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PHYLOGENY AND BIOGEOGRAPHY OF THE GNATHIIDAE (CRUSTACEA: ISOPODA) WITH DESCRIPTIONS OF NEW GENERA AND SPECIES, MOST FROM SOUTH-EASTERN AUSTRALIA

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Abstract

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The classification of the Gnathiidae is reviewed for the first time since Monod (1926). States of 72 characters are discussed with reference to two outgroups of Flabellifera, forming the basis of a phylogenetic analysis. Ninety-five species are included in the analysis representing all nominal genera and subgenera and covering the perceived variation in the family. Results indicate that the Gnathiidae can be divided into two principal clades representing one (*Thaumastognathia* Monod) and nine genera (*Gibbagnathia* gen. nov., *Paragnathia* Omer-Cooper and Omer-Cooper, *Euneognathia* Stebbing, *Bythognathia* Camp, *Monodgnathia* gen. nov., *Bathygnathia* Dollfus, *Caecognathia* Dollfus, *Gnathia* Leach and *Elaphognathia* Monod).

The new classification differs from that of Monod (1926) in the description of two new genera (*Monodgnathia* and *Gibbagnathia*), the revival of another genus previously in synonymy (*Caecognathia*), the elevation of a subgenus to generic rank (*Elaphognathia*) and the loss of two genera and a subgenus in synonymy (*Heterognathia*, *Akidognathia* and *Perignathia*). The elevation of *Elaphognathia* to generic rank relies on the recognition of paraphyletic *Gnathia*. A key to the proposed genera of Gnathiidae is presented.

Twenty-five new species are described and figured from south-eastern Australia, three from deep water in the Tasman and Coral Seas, and one from New Zealand. *Thaumastognathia* is recorded for the first time since 1926. *Bathygnathia*, *Monodgnathia*, and *Thaumastognathia* are recorded for the first time from Australian waters. Keys to all 45 Australian species are offered with figures of the cephalosomes of the 17 previously described species to aid identification. Habitat and distributional data for all Australian species are presented.

The phylogenetic analysis of the family suggests the most significant evolutionary events in the radiation of the family took place in the cold waters of the southern hemisphere. *Thaumastognathia*, sister group of all other gnathiids, is an endemic genus of four species from the Australian-New Zealand shelf. *Gibbagnathia*, the second clade, is an endemic, monotypic genus confined to Bass Strait, southern Australia. *Paragnathia* is enigmatic in being a single Afro-European species but *Euneognathia* is a single species from the Antarctic shelf. None of these four genera has radiated successfully. *Bythognathia* (1 species) is from the deep sea (4000 m) of the Caribbean. *Monodgnathia* (4 species) and *Bathognathia* (12 species) are both confined to the slope and deep sea. But radiation has been moderate and with the exception of the one species of *Bythognathia* none is found very deep, unlike many other families of isopods.

Two related clades have radiated strongly in more shallow and warmer waters: *Caecognathia* with 43 species distributed more towards the poles than *Gnathia-Elaphognathia* (89 species.) which is more cosmopolitan on temperate and tropical shelves and upper slopes. Small clades of species of *Caecognathia* are confined to Australia. Other species of the highly endemic southern Australian fauna seem to have arisen locally and independently.

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Introduction

The waters around Australia possess a rich crustacean fauna (Barnard, 1991; Poore et al., 1994), best documented in the south-eastern temperate region where extensive recent research has been completed. The isopod family Gnathiidae is one of many contributing to this diversity but contains numerous undescribed species.

Gnathiids are most unusual isopods, polymorphic in the extreme. Males are immediately recognisable by their large forwardly-directed mandibles and five pairs of walking legs. Females have more reduced jaws and a thorax swollen with ovary or eggs. The juveniles, or praniza larvae, pass through three instars in the only species studied (Wägele, 1987, 1988), each feeding on blood as ectoparasites of fishes. The praniza appears like a thinner female, also with five pairs of legs and sometimes with guts engorged with blood.

The morphology and classification of the Gnathiidae was placed on an excellent footing by Théodore Monod. Monod's (1926) volume described in detail the anatomy and biology of the group and illustrated the 62 species then known. Camp (1988) listed a further 42 species described since Monod's (1926) work. Eighteen species have been described since Camp's work, two were overlooked by him (Table 1), and a further 29 are described here. This brings the total number of described species of Gnathiidae to 155. There has been no reappraisal of the relationship of the genera since that by Monod (1926).

Prior to this study 17 species of Gnathiidae were known from Australia, only six from the temperate waters of the south-east. Holdich and Harrison (1980) suggested that poor sampling effort, rather than low species diversity, was responsible for the low number of Australian species and that further sampling should uncover more species. This has proved true. This paper addresses the fauna of south-eastern Australia, from near Nowra, New South Wales (35°S, 150°E) around Tasmania (43°S) and across to Pearson Island (34°S, 134°E) west of the Spencer Gulf, South Australia. It describes four times as many species as were previously known from this region, recognises two new genera, is the first record of *Thaumastognathia* in over 65 years, the first records of *Bathygnathia* and *Thaumastognathia* from Australia and the first records of gnathiids from Tasmanian waters. Four significant Australasian species from outside this region are also described, all from deep water. It is now apparent that Australia possesses a rich gnathiid fauna with approximately one-quarter of all the species so far described.

New species are described and figured. Most species previously described from Australia were well illustrated and described by Monod or later authors. Figures of their cephalosomes (Fig. 2) have been copied to aid in identification when using the keys.

As well as describing numerous new species from Australian coastal, shelf and slope environments we present a new phylogeny and classification of the family. This phylogeny is based on a cladistic analysis of 95 described species from world-wide localities. On the basis of this analysis two new genera are described, one is revived, a subgenus is elevated to generic rank, and other genera are lost in synonymy. A key to the ten

Table 1. Gnathiidae described since 1987 (including two overlooked by Camp, 1988). Species have been reallocated to genus according to the classification scheme adopted in this paper. Each species is followed by its type locality, depth of capture and size of male, when available. Species described prior to this date were listed by Monod (1926) and supplemented by Camp (1988). Coordinates of type localities are those listed by original authors; where size was not stated it was measured from figures.

Bythognathia yucatanensis Camp, 1988: Yucatan Channel, Caribbean Sea, 21°07.0′–13.0′N, 85°31.5′–32.0′W; 3700–3800 m; 20.8 mm.
Caecognathia amakusaensis (Nunomura, 1992): Use, Reihoku-cho, Kumamoto Pref., Japan; 30–35 m; 5.1 mm.
Caecognathia kikuchii (Nunomura, 1992): Shiraiwazaki, Reihoku-cho, Kumamoto Pref., Japan; 3.7 mm.
Caecognathia saikaiensis (Nunomura, 1992): off Tomoezaki, Japan; 3.1 mm.
Elaphognathia cornigera (Nunomura, 1992): Tûjishima Islet, Itsuwa-chô, Kumamoto Pref., Japan; 2.4 mm.
Elaphognathia discolor (Nunomura, 1988): Isohara, Kita-ibaragi shi, Ibaragi, Central Japan; 6.2 mm.
Elaphognathia wolffi (Müller, 1989a): Coral Reef near Tiwi, Mombasa, Kenya; 1.6 mm.
Gnathia calsi Müller, 1993b: La Trinité, Anse Rivière, Martinique, Freneh Antilles; 0–2 m; 1.9 mm.
Gnathia cooki Müller, 1989c: Cooks Bay, Moorea, Soeiety Is; 1 m; 3.7 mm.
Gnathia firingae Müller, 1991: La Réunion L'Ermitage-les-Bains; 0.5–1 m; 2.1 mm.
Gnathia galzini Müller, 1989c: Moorea, Society Is; 0.5 m; 1.6 mm.
Gnathia gonalezi Müller, 1988: Punta de Betin, Sta Marta, Colombia; 15 m; about 1.5 mm.
Gnathia hirayamai Nunomura, 1992: Tomioka, Amakusa, Kumamoto Pref., Japan; 8.5 m; 3.9 mm.
Gnathia incana Menzies and George, 1972: Peru-Chile Trench, 11°50′S, 77°58′W; 935–907 m; 3.6 mm.
Gnathia lacunacapitalis Menzies and George, 1972: Peru-Chile Trench, 07°59′S, 80°37′W; 991–1015 m; 4.5 mm.
Gnathia lignophila Müller, 1993a: Pulau Babi Besar, Tioman Archipelago, Malaysia; lower-intertidal; 1.9–2.9 mm.
Gnathia magdalenensis Müller, 1988: Bahía de Nenguangue, Colombia; 18 m; about 2.7 mm.
Gnathia malaysiensis Müller, 1993a: Pulau Babi Besar, Tioman Archipelago, Malaysia; 1–2 m; 2.3 mm.
Gnathia nasuta Nunomura, 1992: off Tomoezaki, Kumamoto Pref., Japan; 8.5 m; 3.3 mm.
Gnathia nicembola Müller, 1989b: Entranee channel to Suva Harbour, Fiji; 76–84 m; 2.6 mm.
Gnathia samariensis Müller, 1988: Isla de Morro Grande, Colombia; 30 m; about 1.95 mm.
Gnathia vellosa Müller, 1988: Isla de Morro Grande, Colombia; 25–30 m; about 1.2 mm (excluding pleon).

world genera now recognised and a checklist of species in the new classification are presented. Updated keys to the species of Australia are offered.

Materials

Much of the material on which this study is based has eome from large benthic surveys of the bays, shelf and slope of southern and eastern Australia:

Crib Point Benthic Survey, 1965–1972 (CPBS) carried out in Western Port, Victoria, by the Marine Studies Group, Ministry for Conservation, Melbourne;

Bass Strait Survey, 1979–1985 (BSS) carried out by the Museum of Victoria, Melbourne (see Wilson and Poore, 1987 for station locations and methods);

south-eastern Australian slope study, 1986, 1988 carried out by the Museum of Victoria, Melbourne (see Poore et al., 1994, for station locations, methods and a discussion of the diversity of Isopoda);

the 1986 *Cidaris* cruise in the western Coral

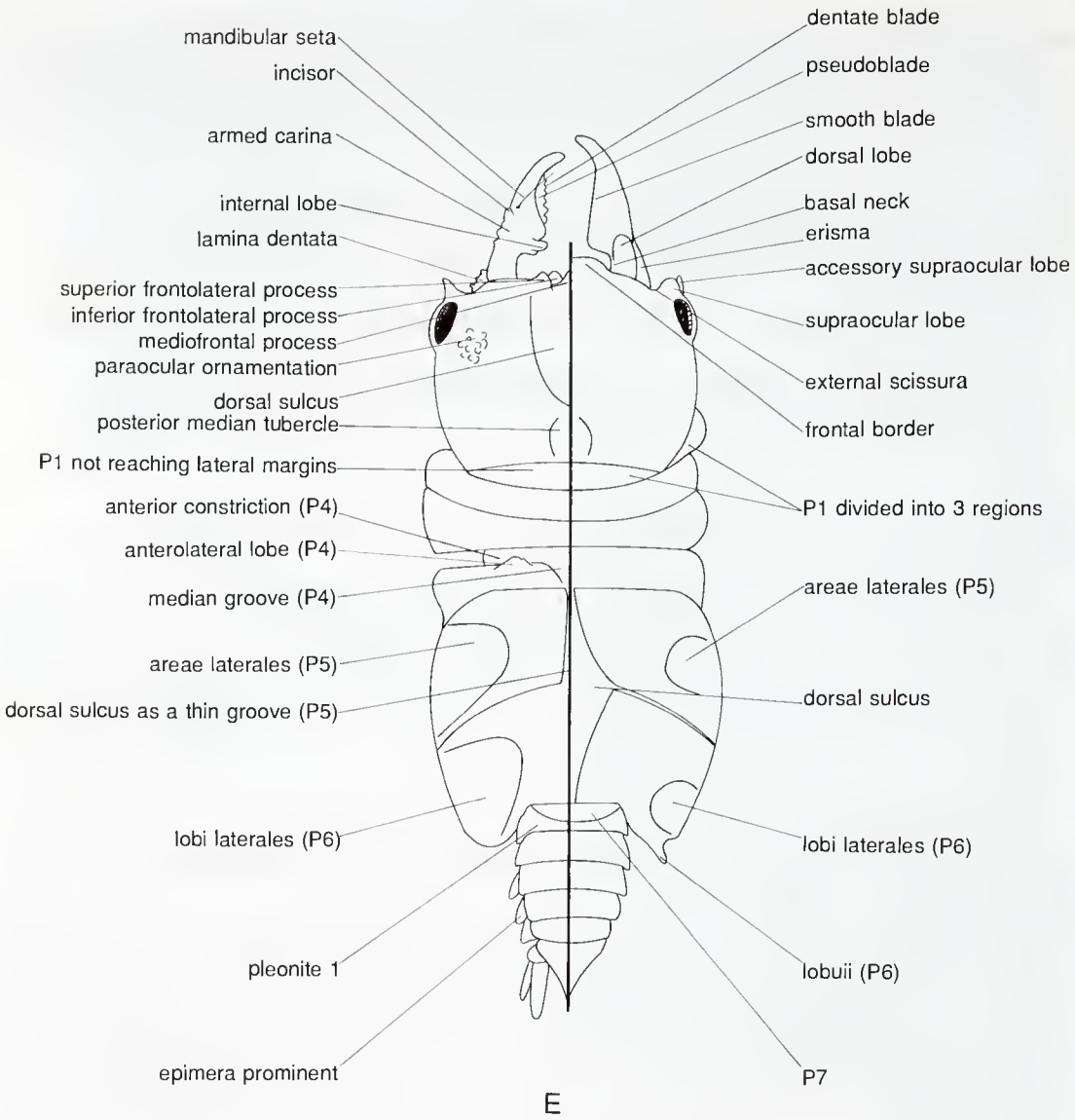


Figure 1. Stylised male gnathiid (dorsal view) showing main anatomical features.

