even if *ursinus* is accepted as a valid species, it is still larger than *W. wakefieldi*.

The detailed morphology of the mandible of *Warendja* reflects this small size. The slender jaw has shallow masseteric and pterygoid fossae, and a small articular condyle, compared with the deep pterygoid fossae, deep to very deep masseteric fossae, and wide, robust articular condyles in other vombatids. In *Phascolonus* and *Ramsayia* the mandible is very robust, but deep and comparatively narrow. In *Lasiorhinus* and *Vombatus* the mandible is very broad, with thick, relatively shallow rami, which support very powerful musculature. *Warendja* differs from all of these in the delicate build of the mandible and the lesser development of the masseteric and pterygoid fossae. While this light build is to some extent probably just a reflection of small size, two features of the mandible are especially un-wombatlike. The size and smoothness of the mandibular symphysis indicate that the left and right mandibular rami never fused, as happens in other wombats. The extremely low position of the articular condyle relative to the plane of the molar row is unique in vombatids, and indeed unusual compared with most other diprotodont families (Table 4).

In general, the articulation of the jaw tends to be in line with the tooth row in carnivores, but is much higher than the tooth row in herbivores. The high position increases the lever arm of the masseter muscle. The low angle in *Warendja* is more comparable to that found in carnivores, such as *Sarcophilus*, *Dasyurus* and *Thylacoleo* (Finch 1971), rather than herbivores. The only diprotodont groups which exhibit a low-set condyle are the phalangerids and potoroines. The jaw structure in rat-kangaroos such as *Aepyprymnus* and *Bettongia* differs in other ways from that in *Warendja*. The phalangerids, *Phalanger* and *Trichosurus*, are quite similar, however, not only in the position of the condyle, but in the relative proportions of the masseteric and pterygoid fossae and the ascending ramus. A comparative study of the jaw mechanics of these taxa might elucidate the feeding habits of *Warendja*.

These characteristics of the mandible of *Warendja* indicate a very different system of jaw musculature from other wombats, and this has implications for the structure of the as yet

TABLE 4

Comparative measurements of the angle of inclination of the ascending ramus (angle a) and of the elevation of the condyle (angle b). Angles approximate only

Taxon	a	b
VOMBATIDAE		
<i>Warendja wakefieldi</i>	56°	18°
NMV P48980	59°	—
NMV P48982	70°	30°
<i>Vombatus ursinus</i>	65°	35°
<i>Lasiorhinus latifrons</i>	75°	40°
<i>Phascolonus gigas</i> ¹		
DIPROTODONTIDAE		
<i>Raemoeotherium yatkolai</i> ²	62°	<32°
<i>Diprotodon optatum</i>	105°	65°
PHASCOLARCTIDAE		
<i>Phascolarctos cinereus</i>	75°	38°
PHALANGERIDAE		
<i>Trichosurus vulpecula</i>	65°	28°
<i>Phalanger orientalis</i>	58°	10°
PETAURIDAE		
<i>Pseudocheirus peregrinus</i>	75°	38°
MACROPODIDAE		
<i>Bettongia leseuer</i>	55°	25°
<i>Aepyprymnus rufescens</i>	57°	22°
<i>Wallabia bicolor</i>	90°	40°
<i>Macropus giganteus</i>	75°	40°
THYLACOLEONIDAE		
<i>Thylacoleo carnifex</i> ³	35°	10°
PERAMELIDAE		
<i>Isodon obesulus</i>	60°	30°
<i>Perameles nasuta</i>	48°	30°
DASYURIDAE		
<i>Dasyurus maculatus</i>	60°	12°
<i>Sarcophilus harrisi</i>	62°	10°

¹ Measured on Plate XL, Stirling (1913).

² Figures quoted from Rich *et al.* 1978.