Sea, carried out by James Cook University of North Queensland; and

other material from the collections of the Australian Museum, Sydney and the Museum of Victoria, Melbourne.

All type material is lodged in the collections of the Museum of Victoria, Melbourne (NMV), Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM) and New Zealand Oceanographic Institute, Wellington (NZOI).

Only males were described because of the difficulty of identifying praniza stages and females. In the species-rich environment of south-eastern Australia, dredge samples with more than one species of gnathiid were common, therefore association of females and pranizas with males was not considered a sufficient criterion for identification. No obvious characters were found that enabled females or pranizas to be accurately identified to species and this problem

was not explored. Identification of females and pranizas to the species level would be a major project and was not attempted here.

We follow the anatomical terminology used by Monod (1926) and Holdich and Harrison (1980) except for numbering of pereonites and pereopods (Fig. 1). The first body segment posterior to the cephalon, pereonite 1 (correctly thoracomere 2, not pereonite 2 as in Monod's and Holdich and Harrison's works), is fused to the cephalon forming a cephalosome. In some species pereonite 1 may be dorsally indistinguishable from the cephalon. The pylopod (pereopod 1) attaches to pereonite 1. Pereonites 2–6 follow posteriorly with pereonite 2 possessing the most anterior of the five pairs of walking legs. The pereopods are labelled according to the pereonite to which they are attached (pereopods 2–6). Pereonite 7, when distinguishable, is very small and functionally forms part of the outline of the pleon.

The scale bar is 1 mm and refers only to drawings of whole animals in dorsal view. Figure labels are as follows: A1, A2, antenna 1 and 2; PY, pylopod (pereopod 1); MP, maxilliped; P2–P6, pereopods 2–6 (walking legs 1 to 5); U, uropods; l, r, left and right. All illustrations are of the male holotype unless otherwise stated. Figure 1 is of a stylised male gnathiid and is labelled to show parts of the animal and its ornamentation.

Monod's (1926) review of the Gnathiidae was extremely detailed and included over 300 references. His synonymies were detailed, therefore, they are not repeated here in full. Hesse (1864) highlighted the similarity of gnathiids to ants (Formicidae) with the specific name *Anceus formica*. The specific epithets of new species here described are genera of Australasian ants (Taylor, 1987) chosen only for their euphony, not to reflect any specific feature of either the isopod or the ant. All are nouns in apposition.

Morphological characters were coded into the taxonomic database program DELTA (Dallwitz and Paine, 1986) for all Australian species. Descriptions were generated from this program but were heavily edited. The database is available on request by DELTA users from the Department of Crustacea.

Phylogenetic methods

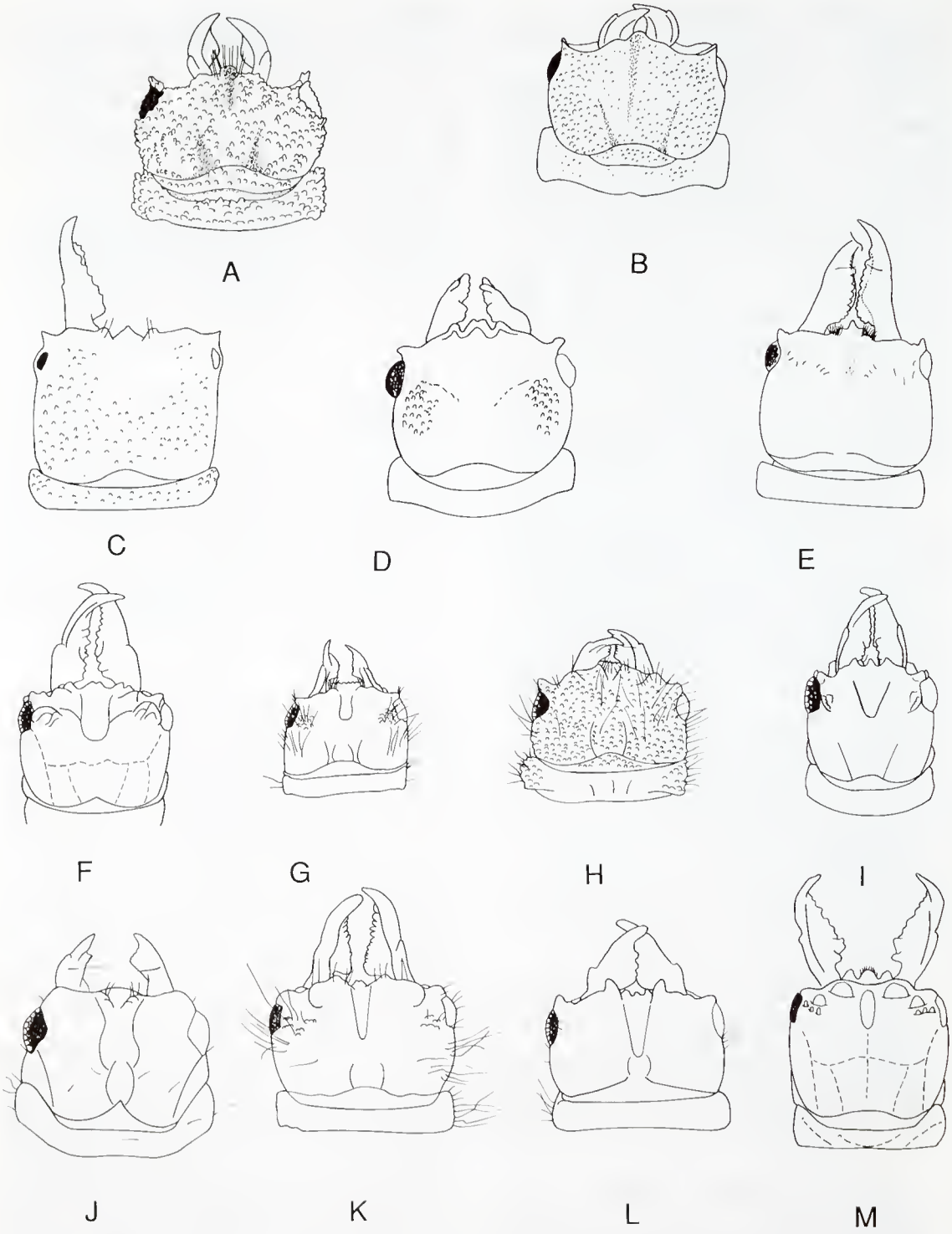
Hennigian phylogenetic (cladistic) methods were used to generate cladograms as hypotheses of the relationship between species of the family Gnathiidae. As many species as were practical, rather than the nominal genera, were chosen for the analysis because of doubt about the monophyly of some genera. The information on character states comes mostly from illustrations and descriptions in the literature and was supplemented from specimens in the collections of the Museum of Victoria. Published details on many species were inadequate for this purpose. These species were omitted but it is felt that the 95 species described in sufficient detail covered the range of form seen in the family. Specimens of *Enneognathia gigas* (Beddard, 1886), *Paragnathia formica* (Hesse, 1864) and *Gnathia maxillaris* (Montagu, 1804) were lent or donated.

The programs PAUP version 3.1.1 and HENNIG86 version 1.5 were used to establish relationships between species and to derive a practical classification which reflected these relationships. The same data set with the same assumptions was run under PAUP with the heuristic search option (general and branch-and-bound) and under HENNIG using *mh** and *bb** routines. Outgroups were chosen from the Isopoda Flabellifera in order to polarise characters. The following sections describe the outgroups, taxa chosen and character transformations.

Outgroups

Brusca and Wilson's (1991) analysis of the relationships of the Isopoda placed the Gnathiidae among the "long-tailed" taxa, part of the non-monophyletic Flabellifera. They concluded that the family no longer deserves the subordinal status traditionally used. Outgroups, therefore, were sought from among the Flabellifera. Wägele and Brandt (1988) suggested that the protognathiid, *Protognathia bathypelagica* (Schultz, 1977) is a "missing link" or intermediate stage between the Cirolanidae and the Gnathiidae, and that these two families are closely related. Brusca and Wilson (1991) argued that *Protognathia* is not closely related to the Gnathiidae but rather Protognathiidae is part of the Cirolanidae-Anuropidae-cymothoid line. They argued that the Cirolanidae is more closely related to the Gnathiidae than Protognathiidae is to Gnathiidae. Both the Cirolanidae and the Protognathiidae were selected as outgroups. *Eurydice acuticauda* Bruce, 1981 was chosen to represent the Cirolanidae for many characters.

Protognathia bathypelagica is known only from immature specimens; states describing the sexual characters of adult males are coded as


A
B
C
D
E
F
G
H
I
J
K
L
M

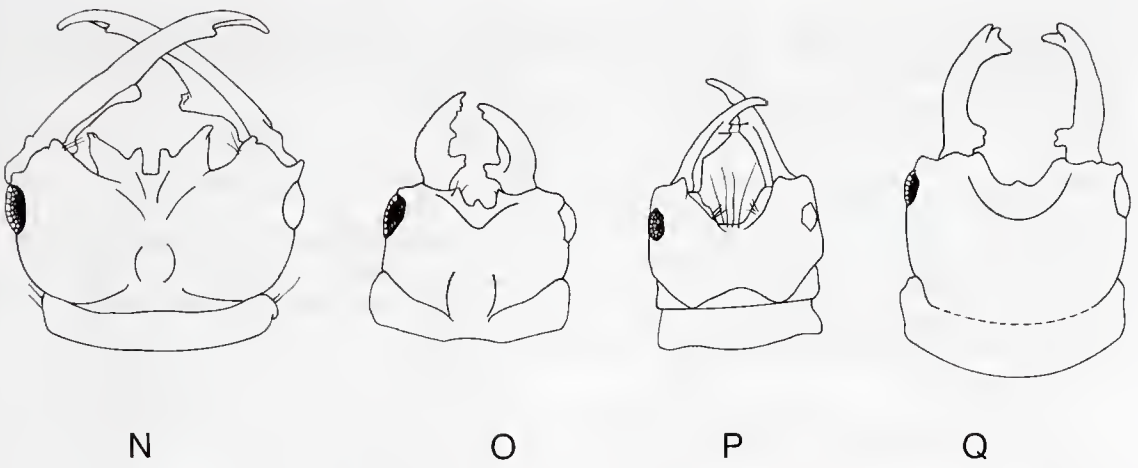


Figure 2. Cephalosomes of 17 Australian species of Gnathiidae not described in this work. A, *Caecognathia agwillisi* (Seed). B, *C. pustulosa* (Hale). C, *Gnathia latidens* (Beddard). D, *G. calamitosa* Monod. E, *G. halei* Cals. F, *G. cornuta* Holdich and Harrison. G, *G. meticola* Holdich and Harrison. H, *G. asperifrons* Holdich and Harrison. I, *G. falcipenis* Holdich and Harrison. J, *G. variobranchia* Holdich. K, *G. biorbis* Holdich and Harrison. L, *G. calmani* Monod M, *G. mulieraria* Hale. N, *Elaphognathia bifurcilla* (Holdich and Harrison). O, *E. forceps* (Holdich and Harrison). P, *E. rimifrons* (Holdich and Harrison). Q, *E. ferox* (Haswell).

Figures copied from original authors except *G. latidens* copied from Monod (1926), and *G. calmani* and *E. ferox* copied from Holdich and Harrison (1980).

unknown (? in Table 3). For both outgroups, a number of the mandibular characters were coded as inapplicable due to the difficulty in drawing homologies between the highly modified mandibles of the Gnathiidae and the mandibles of other Isopoda. Inapplicable characters were coded as states separate from those found in the Gnathiidae (Table 2). The praniza stage of gnathiid ontogeny was also considered when there was difficulty assessing the plesiomorphic condition of some characters.

Taxa chosen

It proved impossible to include every described species of Gnathiidae in the analysis. Many species were excluded because they were not described in sufficient detail to enable complete coding of all character states. Ninety-five species from all round the world were included (Table 3) representing all nominal genera and subgenera.

Four species represented the monotypic genera *Euneognathia* (*E. gigas*), *Paragnathia* (*P. formica*), *Heterognathia* (*H. calva*) and *Bythognathia* (*B. yucatanensis*). All species of *Thaumastognathia* were included, three of which are newly described. Of the remaining genera, *Akidognathia*, *Bathygnathia* and *Gnathia*, the type species and all species described in sufficient detail were included in the analysis. Thus, *A. oedipus*, *A. cristatipes*, *B. affinis*, *B. magnifica*, *B. porca* and six similar new species provided data. *Akidognathia* and *Bathygnathia* seemed *a priori* to be closely allied and the 11 species included covered the variation within these two genera and the supposed differences between them, principally in the form of the pereopods, mandibles and frontal border.

The remaining species are or could be members of *Gnathia* and its three subgenera, *Gnathia* s.s., *Perignathia* and *Elaphognathia* as presently defined. The monotypic subgenus *Perignathia* was represented by *P. triospathiona* although its type species is in doubt (see below). *Gnathia* s.s. and *Elaphognathia* were represented by numerous species. *Caecognathia stygia*, type species of a genus considered by Monod (1926) a junior synonym of *Gnathia* was also included.

Character discussion

The 72 characters used in the phylogenetic analysis are discussed in turn below. All are potential synapomorphic characters (i.e., none is apomorphic for a single species). The character states are given in Table 2 and the data matrix in Table 3.

Eyes. Almost all Gnathiidae have sessile, lateral eyes during all stages of development; this condition is plesiomorphic. Eyes have been lost

Table 2. Character transformations used in the phylogenetic analysis of 95 speeies of Gnathiidae. The plesiomorphie state is listed first and separated by ; from the apomorphic state or states. In the data matrix plesiomorphic states are indicated by 0 and apomorphic states by 1 or more. Characters with consistency and retention indices of 1 are marked with *.