³ Relative to occlusal plane of P₃.

unknown skull of *Warendja*. By analogy with the skulls of *Trichosurus* and *Phalanger*, *Warendja* is likely to have had a more rounded cranium, with greater areas for insertion of the temporal muscles than in other wombats, and possibly some development of a sagittal crest. In *Vombatus* and *Lasiorhinus*, the structure of the zygomatic arch is distinctive, with no development of the masseteric process, but rather a broad area excavated beneath it for the insertion of the masseter muscle. Given the probable lesser development of the masseter in *Warendja*, the structure of the zygoma may have been more like that of the phalangerids,

with the anterior zygomatic surface vertical rather than horizontal (as in other wombats), and with a masseteric process. In summary, the skull of *Warendja* will probably look more like that of *Trichosurus* than any wombat. This is not to imply any special relationship between phalangerids and *Warendja*; these characters are probably plesiomorphic for diprotodonts generally.

Dawson (1981) carried out a cladistic analysis of the five vombatid taxa she recognised, using a set of seven dental and palatal characters. The resulting cladogram linked *Vombatus ursinus* with *Phascolonus gigas*, and *Ramsayia magna* with *Lasiorhinus latifrons* and *L. medius*. For most of Dawson's dental characters, *Warendja* exhibits the plesiomorphic state. The one exception is the depth of the lower incisor, where the apomorphic state, I_2 being deeper than wide, is found in *Warendja*. *Warendja* is intermediate with regard to the structure of the lower premolar, but Dawson concluded that convergence had occurred in this character among vombatids. Dawson's cladistic analysis does not clarify the relationship of *Warendja* to other vombatid taxa, since it is plesiomorphic in most observable characters.

Warendja fits rather better into the as yet unpublished phylogenetic scheme of Wilkinson (1971; in prep). As shown above, it is linked to the *Phascolonus-Ramsayia* group by premolar and molar morphology, and more particularly by the morphology of the lower incisor. It has almost nothing in common with either *Lasiorhinus* or *Vombatus*, apart from family characters. The suggestion by Dawson that these latter genera have evolved separately, and gained similarity by convergence, cannot be sustained when skeletal characters are considered. The skulls of *Vombatus* and *Lasiorhinus* are basically similar, but readily distinguished, as are the skeletons of *V. ursinus* and *L. latifrons*. However, the skeleton of *L. krefftii* blurs the generic boundary to a remarkable degree, which is more readily explained by common ancestry than by convergence.

Warendja probably represents an ancestral vombatid type, from which the *Phascolonus-Ramsayia* group evolved. '*Phascolomys*' *medius* (whose generic assignment is prob-

lematical) is the link between *Phascolonus-Ramsayia* and *Lasiorhinus*, from which *Vombatus* has in turn been derived. In the light of this, the provenance, probable age and faunal association of *Warendja* are of especial interest.

Age and Palaeoenvironment

McEacherns Cave is formed in the Gambier Limestone, of Oligocene-Miocene age. It is approximately 60 m long, along a NW-SE axis, averages 3 m in width and 3 m in height and is connected to the surface by a vertical shaft 13 m deep and 1.5 m in diameter. The cave fill consists of sandy fossiliferous units and extensive roof-fall. The cave itself and the early excavations of the fossil-bearing sediments, in the northwest chamber of the cave, are described by Wakefield (1967) and Link (1967).

Wakefield recognised a series of stratigraphic units in the sandy floor sediments. The oldest of these, which he called the 'Pleistocene' sediments, consist of a block of compacted grey sands laid down on limestone boulders, part of an earlier roof-fall. Overlying this block is a 'calcarenite' deposit, about 5-10 cm thick, consisting of finely laminated layers of calcium carbonate beneath 5-20 cm of grey clay. Above and on each side of the block of grey sand with its calcarenite capping are successive layers of white, red and black sands, Wakefield's 'Recent' sediments. Laterally the white sands are in fact at a lower level than the grey block, filling a cavity formed by slumping and collapse.

The new excavations by Hope at McEacherns Cave confirm this basic stratigraphy, although some details are at variance with Wakefield's report, and the stratigraphy of his 'Recent sands' is probably more complicated than he recognised.