Eyes

1. Eyes present; absent.

Cephalon

2. Cephalon broader than long; as long or longer than broad.
3. Dorsal sulcus absent; present.
4. Paraocular ornamentation absent; presenl.
5. Granules/tubercles absent; present on cephalon; present on ccphalon and pereon.
6. Cephalon lacking posterior, laterally deflected grooves; grooves present.
7.* Cephalon lacking anterior median furrow; furrow present.
8. Posterior cephalon not divided by shallow grooves; posterior cephalon divided by grooves (often marked with chromatophores).

Frontal border

9. Frontal border rounded/produced; transverse.
10. Frontal border not greatly produced; greatly produced.
11.* Frontal border not excavated; excavated.
12. Frontal border without frontal processes; with frontal processes.
13.* Frontal border not clearly delineated; clearly delineated (chalky white appearance).
14.* Buccal cavity wall not visible dorsally; visible beyond rostrum.
15. Entire frontal margin including region lateral to the base of mandibles not produeed; entire margin produced.
16. Frontal border lacking small median indentation; indentation present (not to be confused with excavation found in *Elaphognathia*).
17. Setae on frontal border absent; present.
18. Mediofrontal proeess absent; single process; multiple processes.
19. Mediofrontal process not inferior; inferior.
20. Superior frontolateral process absent; present.
21. Inferior frontolateral process absent; present.

Mandible

22. Armed carina inapplicable; absent; present.
23. Incisura inapplicable; absent; present; pronounced.
24. Internal lobe inapplicable; absent; present.
25. Mandible elearly less than 5 times as long as wide; 5 times as long or longer.
26. Apical cusps absent; present.
27. Blade dentate/crenulate; not dentate; absent/highly reduced.
28. Pseudoblade absent; present.
29. Setae inapplicable; absent; present.

Antennae

30. Antenna 1 shorter than or equal to antenna 2; antenna 1 longer than antenna 2.
31. Antenna 1 flagellum with 7 or more articles; 6; 5; 4; 3; 2 or fewer articles.
32. Antenna 2 flagellum with 8 or more articles; 7; 6; 5; 4; 3 or fewer artieles.
33.* Antenna 1 peduncle length greater than 4 times width; less than 4 time width.
34.* Antenna relatively straight; curved under mandibles.

Pereon

35. Pereon devoid of or with only few setae; setae present anteriorly; setae present all over.
36. Pereon wide (length $\leq$1.85 width); medium; narrow ($\geq$2.5).
37. Pereon pear-shaped (clearly widest at pereonite 5); not pear-shaped.
38. Pereon wider than cephalon; narrower than or as wide as cephalon.
39. Pereonite 1 clearly extending to margins of pereon; surrounded completely by cephalon and pereonite 2; not visible;
40. Anterior constriction of pereonite 4 absent; present.
41. Pereonite 4 lacking mid-dorsal spine; spine present.
42. Pereonite 6 without lobuii; lobuii present.
43. Posterior margin of pereonite 6 not deeply coneave; posterior margin deeply coneave.

44. Pereonites 5 and 6 not fused; partially fused; completely fused.
45. Pereonite 6 lobuii not conical/globular; lobuii conical/globular [see figs 19, 22, 40].
46. Peronite 7 visible dorsally; not visible.

Pleon, pleotelson and uropods.

47. Pleotelson short (as wide or wider than long); medium; long (twice as long or longer than wide).
48. Uropod rami clearly shorter than pleotelson; approximately equal to length; clearly greater than length of pleotelson.
49. Endopod clearly longer than exopod; exopod subequal or longer.

Maxilliped.

50. Mouthparts typical of family; small/reduced (difficult to see).
51. Maxilliped of 5 articles; fewer than 5 articles; absent.
52. Palp clearly less than 5 times as long as broad; about 5 times as long as broad.
53. Endite with 4 or more coupling hooks; 1–3 hooks, no hooks.

Pylopod

54. Pylopod pediform/cylindrical; slightly widened; operculate (pylopods overlapping)
55. Pylopod of 7 articles; 6; 5; 4; 3 or fewer articles.
56.* Pylopod with no articles greatly enlarged; first article enlarged; second article; first, third and fourth articles enlarged.
57. Article 3 not reduced; reduced; absent.
58. Aerolae absent; present.
59. External margin inapplicable; devoid of plumose setae; a few, well spaced plumose setae; many setae/dense cover.
60. Pylopod inapplicable; with many setae on ventral surface (about 15 or more); few setae; no setae.
61. Article 2 not circular or conical; conical (see figs 21, 24, 36, 42); circular.
62. Spine(s) present on article 3; spines absent.
63.* Ventral surface setae inapplicable; plumose; simple or absent.

Pereopods

64. Pereopod setae plumose; simple or absent.
65. Pereopod setae dense; sparse or absent.
66. Pereopod 4 basis lacking distal extension; distal expansion present.
67. Merus of pereopods 3–6 not medially expanded along anteroposterior axis; merus expanded.
68.* Pereopod 4 basis lacking a quadratic lobe; possessing lobe.
69. Pereopod 4 ischium not expanded; ischium expanded; ischium expanded as a cusp.
70. Pereopod 5 ischium not expanded; ischium expanded.

Pleopods

71. Pleopods setose; not setose.
72. Appendix masculina inapplicable; greater than or subequal to length of rami; half to three-quarters length of rami; absent.

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in the adults of only a few species, nearly all of which occur in the deep sea (character 1).

Cephalon. The dorsal surface of the plesiomorphic cephalon is smooth, featureless and broader than long, similar to the cephalon of the cirolanid, *E. acuticauda*. While the Cirolanidae are mostly free-roaming predators or scavengers (Bruce, 1986), adult Gnathiidae are cryptic, often inhabiting substrate that offers protection. Some species may construct burrows. From within these hiding places the gnathiid's mandibles can protrude to deal with potential trouble while the remainder of the animal remains protected (Seed, 1979). Compared to other Isopoda, the mandibles and cephalon of many gnathiids are strengthened. Apomorphic states of the cephalon include sculpture and ornaments which may increase the strength of the cephalon; these include furrows and depressions and raised bumps and tubercles.

A peculiar feature found mid-dorsally on the anterior cephalon or rostrum of a few gnathiids is a thin translucent region of variable shape and size, located above the buccal cavity. The function of this structure and its evolutionary importance are unknown.

Table 3. Species-character matrix of species of Gnathiidae (95 species by 72 characters). The first two taxa are outgroups. Unknown character states are shown by "?"

Cirolanidae	0000000000	0000000000	0000000000	4000000000	0000000000	0020000010	0001100000	00
Protognathia	1000000000	0000000000	0000000000	1000011000	0000002110	0020000000	0000000000	0?
B. adherza	0110000001	000100?000	0132102020	2?10021101	0100001210	0002220012	0021000010	01
B. affinis	1000000001	0001001000	0131102011	2210021101	0000001110	00?2220032	0021101000	02
B. cardicondyla	1010200001	0001001000	0131102020	2210021111	0110000110	0002220012	0021000010	00
B. magnifica	0110000001	0001001000	0112102010	2010021101	011000???0	0002220021	0?21000021	02
B. oedipus	1000000001	0001100000	0112102010	1010021101	0100002210	0002220021	0021000021	01
B. porca	11?0000001	0001001000	0131102010	2110021101	0000001110	0002220032	0021001010	02
B. tapinoma	1000000001	0001101000	0112102020	2010021101	0100001210	0002220121	0021000010	01
B. vollenhovia	1000000001	0001001000	0131102010	2210021101	0000001210	0002220021	0021001000	02
Bythognathia	1010000001	0000000000	0131002010	0110021101	0010000210	0000100032	0120001000	01
C. abyssorum	0000200001	0000010000	0121001010	3210001111	0110001210	0022411122	2121100000	12
C. agwilusi	0000211000	0000001000	0121001010	2110110001	0002001110	0012412012	2121000000	02
C. akaroensis	0000200000	0000011000	0221000010	3110111111	0010000210	0022411???	2121100000	02
C. branchypomera	0100000000	0000001000	0111001011	2510010010	0110101000	0122411032	1110000000	02
C. calva	0000211000	0000000000	0121001010	2110011111	0110001110	0012411012	2121100000	12
C. consobrina	0000200000	0000011000	0121000010	2?10011111	0110000110	0022411132	2121100000	01
C. crenulantrons	00?0100001	0000000000	0111000010	2110011101	0010001110	0022411?32	2121100000	?2
C. dracamma	0100000000	0000001000	0111001011	2310010000	0110100010	0122411031	1110000000	02
C. dolichoderus	0000000001	0000001000	0231002010	22?0211120	0110001100	0012411012	2120000000	02
C. elongata	00?0200100	0000001000	0121001010	2110021101	0110001110	0022411132	2121100000	12
C. galzini	0000200000	0000011000	0121001010	3210211101	0010001210	0022412132	2121100000	?2
C. gnamptogenys	0000000000	0000001000	0111002010	2110211120	0110001110	0022411131	2121010000	01
C. hirsuta	0000200001	0000001000	0121001010	??10101110	0110001210	0022411????	2121100000	12
C. huberta	0000211000	0000001000	0221001021	3410211111	1000000200	0012412012	2121100000	12
C. leptamilla	0100000001	0000001000	0111001011	2310210010	0110100110	0122411031	1111000000	02
C. pactca	0000200000	0000010000	0121000010	3110011111	0110000210	0022411???	2121100000	02
C. paratrecha	0000211000	0000001000	022?001020	2310210001	1000010110	0022412011	2121100000	02
C. polaris	0000211000	0000000000	0121001010	2110011111	1010001110	0012411032	2121100000	12
C. polythrix	0000200000	0000000000	0211001010	2110011111	0110001210	0022411???	2121100000	02
C. sanctaecrucis	0000200000	0000000000	0111001010	2110211100	0100001110	0012411131	2121000000	12
C. schisanthrons	000010002?	0000010000	0111001010	2110001111	0110001210	0022411031	2121100000	12
C. serrata	0000200001	0000101000	0111002010	2110221120	0110001110	0022411021	2121?10000	12
C. trachymesopus	0100000000	0000001000	0111001011	2410010010	0110101000	0122411031	1110000000	02
C. wagneri	0000000000	0000001000	0111001011	1110021101	0100001110	0012411132	2121100000	12
E. amboinensis	0010200010	1100000100	0112002020	3110011120	0000000210	0022411132	2121100000	02
E. bacescoi	0010000110	1100000201	0122101010	2110011101	0000001210	0022412032	2121100000	?2
E. bituricilla	0000000010	1100001211	0112102010	2110001111	0000000210	0022411022	2121100000	00
E. ferox	0000000010	1?00000?00	0112112010	4110001120	0000001210	0022411122	2121100000	02
E. forceps	0010000010	1100001100	0112001010	4010011121	0000000210	0022412122	2121100000	02
E. horgattella	0000000010	1100001211	1112102010	2110001110	0000000210	0022411022	2121000000	02
E. rangifer	0000000010	1?00000000	0112112010	3110001120	0100000210	0022412032	2121100000	02
E. sugashimaensis	0000000010	1100001001	0112102020	2110011111	0000001210	0022411032	2121100000	?2
E. wolffi	0000100010	1100001201	0112112020	3110001120	0000000210	0022411132	2121100000	?2
Eumegnathia	0011000010	0100000200	113200011 0	2010011110	0110002110	0011200032	0121100000	02
Gibbagnathia	0000200000	0100001001	0111002010	3300211111	0010000101	1020300013	0120000000	02
G. albescens	1010100011	0100101001	0121000020	2110021011	0000001100	0012411132	2121100000	?2
G. aspertrons	0000210010	0100001001	0121000020	?210210000	0110001010	0022411032	2121100000	12
G. beethovem	0010000010	0100001211	0111000020	3110211110	0000001210	0022412032	2121100000	?2
G. bicolus	0011000010	0100001211	0121000010	2110011101	0000001210	0022411132	2121100000	12
G. cahmani	0010000010	0100001211	0121000010	2110011101	0000000210	0022411132	2121100000	02
G. camponotus	0011200010	0100001111	0122000110	2110011111	0000000110	0022411132	2121100000	01
G. clementensis	0010200010	0100001211	0121000010	1110211100	0110101110	0012411131	2121000000	02
G. cooki	0011000010	0100001211	1121000020	3210211111	0000000210	0022411132	2121100000	?2
G. cornuta	0011000110	0100001211	0122000010	2110021101	0000001110	0022411132	2121100000	02
G. coronadensis	1010000010	0100001111	0121000010	2110011100	0110001200	0022411031	2121000000	?2
G. epopostruma	0011000010	0100001200	0121000020	2110211111	0000001210	0022411132	2121100000	02
G. falcipenis	0011010010	0100001200	0122000010	2110021111	0000001210	0022411132	2121100000	02
G. gonzalezi	0010000010	0100001001	0121000020	4210211110	0010001110	0012411022	2121100000	?2
G. halei	0010000011	0100001111	0111000120	2110011101	0102001100	0022411132	2121100000	01
G. illepida	0011200010	0100000111	1121000020	2110011111	0010001210	0022411022	2121100000	02
G. inopinata	0012200010	0100001211	0221000010	2110011011	0000000210	0022411???	2121100000	02
G. tridonivermex	0010000010	0100001211	0111000020	2110111111	0000000210	0022411132	2121100000	01
G. johanna	0010000010	0100001111	0122000020	2110211111	0010001210	0022412132	2121100000	12
G. lanmacaptalis	1011000010	0100001111	0121000010	2110021101	0100001100	0022412032	2121100000	02
G. magdalcnsis	0011100010	0100001200	0122000020	2110211121	0000001210	0022411132	2121100000	?2

G. margaritarum	0011200010	0100001211	1121000020	3110211111	0000000200	0022411132	2121100000	?2
G. maxillaris	0001200010	0100001111	0121000010	2110011111	0000000110	0022412132	2121100000	12
G. meticola	0010000110	0100001001	0121000010	1110011001	0000001200	0022411032	2121100000	02
G. mortensen	0020200010	0100001101	0122000010	2110011001	0100000210	0022411?22	2121100000	02
G. mulleraria	0010000110	0100001111	0122000010	2110021101	0000000110	0022411132	2121100000	02
G. mystrium	0011000010	0100001211	1121000020	2110011121	0000001110	0022411132	2121100000	01
G. necembola	0010000010	0100001111	1121000020	3110011101	0010001110	0022411032	2121100000	?2
G. notostigma	0011000010	0100001200	0122000120	2110011111	0000000110	0022411132	2121100000	01
G. odontomachus	0010000010	0100001111	0121000020	2110211101	0000000100	0022411132	2121100000	01
G. oxyuraea	0001000010	0100001110	0211000020	3110011121	0010001110	0022412132	2121100000	02
G. prolasius	0011000010	0100001200	0111000020	2110021111	0000010210	0122411012	2121100000	12
G. rathi	0010200010	0100001001	0121000020	3110021111	0000000200	0022411032	2121100000	?2
G. regalis	0010200010	0100000111	1121000010	3110011111	0110000200	0022411032	2121100000	02
G. thylidoponera	0010000011	0100001111	0111000120	2110011111	0100001100	0022411132	2121100000	00
G. samariensis	0010000010	0100001200	0121000010	3110201121	0000001200	0022411132	2121100000	?2
G. serrulatifrons	0001200010	0100001211	1121000110	?210011111	0110001110	0022411?32	2121100000	02
G. stigmacros	0011000010	0100001101	0111001020	2110021111	0000010210	0112411012	2121100000	02
G. triospathiona	0000000010	0100000100	1121001010	2010020011	0000001110	0??2410032	11?1100000	02
G. variobranchia	0010000010	0100001001	0121000020	2110211011	0000000110	0022411032	2121100000	02
G. vellosa	0010200010	0100001200	0121000010	3110201121	0000001200	0022411132	2121100000	?2
G. venusta	0011000010	0100001111	1121000120	2110021121	0100001200	0022411?32	2121000000	02
G. virginalis	0010200010	0100001200	0121000010	3110211121	0000000210	0022412132	2121100000	?2
G. vorax	0000000010	0100001111	1121000010	2110021111	0000001110	0022412032	2121100000	02
M. colobstruma	1010010001	0010101000	0111001010	2110021111	0100000110	0002220111	0021000120	02
M. cristatipes	1010000000	0020000000	0111001010	2110021101	0110000210	0002220012	0021000121	11
M. ponera	1010000000	0010000000	0121001010	2010021011	0100001110	0002220011	0021000120	11
Paragnathia	0010000000	0000001000	0121000010	3010021111	0010000210	0011130012	0120100000	12
T. diceros	0000200000	0000001000	0221000011	2501000010	0000010111	1020300013	0121100000	11
T. metaphone	0000000010	0100001200	1111000021	4501000010	0001010001	2020200013	0121100000	12
T. orectognathus	0000000001	0000001000	0111000021	4401010110	0002010201	1020300013	0121100000	12
T. wasmanna	0000000010	0000001000	0131000021	5401200010	0001010111	2020300013	0121100000	12

Characters 2–8 summarise character changes in the cephalon.

Frontal border. The frontal borders of the Gnathiidae are variable and often complex. Monod (1926) introduced terms to describe many of the unique structures found there (see fig. 1). The plesiomorphic frontal border is simple, smoothly rounded, only slightly produced and devoid of setae, similar to that of most cirolanids. The apomorphic frontal border may have one or more frontal processes originating from different vertical levels and may be greatly produced or deeply excavated.

Gnathiids belonging to the Section Transversae (see Monod, 1926) possess a relatively linear frontal border which is punctuated with one or more frontal processes. All species of *Bathygnathia* lack frontal processes but possess a frontal border produced into a rostrum. The rostrum can be as long as the rest of the cephalon beyond which the buccal cavity wall may be visible. The frontal border of *Elaphognathia* has been deeply excavated. The frontal border region of some species of *Monodgnathia* is clearly delineated from the rest of the cephalon and has a chalky-white appearance in the two newly described Australian species.

Mandibles. Pronounced, anteriorly protruding mandibles characterise the adult male Gnathiidae. These mandibles are believed to be for display or defence and not involved in feeding (Brusca and Iverson, 1985). Male *Gnathia* have been observed capturing females with its mandibles to gather a harem in its burrow. Homologies between the mandibles of gnathiids and of other isopods are difficult to draw. The molar, spine row and lacinia mobilis are reduced if present. The mandibular palp may be represented by the mandibular seta in gnathiids but this is not assumed.

For the purposes of this analysis, the plesiomorphic state of the mandibles in gnathiids is of a relatively straight and symmetrical mandible with a single dentate blade, homologous to the lacinia mobilis of cirolanids. Monod (1926) introduced new terms to describe what are believed to be features unique to the gnathiid mandible. No homologies are drawn between the internal lobe and molar process of the mandible of other Isopoda and the armed carina and incisura of gnathiids and the incisor process of other isopods. These characters have been coded as inapplicable for the outgroups. Other apomorphic states include the dramatic lengthening

of the mandibles and addition of apical cusps as found in *Elaphognathia*.

Characters 22–29 summarise character changes in the mandibles.

Antennae. The antennae are similar to the antennae of other Isopoda: antenna 1 with a 3-articled peduncle and a short first flagella article; antenna 2 with a 5-articled peduncle. The first article of antenna 2 is very short and not figured in gnathiid illustrations. Reduction in the number of antennal flagella articles, reduction in width of the peduncle of antenna 1, and reduction in the length of antenna 2 (relative to antenna 1) are all apomorphic states.

Characters 30–34 refer to the antennae.

Pereon. The Gnathiidae differ considerably from the body plan of Cirolanidae. Many gnathiids have a more elongate and flexible habitus; are proportionally narrower and longer, and are better articulated between pereonites 3 and 4 (characters 36–38 and 40).

Cephalisation is characteristic of the Gnathiidae, pereonite 1 is partially fused with the cephalon in all species. Further cephalisation has occurred in a few species; pereonite 1 has become immersed or completely fused with the cephalon (character 39). Pereonite 7 is reduced and appears to form part of the pleon. In a few species, pereonite 7 is not visible dorsally. Various ornamental changes of unknown function have also occurred and are summarised in characters 41–43 and 45. These changes may serve to strengthen the pereon which is relatively soft, especially in the pranizas and females.

Pereonites 5 and 6 of pranizas have been completely fused together into an elastic stomach region (Wägele, 1987). Pranizas are able to engorge themselves on their fish host (Paperna and Por, 1977; Wägele, 1987) and this elastic stomach region expands and contracts with the meal. A few adult gnathiids retain this apomorphy (character 44).

Pleon, pleotelson and uropods. The tailfan is longer and more slender than the tailfan of Cirolanidae (Wägele, 1987). This may aid in locomotion, particularly for the praniza which must swim to and from suitable fish hosts. The pleotelson of most gnathiids is triangular with a marked apex (though the truncated pleotelson of *C. agwillisi* (Seed) is a notable exception). The uropodal rami of Cirolanidae are short, shorter than or about as long as the pleotelson. Elongation of the rami relative to the pleotelson and of the exopod relative to the endopod are considered apomorphies.

Characters 47–49 summarise these changes.

Maxilliped. The plesiomorphic maxilliped is 5-articled with a palp approximately two to three times as long as broad. The maxilliped is similar in most gnathiids; apomorphic changes include the loss of some or all of the coupling hooks found on the internal margin of the endite and the lengthening of the palp to approximately five times its width.

The exceptions are the genera *Thaumastognathia* and *Gibbagnathia* whose maxillipeds are greatly reduced to only one or two articles or lost altogether (characters 50–53).

Pylopod. The pylopod is the highly modified pereopod 1 and defines the Gnathiidae. The pylopod is directed anteriorly and forms the most ventral mouthpart. The function of the pylopod has not been fully investigated but it has been suggested that in most genera it acts as a operculate cover for the other mouthparts and/or as a large surface area across which gas exchange takes place (Seed, 1979). An analogue is seen in the third maxilliped of decapods.

The plesiomorphic state of the pylopod, a simple pereopod, is seen in the "gnathopode" of the larval *Paragnathia formica* (Monod, 1926: fig. 34). In adult males of all genera except *Bythognathia* the pylopod is simplified and lacks the terminal unguis. The apomorphic states involve a reduction in the number of articles from more than five to as few as three or two, a change from a cylindrical shape to an operculate shape and the loss of setae. The fringe of plumose setae seen on the external margin of article 1 on the pylopod of many species has been secondarily derived and is not directly homologous with any setae on a typical pereopod. This condition is apomorphic.

Characters 54–63 are changes in the pylopod.

Pereopods. Adult gnathiids have only five pairs of functional walking legs: thoracopods 3–7 or pereopods 2–6 of other isopods. Pereopod 1 has been modified into the pylopod and pereopod 7 is absent, a neotenous state shown in all isopod mancas (first instar). The five remaining pereopods (2–6 in our numbering) primitively are very similar to each other and to the pereopods of other isopods except for a dense covering of plumose setae. Pranizas use these plumose setae to swim towards a suitable fish host (Wägele and Brandt, 1988).

The proportions of the basis, ischium and merus on pereopods 4–6 are diagnostic of species of *Bathygnathia* and *Monodgnathia*. The

merus of pereopods 4–6 in some species of *Bathygnathia* is medially expanded along the anteroposterior axis. The ischium of pereopod 4 of species of both *Monodgnathia* and *Bathygnathia* may be distally expanded, occasionally as a circular cusp which appears to function as a large foot or support. The distal articles below the ischium cusp can be directed along the same plain as the ventral face of the cusp further increasing the surface area available for support; these articles no longer appear to be part of a functional walking leg (see *Monodgnathia ponera*). The ischium of pereopod 5 may also be expanded. The basis of pereopod 4 of some species previously assigned to *Akidognathia* has developed a pronounced quadratic lobe on the lateral face (see figs 74 and 76). The function of this structure has not been investigated though it appears to be capable of locking pereopod 4 against the pereon.

Characters 64–70 explain changes in pereopods.

Pleopods and penes. The pleopods are useful taxonomic characters for the study of many crustacean taxa but do not vary greatly among species of Gnathiidae. The plesiomorphic pleopods have setose margins (e.g., Cirolanidae) and the appendix masculina is as long or longer than the endopod of pleopod 2. Loss of setae from the pleopodal rami (character 71) and reduction (character 72, state 1) or loss (state 2) of the appendix masculina are apomorphic states. The penes of most gnathiids are small; only in a few species are they greatly enlarged.

Results

Cladogram

While processing earlier versions of the data matrix using the programs PAUP and HENNIG it was not uncommon for one program to find shorter trees than the other. Neither program consistently found the shorter trees, therefore, when dealing with large data sets we strongly recommend that more than one tree-calculating program is used.

For the final data matrix (Table 2) both HENNIG, using the *mh** and *bb** search options, and PAUP, using the heuristic search option, found equally parsimonious trees of the same length – 594 steps (consistency index = 0.19, retention index = 0.63).

Almost 1000 equally parsimonious trees were saved by HENNIG and 3000 trees by PAUP but given the limited memory available on the computers used for the analysis, the number of trees saved represent only a fraction of the true number of equally parsimonious trees for this data set. Because of the large number of equally parsimonious trees found it was necessary to calculate consensus trees with their resulting loss of information and resolution. Nelson strict-consensus and 50% majority-rule trees were generated. These differed from each other only at the subgeneric level, the major clades which could be used to define genera were identical in both. Numerous versions and subsets of the data matrix supported the major clades, therefore, we are confident of the monophyly of these major clades. The strict consensus tree is shown in fig. 3. Two major clades are evident. The smaller clade is comprised solely of the genus *Thaumastognathia*; the other clade contains the remaining nine genera.

Ten characters (14%) retained ci and ri equal to 1 and are marked with * in Table 2. A further 15 characters (21%) had ci equal to or greater than 0.5.

The transformation series, apomorphic changes at all nodes of the cladogram, were investigated using the *apolist* option in PAUP and the program CLADOS. Ambivalent characters were revealed with the *xs h* option in HENNIG86. Thirty-two characters were ambivalent at one or more nodes; 18 occurred at nodes that separated the major clades. The implication of this is that these characters could not be used in defining genera unless post hoc decisions on their value were made.