Wakefield obtained only one radiocarbon date from the site based on 373.4 g of mammal bones extracted from the uppermost layers of the grey block, about 0.5 cm below the calcarenite layer. This material gave a date of $15,200 \pm 320$ years before present (GaK-509). This date for the top of the grey sand, along with the absence of any element of the extinct Pleistocene fauna from the overlying white and red sands (except as reworked material) was in-

terpreted by Wakefield as indicating that the older grey sand was late Pleistocene in age, while the remaining sediments were all Holocene in age. He suggested that the calcarenite layer indicated a period of aridity, attributed to 'a mid-Holocene warm-arid period'. Link (1967), however, argued that the calcarenite might have been formed by frost brecciation of the walls of the cave during an arid and possibly cold phase about 8-11,000 years before present.

The results of the 1977 excavations at McEacherns Cave suggest that the sedimentary sequence is in fact much older. Preliminary radiocarbon dates indicate that the younger sands were deposited between 15,000 and 2000 years before present. A sample of the laminated calcarenite layer has also been dated, and this gave an age of $28,580 \pm 850$ years (ANU-2030). It was expected that this date might be similar to Wakefield's original date of 15,200 years before present on bone from immediately under the calcarenite layer, on the grounds that since the bone date was likely to be affected by contamination, the calcarenite and bone carbonates might have equilibrated.

It has proved difficult to obtain suitable charcoal from the older grey sand for dating. One sample has given a preliminary date of about 24,000 years before present (ANU-2372), but given the reversal between this and the calcarenite date, it is likely that some as yet unclear source of contamination is affecting organic materials in this unit.

There is some circumstantial evidence to suggest that the grey sands may be considerably older than the last Pleistocene glaciation and thus probably beyond the range of radiocarbon dating. There is clear evidence in the excavated section that the grey block is in effect a residual, left stranded after a period of collapse, and subsequently surrounded by the younger sediments. Elsewhere in the cave, remnants of similar sediments containing a similar fauna, including extinct species, are plastered on the cave walls up to 3 m above the top of the grey block. The exact relationship of these sediments to the grey block cannot yet be determined, but they may relate to the same event of cave fill, most of which has now disappeared.

A considerable period of time must be allowed for the almost complete filling of the cave by the older sediments, the deposition of the laminated calcarenite layer, and for the subsequent removal of much of these sediments, before the younger phase of deposition began, sometime before 15,000 years ago. Further, given the relative positions of the remnants of the older sediments, the excavated block of grey sediment may in fact date from the earlier stages of the older depositional event. An absolute age for the grey sediments is likely to prove impossible to obtain, but a hypothetical age for the calcarenite deposit and the sediment removal can be suggested, on the assumption that these are related to changes in regional watertable.

During the last interglacial maximum episode, from about 135-120,000 years ago, the maximum sea level relative to the New South Wales coast is considered to have been 5 ± 1 m above present sea level (Chappell and Thom 1978). In western Victoria, high sea level stands of approximately the same magnitude, 7.5 m and 4 m (the later regarded as a stage during the retreat of sea level), are also attributed to this time period (Gill and Amin 1975). Interstadial high sea levels younger than 118,000 years are thought to have been at least 8 m lower than the 135-118,000 year levels (i.e. below present sea level) (Chappell and Thom 1978).

McEacherns Cave lies approximately 550 m south of the Glenelg River, which is tidal at this point, and the surface of the younger cave deposit is approximately 6 m above the present river level. Therefore during the last interglacial maximum, the lower levels of the sediments in the cave were likely to have been affected by a higher regional watertable, related to the higher sea level.

Corroborative evidence may come from a study of the calcarenite sediments, whose origin is unclear at the moment. Wakefield suggested that they were of aeolian origin, while Link proposed frost action; a further possibility is that they were laid down under standing water. If in fact the formation of the calcarenite layer and the subsequent roof-fall and removal of much of the older fill were related to the rise

and then lowering of the watertable, then these events may have occurred during and at the end of the last interglacial, 135-118,000 years ago. The grey sediments themselves would be even older.