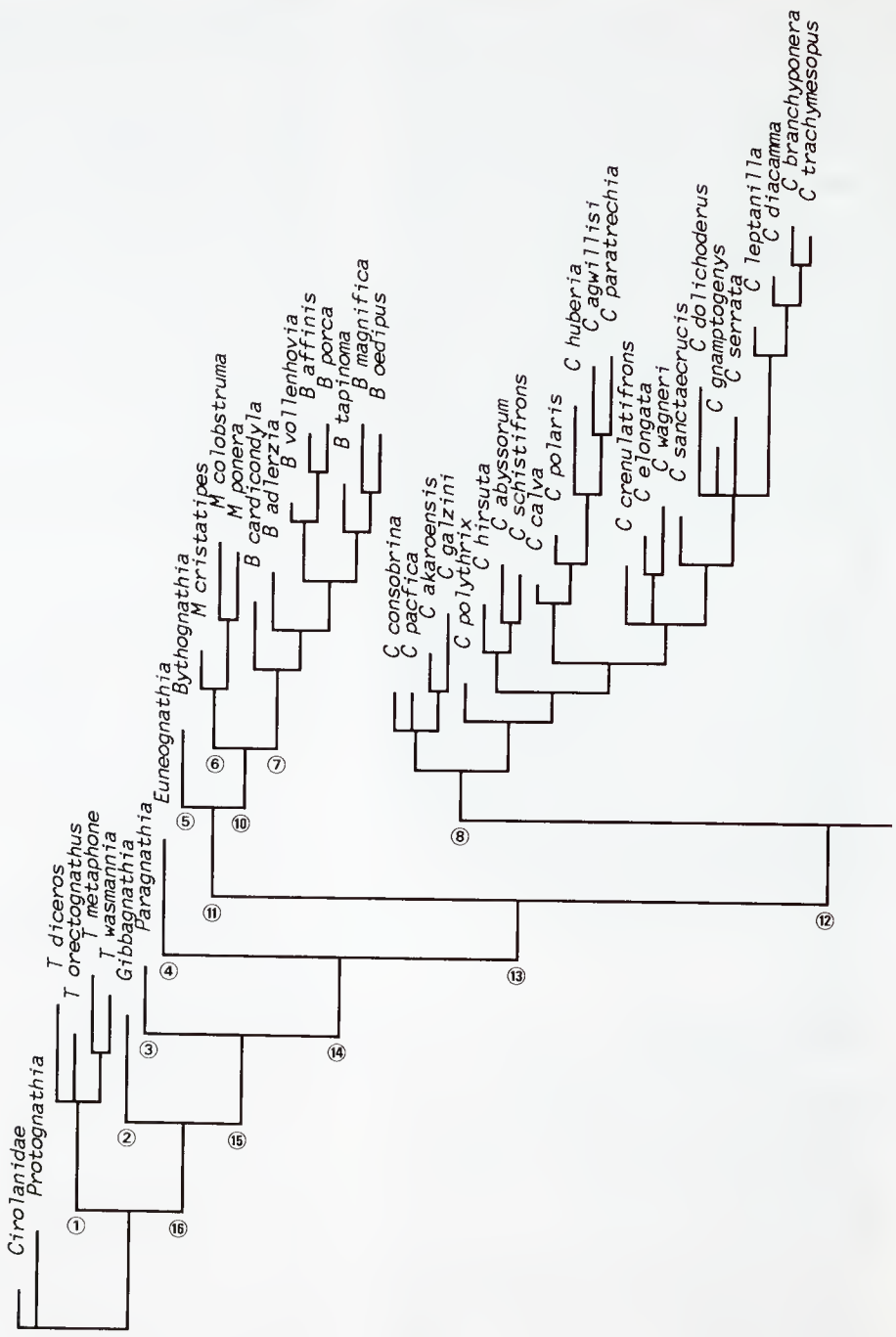
The successive weighting option (PAUP *reweight*) resulted in longer equally parsimonious trees (after weights had been reconverted to unity). These trees resolved some clades, principally within the *Caecognathia* and *Gnathia* clades, suggesting that a more robust analysis may reveal that these two genera can be further divided and refined. Because of their greater length, trees generated by the successive weight option were not considered further.

Character changes defining clades and genera

Character changes defining the major clades are discussed below. The major clades for which taxonomic status exists or is proposed are outlined and discussed in further detail. No conclusion is drawn about the relationship of the Gnathiidae to the outgroups.

The family is divided into two clades, 1 and 16, interpreted as one and nine genera respectively.

Thaumastoganthia (clade 1) shares the following apomorphies that are never reversed:


Cirolanidae
Protognathia
T diceros
T orectognathus
T metaphone
T wasmannia
Gibbagnathia
Paragnathia
Euneognathia
Bythognathia
M cristatipes
M colobstruma
M ponera
B cardicondyla
B adlerzia
B vollenhovia
B affinis
B porca
B tapinoma
B magnifica
B oedipus
C consobrina
C pacifica
C akaroensis
C galzini
C polythrix
C hirsuta
C abyssorum
C schistifrons
C calva
C polaris
C huberia
C agwillisi
C paratrechia
C crenulatifrons
C elongata
C wagneri
C sanctaecrucis
C dolichoderus
C gnamptogenys
C serrata
C leptanilla
C diacamma
C branchyponera
C trachymesopus
①
②
③
④
⑤
⑥
⑦
⑧
⑩
⑪
⑫
⑬
⑭
⑮
⑯

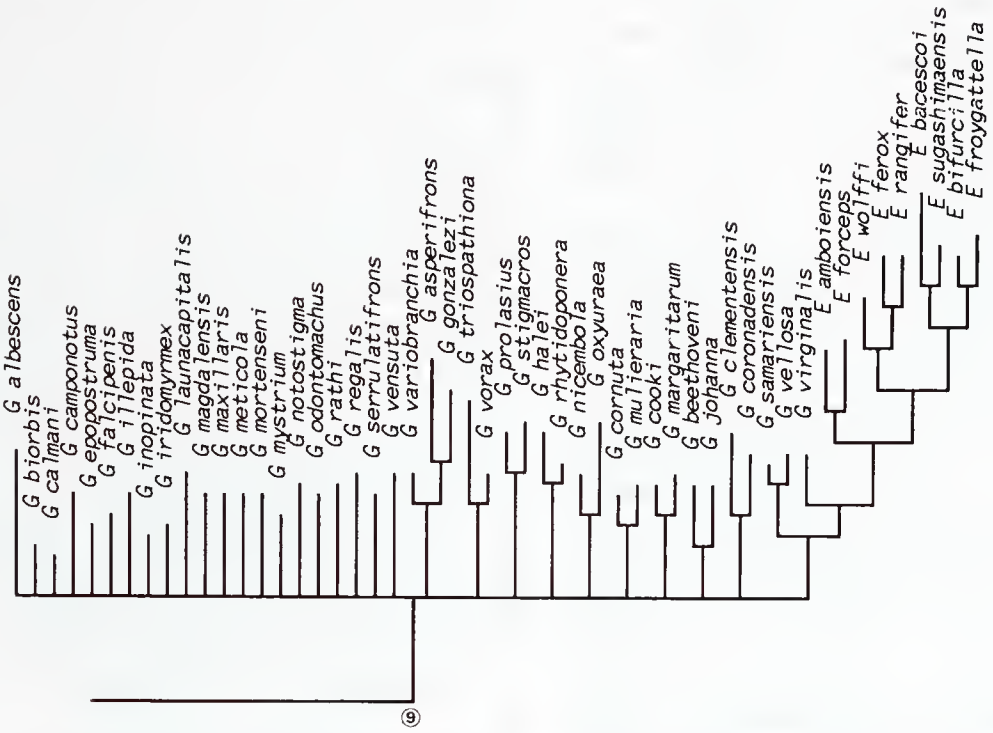


Figure 3. Strict consenus tree calculated from over 3000 equally parsimonious trees (The tree does not indicate branch length but is organised for clarity only).

mouthparts small; maxilliped of fewer than 5 articles; antenna curved under mandibles; antenna 1 longer than antenna 2, antenna 2 peduncle stout (less than 4 times width) and flagellum of 3 articles or less; pereonite 7 not visible dorsally and pleopods without setae. The following plesiomorphies also unite *Thaumastognathia*: pylopod pediform, not operculate and pereon widest at pereonite 5.

Clade 16 (*Gibbagnathia*, *Paragnathia*, *Eueognathia*, *Bythognathia*, *Monodgnathia*, *Bathygnathia*, *Caecognathia*, *Gnathia* and *Elaphognathia*) share the following characters that are sometimes reversed: antenna 1 flagellum of four or more articles; pereon even-sided; pereonite 4 possessing an anterior constriction; pereonite 7 visible and antenna 2 longer than or subequal to antenna 1.

Gibbagnathia (clade 2) is a monotypic genus defined by numerous autapomorphies not included in this analysis (see *Methods*). In this analysis *Gibbagnathia* is characterised by the following apomophies convergent in other taxa: mouthparts small; pylopod pediform; maxilliped of fewer than 5 articles; frontal border with processes; superior frontolateral process present; mandibular blade reduced or absent and cephalon and pereon covered with numerous granules and setae.

Clade 15 unites eight genera which share the following characters that are sometimes reversed: mouthparts not reduced; pylopod not pediform, with setae on ventral surface; maxilliped of 5 articles (sometimes with coupling hooks); antenna 1 peduncle length greater than four times width and dorsal sulcus present.

Paragnathia (clade 3) is also a monotypic genus defined by numerous autapomorphies not included in this analysis (see Monod, 1926). In this analysis *Paragnathia* is characterised by the following which are convergent in other taxa: pylopod 6-articled, operculate (articles 1, 3 and 4 enlarged); frontal border without processes; pleopods without setae; pereopods covered in plumose setae and uropodal rami clearly extending beyond the apex of the pleotelson.

Clade 14 unites seven genera with the following synapomorphies that are sometimes reversed: pylopod of 5 or fewer articles (except *Bythognathia*) and external margin of pylopod with at least a few setae.

Enneognathia (clade 4) is a monotypic genus defined in this analysis by the following apomorphies convergent in other taxa: pylopod 5-articled (not operculate), with a dense margin of plumose setae; frontal border transverse, with processes; mediofrontal process with multiple projections; inferior lateral process present; mandibles with a pseudoblade and an internal lobe; cephalon with paraocular ornamentation; and posterior border of pereonite 6 deeply concave with lobuli. For a complete description, including autapomorphies not used in this analysis see Monod (1926).

Clade 13 unites the seven remaining genera which possess an operculate pylopod (except *Bythognathia*).

Clade 11 links three genera *Bythognathia*, *Monodgnathia* and *Bathygnathia* who share three apomophies, never reversed: produced frontal border; absence of a dentate mandibular blade and presence of four or more coupling hooks on the maxillipedal endite. Other character changes are reversed in some species or genera. These include: absence of eyes (present in two species of *Bathygnathia*) and appendix masculina one-half to three-quarters length of the pleopodal endopod. *Bythognathia* (clade 5), the least derived genus, is monotypic and defined by numerous autapomorphies (Camp, 1988 for complete description). *Bythognathia* is defined in this analysis by the following apomorphies convergent in other taxa: antenna 1 flagellum 7-articled; uropodal rami clearly extending beyond the apex of pleotelson; pylopod 6-articled, pediform, external margin with dense cover of plumose setae; pereonite 1 extending to lateral margins of pereon; pereopods with dense cover of plumose setae and pereopods 3–6 with laterally expanded merus.

Monodgnathia and *Bathygnathia* form a strong and consistent group (clade 10) based primarily on the structure of the pylopod. These two genera share synapomorphies: pylopod 5-articled, operculate; pylopod article 2 greatly enlarged with spine(s) present on article 3. *Monodgnathia* (clade 6) is further defined by synapomorphies: mandibular blade present; pereopod 4 basis with a lateral quadratic lobe, ischium distally expanded into a circular cusp and frontal border as a distinct (chalky white in Australian species) region. *Bathygnathia* (clade 7) is defined by one synapomorphy and two apomorphies convergent in other taxa: buccal cavity wall protruding beyond rostrum, frontal border greatly produced and the presence of setae on the frontal border. Other apomorphies reversed in some species include: mandibles long (length about 5 times width); percopods 3–6 with laterally expanded merus and the ischium of pereopod 4 expanded distally (though not necessarily as a circular cusp).

Clade 12, comprising *Caecognathia* and *Gnathia*, is defined by three apomorphies, all of which involve the pylopod: pylopod 2- or 3-articled, article 1 enlarged and article 3 reduced. Other apomorphic character changes that are reversed in some species include: pylopod with dense margin of plumose setae and article 2 of pylopod circular. *Caecognathia* (clade 8) is defined by three apomorphies reversed in some species: a rounded frontal border; a mandibular blade which is not dentate or crenulate (reversed in *P. crenulatifrons*) and pleopods without setae.

Clade 9 is characterised by two non-reversed apomorphies of the frontal border: frontal border transverse and with processes. Two other apomorphies are reversed in some species: the presence of a superior frontolateral process and a mandibular incisor. This clade contains 56 species previously allocated to *Gnathia* and *Elaphognathia*.

Our analysis did not result in further dichotomies between major clades. The species *G. triospathiona* Boone, which Monod (1926) placed in the subgenus he incorrectly called *Perignathia*, was not significantly different from other species of *Gnathia*. Nine species belonging to the subgenus *Elaphognathia* did cluster in a monophyletic clade sharing several synapomorphies: frontal border excavated, mandibles possessing an internal lobe and lacking a dentate blade. Other character changes are reversed in some species: mediofrontal process and mandibular seta absent. Recognition of this taxon relies on recognition of a paraphyletic nominal taxon *Gnathia*. *Elaphognathia*, with its deeply

excavated frontal border, is immediately distinguishable from *Gnathia*, therefore, both *Elaphognathia* and *Gnathia* are given generic status.

A new classification of Gnathiidae

Monod (1926) in his major revision of the Gnathiidae recognised six genera: *Akidognathia*, *Thaumastognathia*, *Paragnathia*, *Euneognathia*, *Bathygnathia* and *Gnathia*. The genus *Gnathia* was further divided into three subgenera; *Gnathia*, *Elaphognathia* and "*Perignathia*". Since then, *Bythognathia* was erected by Camp (1988). Of these genera and subgenera *Euneognathia*, *Bythognathia*, *Paragnathia* and *Thaumastognathia* remain as originally defined but a new classification is needed for the others.

The strict-consensus tree, the most conservative consensus tree, gives a good deal of confidence in the robustness of the clades and is used as an hypothesis on which to base a new classification as follows:

Family Gnathiidae Leach, 1814
- *Bathygnathia* Dollfus, 1901
- *Bythognathia* Camp, 1988
- *Caecognathia* Dollfus, 1901
- *Elaphognathia* Monod, 1926
- *Euneognathia* Stebbing, 1893
- *Gibbagnathia* gen. nov
- *Gnathia* Leach, 1814
- *Monodgnathia* gen. nov.
- *Paragnathia* Omer-Cooper and Omer-Cooper, 1916
- *Thaumastognathia* Monod, 1926

The significant taxonomic changes proposed by this classification are:

1. Synonymy of the genus *Akidognathia* Stebbing, 1913 with *Bathygnathia* as a result of its type species being placed in the clade containing all species of *Bathygnathia*.
2. Erection of a new genus *Monodgnathia* to house non-type members of the former genus *Akidognathia*.
3. Erection of a new genus (presently monotypic) *Gibbagnathia*.
4. Resurrection of the genus *Caecognathia* based largely on the Section Productae of *Gnathia* (Monod, 1926).
5. Restriction and redefinition of the genus *Gnathia* as a paraphyletic taxon.
6. Elevation of the subgenus *Elaphognathia* to generic status on the basis of monophyly.
7. Synonymy of the subgenus *Perignathia* Monod, 1926 with *Caecognathia*.
8. Synonymy of the genus *Heterognathia* Amar and Roman, 1974 with *Caecognathia* (see Wägele, 1987).

Table 4 lists all currently known species in the new classification.

Biogeography

The family Gnathiidae is widespread, found from the Arctic through to the Antarctic and the intertidal, shelf and upper slopes of the major oceans. The South Atlantic, Indian Ocean and the Eastern Pacific Ocean have yielded few species of Gnathiidae compared to the seas around Europe, the Caribbean and the Western Pacific. Whether this reflects the amount of taxonomic work undertaken in the various regions or a natural pattern is unclear, though there is no *a priori* reason to expect the Pacific and Indian Oceans to possess a less diverse gnathiid fauna.

The cladogram contains information about the evolution of the family. The most significant evolutionary events in the radiation of the Gnathiidae took place in the cold and cool waters of the southern hemisphere. *Thaumastognathia*, four species on the shelf of Australia-New Zealand, is the sister group of all other gnathiids. Its presence on coasts on both sides of the Tasman Sea indicates that the genus is at least 80 million years old, the time usually given for the separation of these two land masses. The monotypic *Gibbagnathia*, the second clade in the cladogram is also a southern Australian shelf species. *Paragnathia* is enigmatic in being a single Afro-European species but *Euneognathia* is a single species from the Antarctic shelf.

None of these four genera has radiated successfully. But the next clade of three genera has begun to radiate in cold water. *Bythognathia* (one species) is from the deep sea (4000 m) of the Caribbean. *Monodgnathia* (four species) and *Bathognathia* (12 species) are both confined to the slope and deep sea (245–2698 m). *Monodgnathia* has a very disjointed distribution between the Western Pacific and North Atlantic suggesting that further species await discovery. But radiation has been moderate and with the exception of the one species of *Bythognathia* none is found very deep, unlike many other families of isopods.

Two related clades have radiated strongly in more shallow and warmer waters: *Caecognathia* with 43 species distributed more towards the poles than *Gnathia-Elaphognathia* (89 species) which is more cosmopolitan on temperate and tropical shelves and upper slopes. *Elaphogna-*

Table 4. Species of Gnathiidae assigned to genera according to the new classification proposed here. See Monod (1926) for full synonymies of species published by him or prior to this date. Later authorities are included in the References.

Bathygnathia Dollfus, 1901
B. adlerzia sp. nov.
B. affinis Birstein, 1963
B. bathybia (Beddard, 1886)
B. cardiocondyla sp. nov.
B. curvirostris Richardson, 1909
B. magnifica Moreira, 1977
B. monodi Cals, 1974
B. oedipus (Stebbing, 1913)
B. porca Kensley, 1980
B. segonzaci (Cals, 1982)
B. tapinoma sp. nov.
B. vollenhovia sp. nov.

Bythognathia Camp, 1988
B. yucatanensis Camp, 1988

Caecognathia Dollfus, 1901
C. abyssorum (Sars, 1872)
C. agwillisi (Seed, 1979)
C. akaroensis (Monod, 1926)
C. albescenoides (Menzies, 1962a)
C. amakusaensis (Nunomura, 1992)
C. antarctica (Studer, 1883)
C. bicolor (Hansen, 1916)
C. branchyponera sp. nov.
C. caeca (Richardson, 1911)
C. calva (Vanhöffen, 1914)
C. consobrina (Monod, 1926)
C. coralliophila (Monod, 1926)
C. crenulatifrons (Monod, 1926)
C. diacamma sp. nov.
C. dolichoderus sp. nov.
C. elongata (Kröyer, 1847)
C. floridensis (Menzies and Kruczynski, 1983)
C. galzini Müller, 1989c
C. gnamptogenys sp. nov.
C. hirsuta (Sars, 1877)
C. hodgsoni (Vanhöffen, 1914)
C. huberia sp. nov.
C. kikuchii (Nunomura, 1992)
C. leptanilla sp. nov.
C. nasuta (Nunomura, 1992)
C. nipponensis (Monod, 1926)
C. pacifica (Monod, 1926)
C. paratrechia sp. nov.
C. pilosipes (Monod, 1926)
C. polaris (Hodgson, 1902)
C. polythrix (Monod, 1926)
C. pustulosa (Hale, 1924)
C. regalis (Monod, 1926)
C. robusta (Sars, 1879)
C. saikaiensis (Nunomura, 1992)
C. sanctaecrucis (Schultz, 1966)
C. schistifrons (Stebbing, 1913)
C. serrata (Richardson, 1909)
C. stygia (Sars, 1877)
C. trachymesopus sp. nov.
C. vanhoeffeni (Menzies, 1962c)
C. vemae (Menzies, 1962a)
C. wagneri (Monod, 1925a)

Elaphognathia Monod, 1926
E. amboinensis (Cals, 1978)
E. bacescoi (Bacescu, 1960)
E. bifurcilla (Holdich and Harrison, 1980)
E. cornigera (Nunomura, 1992)
E. discolor (Nunomura, 1988)
E. ferox (Haswell, 1884)
E. forceps (Holdich and Harrison, 1980)
E. froygattella sp. nov.
E. insolita (Stebbing, 1905)
E. lucanoides (Monod, 1926)
E. monodi (Gurjanova, 1936)
E. rangifer (Monod, 1926)
E. rinnifrons (Holdich and Harrison, 1980)
E. sugashimaensis (Nunomura, 1981)
E. wolffi (Müller, 1989a)

Euneognathia Stebbing, 1893
E. gigas (Beddard, 1886)

Gibbagnathia gen. nov.
G. europalothrix sp. nov.

Gnathia Leach, 1814
G. africana Barnard, 1914
G. albescens Hansen, 1916
G. alces Monod, 1926
G. asperifrons Holdich and Harrison, 1980
G. beethoveni Paul and Menzies, 1971
G. biorbis Holdich and Harrison, 1980
G. bungoensis Nunomura, 1982
G. calamitosa Monod, 1926
G. calmani Monod, 1926
G. calsi Müller, 1993b
G. camponotus sp. nov.
G. clementensis Schultz, 1966
G. cooki Müller, 1989c
G. cornuta Holdich and Harrison, 1980
G. coronadensis Schultz, 1966
G. crytopais Barnard, 1925
G. dentata (Sars, 1872)
G. derzhavini Gurjanova, 1933
G. disjuncta Barnard, 1920
G. epopstruma sp. nov.

G. falcipenis Holdich and Harrison, 1980
G. fallax Monod, 1926
G. firingae Müller, 1991
G. gonalezi Müller, 1988
G. halei Cals, 1973
G. hirayamai Nunomura, 1992
G. illepida Monod, 1923
G. incana Menzies and George, 1972
G. inopinata Monod, 1925b
G. iridomyrmex sp. nov.
G. johanna Monod, 1926
G. lacunacapitalis Menzies and George, 1972
G. latidens (Beddard, 1886)
G. lignophila Müller, 1993a
G. magdalenensis Müller, 1988
G. malaysiensis Müller, 1993a
G. margaritarum Monod, 1926
G. maxillaris (Montagu, 1804)
G. meticola Holdich and Harrison, 1980
G. mortenseni Monod, 1926
G. mulieraria Hale, 1924
G. mystrium sp. nov.
G. nicembola Müller, 1989b
G. notostigma sp. nov.
G. odontomachus sp. nov.
G. oxyuraea (Lilljeborg, 1855)
G. panousei Daguerre de Hureaux, 1971
G. phallonajopsis Monod, 1925b
G. philogona Monod, 1926
G. piscivora Paperna and Por, 1977
G. producatridens Menzies and Barnard, 1959
G. prolasius sp. nov.
G. puertoricensis Menzies and Glynn, 1968
G. rathi Kensley, 1984
G. rectifrons Gurjanova, 1933
G. rhytidoponera sp. nov.
G. samariensis Müller, 1988
G. schmidti Gurjanova, 1933
G. serrulatifrons Monod, 1926
G. steveni Menzies, 1962b
G. stigmaeros sp. nov.
G. taprobansis Monod, 1926
G. teisseri Cals, 1972
G. tridens Menzies and Barnard, 1959
G. trilobata Schultz, 1966
G. triospathiona Boone, 1918
G. tuberculata Richardson, 1910
G. tuberculosa (Beddard, 1886)
G. variobranchia Holdich and Harrison, 1980
G. vellosa Müller, 1988
G. venusta Monod, 1925b
G. virginalis Monod, 1926
G. vorax (Lucas, 1849)

Monodgnathia gen. nov.
M. colobostruma sp. nov.
M. cristatipes (Stebbing, 1913)
M. ponera sp. nov.
M. poteriophora (Monod, 1926)

Paragnathia
Omer-Cooper and Omer-Cooper, 1916
Paragnathia formica (Hesse, 1864)

Thaumastognathia Monod, 1926
T. diceros Monod, 1926
T. metaphone sp. nov.
T. orectognathus sp. nov.
T. wasmannia sp. nov.

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thia is confined to the Indo-West Pacific region except for one species, *E. bacescoi*, which is from the Mediterranean. Most species of *Elaphognathia* are confined to warm waters.

Holdich and Harrison (1980) suggested that more Australian species of Gnathiidae would be discovered once detailed surveys were completed in regions which had yet to be investigated. Sampling of the Australian coast, shelf and slope has yielded 28 new species of Gnathiidae, more than doubling the number of described Australian species to 45, of these 34 are found in the south-east. To date, only a few areas of northern Australia and no areas in the south-west have been intensively surveyed. Even in regions where detailed work has been carried out not all the potential habitats have been fully investigated. Further sampling is bound to yield more species of Gnathiidae.

Though only limited areas of the Australian coastline have been sampled, it is still clear that the continent possesses an extremely rich and diverse gnathiid fauna in intertidal, shelf and slope environments (Table 5). About one quarter of all the presently described species of Gnathiidae are found in Australian waters. All but three monotypic genera (*Bythognathia*, *Enneognathia* and *Paragnathia*) are represented.

Cals (1973) and Holdich and Harrison (1980) argued that it was premature to state that Australia has an endemic fauna but it now seems certain that this is true for at least southern Australia. The northern boundary along the eastern coast and the western boundary of all species are uncertain because of absence of sampling but there is little overlap between this fauna and the fauna of tropical Australia recorded by Holdich and Harrison. *G. calmani*, described from Vie-

Table 5. Habitat and distributional data for Australian Gnathiidae following format of Holdich and Harrison (1980: table 1) and incorporating new species and range extensions for previously described species from collections of the Museum of Victoria.

Species	Substratum	Depth (m)	Locality
Bathygnathia alderzia sp. nov.		780–795	NW Coral Sea
B. cardiocondyla sp. nov.	silt to clay	868–1730	Off Freycinet Peninsula, Tas. and off Terrigal, NSW
B. opisthopsis sp. nov.		2632–2698	E of Newcastle, NSW
B. vollenhovia sp. nov.	coarse shelly sand	800	47 km S of Cape Conran, Vic. and W coast of South Island, New Zealand
Caecognathia agwillisi (Seed, 1979)	tubes of *Rhampobrachium* sp. and colonies of *Galeolaria* sp.	intertidal	Aireys Inlet, Vic. and Elliston, SA
C. branchyponera sp. nov.	muddy coarse shell with many sponges	400–426	Nowra, NSW to Point Hicks, Vic.
C. diacamma sp. nov.	fine to coarse sand	15–103	Western Bass Strait and S of Newcastle, NSW
C. dolichoderus sp. nov.	fine to muddy sand	110–130	Eastern Bass Strait and E of Cape Banks, NSW
C. gnamptogenys sp. nov.		1000	S of Point Hicks, Vic.
C. huberia sp. nov.	mud, sand and hard bottom and sponges	27–185	Bass Strait and Broken Bay, NSW
C. leptanilla sp. nov.	sand and shell	22–800	Bass Strait, E coast of Tas. and E of Sydney, NSW
C. paratrechia sp. nov.	shaded, sessile invertebrates	20	Pearson I., SA
C. pustulosa (Hale, 1924)	sponge	intertidal	Glenelg, SA
C. trachymesopus sp. nov.	mud to coarse sand with shells	21–293	Bass Strait
Elaphognathia bifurcilla (Holdich and Harrison, 1980)	sand	10–18.2	Bowling Green Bay, Qld
E. ferox (Haswell, 1884)	sand, silt clay and sessile invertebrates / plant holdfasts	intertidal–24	Port Jackson, NSW to Portland, Vic.
E. forceps (Holdich and Harrison, 1980)	coral rubble on muddy shore	intertidal	Rowes Bay, Qld
E. froygattella sp. nov.	coarse sand	84	35 km SSW of Cape Otway, Vic.
E. rimifrons (Holdich and Harrison, 1980)	sandy mud	6.8–8.8	Halifax Bay, Qld
Gibbagnathia europalothorix sp. nov.	medium to coarse sand	36–104	Bass Strait
Gnathia asperifrons Holdich and Harrison, 1980	rock scrapings	intertidal	Lizard I., Qld
G. biorbis Holdich and Harrison, 1980	dead coral / barnacles	intertidal	Heron I. and Townsville, Qld
G. calanitosa Monod, 1926	coarse sand to mud	29–204	Nowra, NSW to Eddystone Point, Tas. and west into central Bass Strait
G. calmani Monod, 1926	sand, bryozoans and dead coral	intertidal–113	Heron I., Qld and Portland, Vic.
G. camponotus sp. nov.	muddy to coarse sand and shell	55–135	Bass Strait and E of Port Jackson, NSW
G. cornuta Holdich and Harrison, 1980	*Teredo*-bored wood	intertidal	Pallarenda, Qld
G. epopostruma sp. nov.	medium sand	81	44 km SW off Cape Otway, Vic.
G. falcipenis Holdich and Harrison, 1980	wood/coral	intertidal–80	Magnetic I. and Lizard I., Qld and North West Shelf, WA
G. halei Cals, 1973	fine gravel to mud	136–188	Off Moreton I. and Capricorn Channel, Qld
G. iridomyrmex sp. nov.	red coralline algal turf	11	Portland, Vic.
G. latidens (Beddard, 1886)		12.8	Flinders Passage, Qld
G. meticola Holdich and Harrison, 1980	wood / barnacles	intertidal	Townsville, Qld
G. mulleraria Hale, 1924	among *Zostera* sp.	12.8–14.6	Vic. to WA
G. mystrium sp. nov.	muddy sand to shelly sand	57–130	Bass Strait
G. notostigma sp. nov.	coarse sand and gravel	75–200	S of Point Hicks, Vic. and off Broken Bay, NSW
G. odontomachus sp. nov.	find sand and mud to sandy gravel	8–13	Western Port, Vic.
G. prolasius sp. nov.	coarse shelly sand	363–1000	Nowra, NSW to Freycinet Peninsula, Tas.