The specimens of *Warendja wakefieldi* were found among the material from McEacherns Cave in the N. A. Wakefield Collection at the National Museum of Victoria. Some of this material is poorly documented and is difficult to attribute with absolute confidence to a particular stratigraphic layer. In 1964-5 Wakefield excavated five 3 ft wide sections from wall to wall across the width of the cave. These together extended from 15 ft to 30 ft from the cave entrance, and were numbered accordingly in 3 ft blocks, i.e. 15-18 ft, 18-21 ft etc. Most of the material collected during this phase of the excavation was labelled with the section numbers, and also with the depth from the surface, but no record was kept of the lateral position across the cave. Part of the collection, however, was labelled using a code of letters or numbers. Bones so labelled can be allocated a stratigraphic position only by comparison of colour, preservation and faunal composition with better documented material.

One specimen of *Warendja*, P48982, is clearly provenanced within the system. This is labelled '24'-27', 0"-1" below ML' (ML middle layer = calcarenite layer). Unfortunately it is not possible to allocate the remaining specimens to specific positions in the excavation. The colour and degree of mineralisation of all specimens, and of the rest of the bone material with which they are associated, indicates that they are derived from the older Pleistocene unit.

Wakefield (1967) lists the faunal assemblages recorded from the older Pleistocene sediments, and from the younger Pleistocene red and black sands, based on material collected during the initial excavations in 1963 and 1964. He interpreted the faunal sequence from the younger sands (now known to be from more than 15,000 to about 2000 years before present) as indicating a change from a 'mallee' fauna, through a fauna including some woodland species, to the modern dry sclerophyll forest of the district.

In the older Pleistocene sediments the faunal assemblage is dominated by *Rattus fuscipes*, *Antechinus stuartii*, *Perameles nasuta* and the extinct kangaroo *Sthenurus gilli*. Other extinct Pleistocene species present are *Sarcophilus laniarius*, *Zygomaturus trilobus*, *Thylacoleo carnifex*, *Sthenurus* cf. *occidentalis* and *Protemnodon* cf. *brehus*. *Vombatus* sp. also occurs in the assemblage, but only isolated teeth have so far been recovered. Notable by their absence are many elements of the modern woodland and heath communities, such as *Antechinus swainsonii*, *Sminthopsis* cf. *leucopus*, *Isoodon obesulus*, *Trichosurus vulpecula*, *Macropus rufogriseus*, *Conilurus albipes* and *Pseudomys shortridgei*, all of which are abundant in the younger sediments in the cave. Preliminary analyses of the material collected by Wakefield in 1964-65, and by Hope in 1977 support these faunal lists for both the older and younger sediments.

Wakefield interpreted the faunal association from the older Pleistocene sediments as indicative of wet sclerophyll forest, which today occurs in areas of Victoria with an annual rainfall of 1000-1200 mm or more, such as the Otway Ranges and the east-central highlands. The dramatic change in faunal composition between the older and younger sediments also supports the hypothesis of a long hiatus in sedimentation within the cave.

Conclusion

Warendja wakefieldi is an enigma. The open-rooted dentition is clearly vombatid, but it combines some characters that could be seen as plesiomorphic, such as the minimally bilobed form of the molars, and the extent of enamel on I_1 , with others, such as the grooving on P_3 and the depth of I_1 , which could be regarded as apomorphic. The mandible is unique in vombatids, and bears more resemblance to that of phalangerids. It probably represents a plesiomorphic diprotodont morphology.

It would have been no surprise if *Warendja wakefieldi* had turned up in a Miocene site, where its small size and primitive features would have conveniently fitted it for the role of ancestral wombat. *Warendja*, however, has been found in terrigenous sediments within a

cave eroded in Miocene limestone, in association with typical Pleistocene and modern species. Although circumstantial evidence suggests that the sediments from which *Warendja* comes may be older than 120,000 years, there is no reason to suppose they are significantly older, say, of early Pleistocene age. So far, *Warendja* is the only taxon recognised in the site which has not been found elsewhere in Victoria in a late Pleistocene context.