G. rhytidoponera sp. nov.		296–303	Western Coral Sea
G. stigmacros sp. nov.	medium sand to gravel	27–293	Eastern Bass Strait
G. variobranchia Holdich and Harrison, 1980	coral	intertidal	Heron I., Qld
Monodgnathia colobstruma sp. nov.		1000	S of Point Hicks, Vic.
M. ponera sp. nov.		1550	Lord Howe Rise, Tasman Sea
Thaumastognathia metaphone sp. nov.	shaded, sessile invertebrates	20	Pearson I., SA
T. orectognathus sp. nov.	medium to very coarse sand	27–200	Bass Strait
T. wasmannia sp. nov.		122	20 km E of Falmouth, Tas.

toria is also recorded from Heron I., Queensland but this is exceptional. This discovery of extreme endemism on the southern coast is consistent with the generalisations made by Wilson and Allen (1987). The extent to which the tropical Australian species extend into the Indo-West Pacific is unknown because of the low level of sampling elsewhere.

Moreover, even within the small area studied, many species have limited distributional range. The isopod collections of the Museum of Victoria are based on over 400 well-sorted samples of benthos from Bass Strait and the south-eastern Australian slope and of samples from subtidal rocky habitats. Only two species of more than 30 could be said to be moderately well distributed: *Caecognathia leptanilla* with records from 40 samples collected between 22 and 800 metres in Bass Strait and the eastern shelf and slope; and *Caecognathia trachymesopus* from 29 sites in Bass Strait between 21 and 293 metres. All other species are recorded from fewer than 11 samples. The shallow-water species with the greatest geographical range is *G. mulieraria* recorded from Victoria to Western Australia. Because so little collecting has been done in Western Australia the likelihood remains that other species have this sort of distribution.

The south-eastern Australian gnathiid fauna shows evidence of local radiation into endemic species complexes (see cladogram). The *Caecognathia agwillisi*-complex comprises *C. pustulosa* (not included on this analysis but clearly related to this complex), *C. agwillisi*, and *C. paratrechia* in South Australia and western Victoria and *C. huberia* in Bass Strait and New South Wales. The cladogram suggests that the sister taxa of this group are species from Antarctic seas, *C. calva* and *C. polaris*. The *C. trachymesopus*-complex comprises *C. trachymesopus*, *C. leptanilla* and *C. diacamma* from shelf habitats in Bass Strait and south-eastern Australia and *C. branchyponera* from the slope in the same region.

Further evidence of local radiation is seen in *Thaumastognathia* whose four species are confined to the Australian or New Zealand shelf.

Although deep-water Australian species of the genera *Bathygnathia* and *Monodgnathia* are endemic they do not group into local complexes. The species seem to have arisen independently within widespread genera.

The species from the south-eastern slope have been recorded from few localities although two, *G. prolasius*, from 363 to 1000 m and *C. leptanilla*, 22 to 800 m, cover a wide depth range.

Bathygnathia vollenhovia, reported from 800 m, is the only species recorded from both sides of the Tasman Sea. The limited number of specimens of this species from the west coast of New Zealand are not distinguishable from those from the Australian eastern slope. More specimens are needed from both sides of the Tasman Sea to clarify the relationship between the Australian and New Zealand groups.

Only one species, *B. opsithopsis*, has been recorded below 2000 m in Australia and gnathiids are noticeably absent from the limited number of samples taken below this depth (Poore et al., 1994) and rare in other parts of the world. Only *Bythognathia yucatanensis* Camp from 3700–3800 m in the Caribbean, *Caecognathia caeca* Richardson from 2638 m in the western North Atlantic, and *Bathygnathia segonzaci* (Cals) from abyssal depths in the southern Atlantic have been reported from bathyal depths (Camp, 1988).

Gnathiidae Leach

Gnathides Leach, 1814: 432.

Gnathiidae. — Harger, 1880: 408. — Monod, 1926: 281–285 (synonymy) (and other authors)

Diagnosis. Pereopods 1 modified as pylopods which lie under buccal cavity. Pereonite 7 reduced, as wide as pleon. Pereopods 7 absent.

Pleon narrower than pereon. Sexually dimorphic. Male head fused to first pereonite; mandible in male large and projecting foward, visible dorsally. Female and praniza larva with pereonites 4–6 fused, inflated. Praniza ectoparasitic on fish.

Key to genera of Gnathiidae

The key applies only to adult males and is written for ease of identification; it does not reflect the phylogenetic hypothesis.

1. Pylopod large, distinct; maxilliped 5-articled 2
— Pylopod very thin and elongate (difficult to see even under dissecting microscope), pereopod-like; maxilliped absent or greatly reduced 9
2. Pylopod of 5 or 6 articles; article 3 not reduced 3
— Pylopod of 2 or 3 articles; article 3 reduced or absent 7
3. Frontal border with processes, transverse; pronounced paraoccular ornamentation present ..... *Euneognathia*
— Frontal border without processes, rounded or produced; lacking paraoccular ornamentation 4
4. Pylopod pereopod-like, not operculate; pereonite 1 greatly produced ..... *Bythognathia*
— Pylopod operculate, not pediform; pereonite 1 not greatly produced ... 5
5. Pylopod 6-articled, article 2 reduced; mandibular blade dentate; animal small, < 5 mm ..... *Paragnathia*
— Pylopod 5-articled, article 2 greatly enlarged; mandibular blade smooth or absent; animal large, > 5 mm 6
6. Mandibles without blade; buccal cavity wall extension visible at the end of pronounced rostrum ..... *Bathygnathia*
— Mandibular blade smooth; frontal border rounded, without buccal cavity wall protrusion; pereopod 4 basis with quadratic lobe ..... *Monodgnathia*
7. Frontal border without frontal process, often rounded; cephalon lacking paraoccular ornamentation and dorsal sulcus ..... *Caecognathia*
— Frontal border with frontal processes, often transverse; cephalon may possess paraoccular ornamentation and/or a dorsal sulcus 8
8. Frontal border not deeply excavated, mandibles not elongate ....*Gnathia*
— Frontal border excavated; mandibles long, lacking a dentate blade ..... *Elaphognathia*
9. Pereon smooth, oval; pereonite 7 not visible; pleon often folded under pereon and antennae curved under mandibles; mandibles with crenulate blade and incisor ..... *Thaumastognathia*
— Pereon covered in granules and setae, rectangular; large dorsal, anteriorly-directed projection from pereonite 3; pereonite 7 visible, small; mandibles with highly reduced or absent blade, incisor absent ..... *Gibbagnathia*

Bathygnathia Dollfus

Bathygnathia Dollfus, 1901: 240. — Monod, 1926: 319.

Akidognathia Stebbing, 1913: 12. — Monod, 1926: 289 (type species: *Akidognathia oedipus* Stebbing, 1913).

Type species. Anceus bathybius Beddard, 1886 (original designation).

Diagnosis. Eyes absent or present. Frontal border produced as rostrum, often long; without processes; buccal cavity wall visible anterodorsally. Mandibles straight, without blade. Pereonite 1 reaching lateral margins of pereon, not immersed in cephalon. Pylopod 5-articled; operculate, second article enlarged; article 3 with 1 or 2 spiniform setae; external margin lacking dense cover of plumose setae. Pereopod 4 basis without anterior quadrate lobe, ischium distally expanded or not; merus of pereopods laterally expanded in some species.

Remarks. Bathygnathia is characterised by a 5-articled, operculate pylopod, mandibles without obvious blade and the protruding rostrum and buccal cavity wall. Phylogenetic analysis separated the known species of *Akidognathia* into two groups. The first, including its type species, *A. oedipus*, belongs in a clade with species of *Bathygnathia* and is the sister taxon to the second clade. *Akidognathia* is therefore a junior synonym of *Bathygnathia* and a new genus, *Monodgnathia*, is needed for the second clade.

A. segonzaci Cals is very tenatively placed in *Bathygnathia* because of the shape of the mandible and the lack of a quadratic lobe on pereopod 4 but the description of this species is very brief and only the ventral surface was figured.

There are 12 species identified in the literature (Table 4) all confined to the deep sea at depths between 245 and 2698 m. The five newly described species of *Bathygnathia* are the first records of this genus from Australasian waters.

Key to males of *Bathygnathia* from Australia and New Zealand

1. Eyes present ..... *B. adlerzia*
— Eyes absent 2
2. Rostrum elongate, two-thirds length of cephalosome and narrow, one third width of cephalosome; pereopod 4 ischium not dilated distally ..... *B. vollenhovia*
— Rostrum rather broad, not elongate; pereopod 4 ischium dilated distally 3
3. Pereonites 1–4 with ornate margins, raised distally; cephalon covered with numerous granules ..... *B. cardiocondyla*
— Cephalon and pereonites 1–4 relatively smooth 4
4. Mandibles indurate, with pronounced incisor; rostrum and cephalon without diamond-shaped translucent region ..... *B. opisthopsis*
— Mandibles thin and flexible in preserved material, without incisor; diamond-shaped translucent region on anterior cephalon ..... *B. tapinoma*

Bathygnathia adlerzia sp. nov.

Figures 4–6

Material examined. Holotype. North-western Coral Sea (10°32.1′S, 144°12.1′E), 780–795 m, epibenthic sled, ORV *Franklin*, 20 August 1988 (AM stn 06/88 site 3), AM P41294 (1 male).

Paratype. Type locality, AM P42273 (1 male).

Other material. Western Coral Sea (17°35′S, 146°53′E), 458–500 m, epibenthic sled, M. Pichon et al. on RV *Cidaris*, 15 Jun 1986 (stn 142.2), QM W19964 (1 male, anterior half only).

Description. Total length of holotype: 7.82 mm.

Cephalosome pentagonal, 1.4 times as long as wide, lateral margins convex. Rostrum wide and produced with ventrolateral walls of buccal cavity protruding. Holotype very heavily crystallised, no obvious remnants of setae visible on rostrum, rostrum badly torn. Eyes well developed, lateral, sessile and pale. External scissura smoothly rounded. Cephalosome long, one-third length of animal; with broad dorsal sulcus and low, posterior median tubercle. Antenna 1 peduncle article 2 with a large plumose seta distally; flagellum of 5 articles, with 1 aesthetasc. Antenna 2 peduncle twice as long as peduncle of antenna 1; flagellum incomplete, only three articles present. Mandible curved around rostrum, one-third length of cephalosome, cylindrical, lacking obvious blade, with unarmed carina; seta one-third way along; slight mandibular inci-

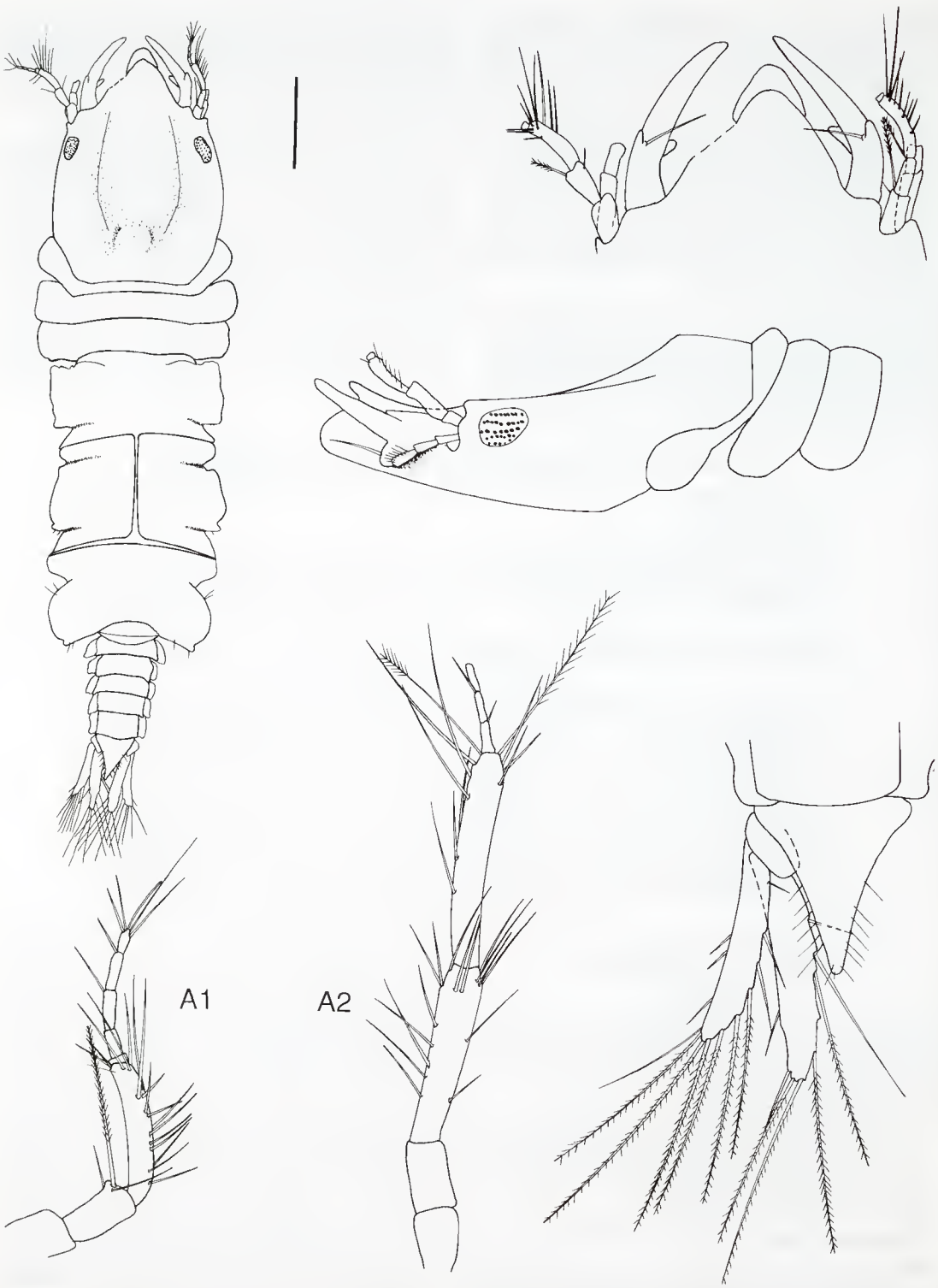

Figure 4. *Bathygnathia adlerzia*. Holotype, AM P41294; A2 of paratype, AM P42180.