The palaeoenvironment suggested by the faunal assemblage associated with *Warendja* is wet sclerophyll forest. The suite of modern species in the assemblage occurs in such forest in Gippsland today. *Warendja*, with its primitive morphology, may be a conservative survivor from the forests of the Tertiary, lingering into the Pleistocene in the forested areas of southeastern Australia.

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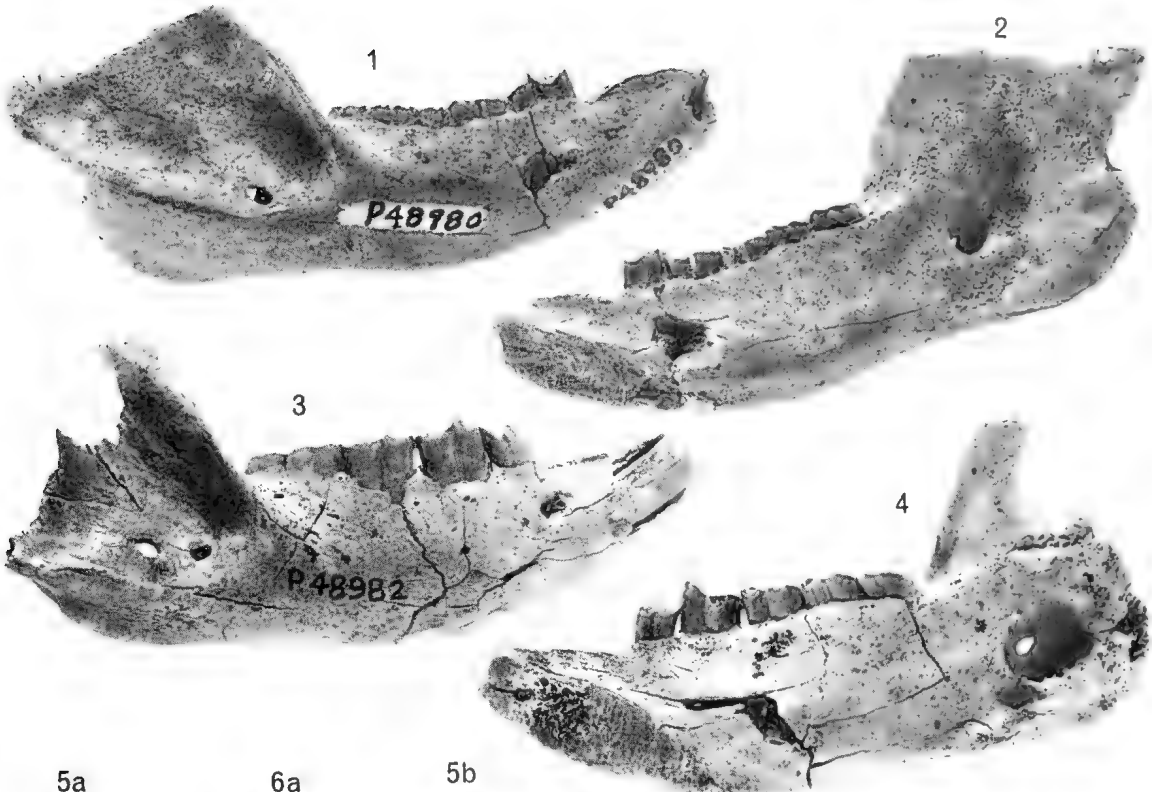
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Explanation of Plate

PLATE 3

Warendja wakefieldi. NMV P48980, holotype, right mandible, McEacherns Cave, Victoria, fig. 1, labial view, $\times 1$; fig. 2, lingual view, $\times 1$; fig. 5, occlusal view, $\times 1$. NMV P48982, right mandible, McEacherns Cave, Victoria, fig. 3, labial view, $\times 1$; fig. 4, lingual view, $\times 1$; fig. 6, occlusal view, $\times 1$.



5a

6a

5b

6b