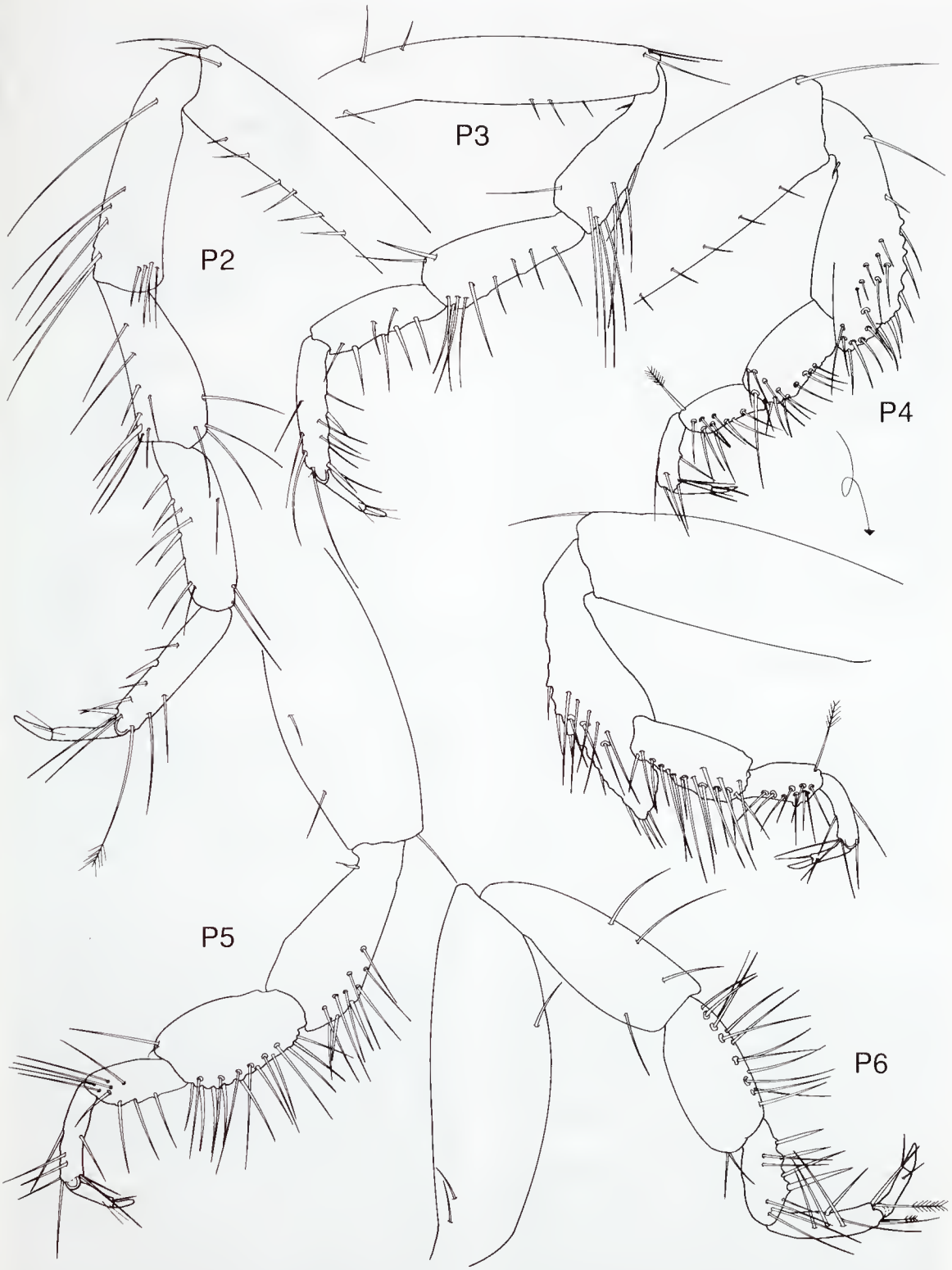

Figure 5. *Bathygnathia adlerzia*. Holotype, AM P41294; P2 of paratype, AM P42180.

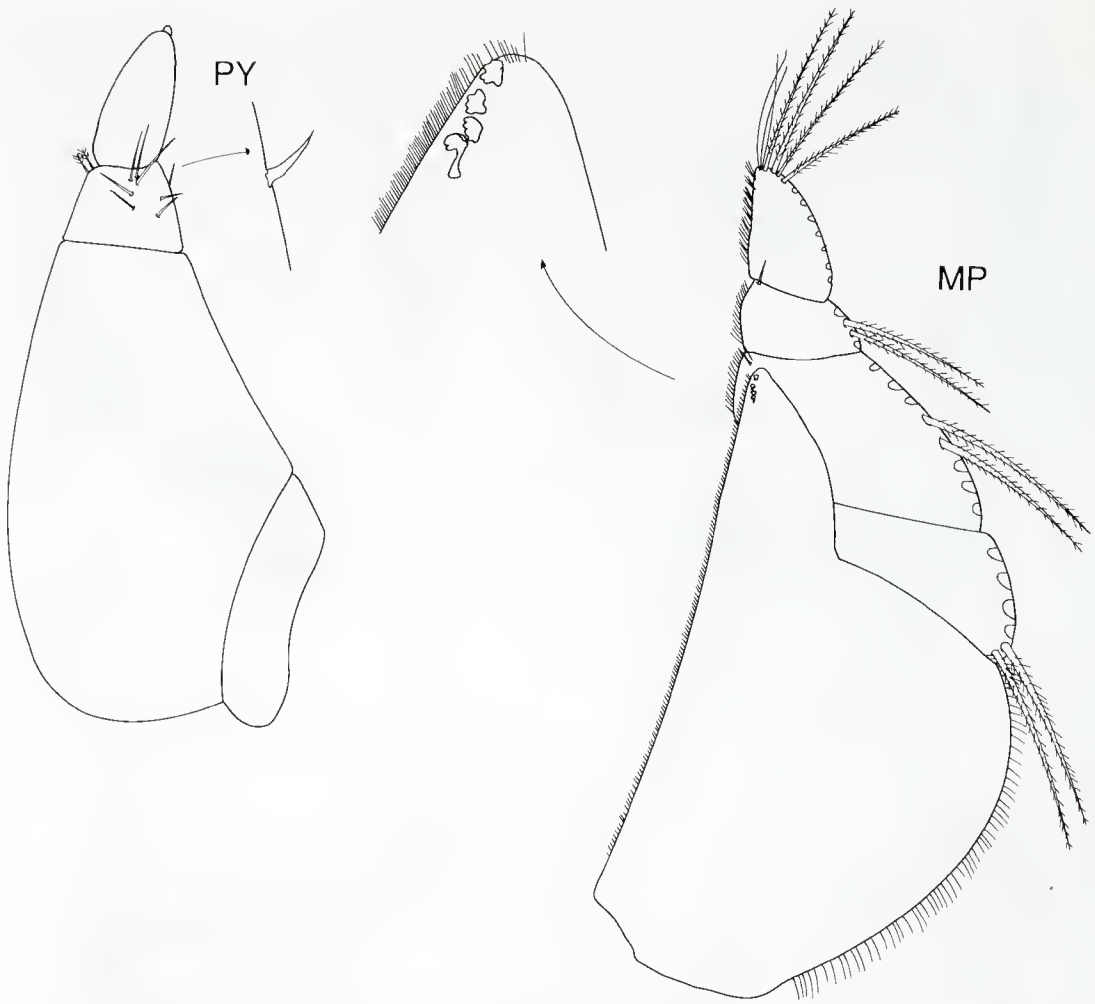

Figure 6. *Bathygnathia adlerzia.* Holotype, AM P41294.

sor near base of seta; 1 conical internal lobe ventrally opposite seta. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, wide, with 4 coupling hooks. Pylopod 5-articled: article 1 elongate, firmly attached to article 2; article 3 with 1 spiniform seta on external anterolateral margin and 7 simple setae medianly on ventral surface; article 5 minute.

Pereon widest anteriorly, slightly wider than cephalosome. Pereonite 1 large, laterally directed forward; dorsally reaching lateral margins and laterally visible as one continuous band. Pereonites 2 and 3 subequal, as wide as perconite 1. Pereonite 4 narrow, with anterior constriction. Pereonite 5 with dorsal sulcus as thin median groove, twice as long as pereonites 2 and 3. Pereonite 6 with small lobuii. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer and narrower, pleonal epimera prominent. Pleotelson subtriangular, longer than wide, with 7-8 pairs of simple setae laterally. Uropodal peduncle without setae; rami subequal, reaching well beyond the apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with many posterior spiniform setae, particularly on carpus and with dense cover of simple setae; bases of pereopods 2 and 3 narrower than bases of pereopods 4-6; pereopod 4 ischium distally produced.

Pleopods setose. Pleopod 2 endopod with

appendix masculina one-quarter length of rami. Penes 2 contiguous papillae.

Distribution. Western Coral Sea, 458–795 m depth.

Remarks. Bathygnathia adlerzia is only the second species of *Bathygnathia* deseribed with funetional eyes and as such, it is easily separated from all others speeies exeept *B. magnifica* Moreira from Brazil. It differs from *B. magnifica* by having a shorter rostrum, mandibles with marked incisors and pereopod 5 lacking a distal expansion of the isehium.

Bathygnathia cardiocondyla sp. nov.

Figures 7–9

Material examined. Holotype. Eastern Bass Strait, 47 km S of Cape Conran, Vic. (38°24.5′S, 148°42.1′E), 1200 m, sand-silt-clay, pipe dredge, R.S. Wilson on RV *Tangaroa*, 15 Nov 1981 (stn BSS 632) NMV J8372 (1 male).

Paratype. Eastern Bass Strait, 121 km S of Cape Conran. (38°55.6′S, 148°46.4′E), 1730 m, silty clay, pipe dredge, R.S. Wilson on RV *Tangaroa*, 16 Nov 1981 (stn BSS 635) NMV J8371 (1 male).

Other material. New South Wales. East of Terrigal (33°26′S, 152°11′E), 868 m, sled-dredge. FV *Kapala*, 6 Dec 1979, (AM stn K79-20-12), AM P42099 (1 male).

Description. Total length of holotype: 6.85 mm.

Cephalosome pentagonal, as long as wide, lateral margins slightly eonvex. Eyes absent. Frontal border produced as broad rostrum; pointed, with 30 setae submarginally. Anterior margin of rostrum raised; buccal cavity wall visible anteriorly (particularly on paratype). Supraocular lobe smoothly convex. Cephalosome covered with numerous granules: broad dorsal sulcus in distal half and small posterior tuberele. Region between dorsal sulcus and frontal margin of rostrum translucent. Antenna 1 flagellum of 5 articles, with 2 acsthetases. Antenna 2 longer than antenna 1; flagellum of 6 articles (possibly some flagellum articles missing). Mandible half length of cephalosome, cylindrieal with narrow apex; a slightly armed carina; pronouneed proximal mandibular incisor; mandibular seta one-quarter way along; eonieal internal lobe ventrally opposite ineisor. Maxilliped 5-artieled; external margins of articles 2 to 4 bearing plumose setae; endite elearly reaching article 3, with 5 coupling hooks. Pylopod 5-articled: article 3 with 2 peetinate setae on external anterolateral margin; articles 2–4 with 13 setae medianly; artiele 5 minute.

Pereon evenly sided, as wide as cephalosome exeept pereonite 5 which is wider around base of pereopods. Pereonite 1 dorsally raised forming saddle-like structure with pereonite 2 laterally; dorsally small, not reaching lateral margins of pereon and partially obscured laterally by pereonite 2. Pereonites 1–4 with granular ornate borders. Pereonite 4 with raised ornate ridge near posterior border. Pereonites 2 and 3 mueh shorter than 4–6, pereonite 5 longest. Pereonite 6 lobuii thin and elongate. Pereonite 7 small, very narrow, overlapping pleon. Pleonites progressively narrower, pleonal epimera prominent. Pleotelson subtriangular, tapering, as wide as long; lateral margins sinuous with 3 pairs of simple setae laterally. Uropodal pedunele with 2 setae; rami subequal, reaching beyond apex of pleotelson, internal margins bearing numerous plumose setae.

Pereopods with dense eover of simple setae particularly on basis; pereopod 2 with 1 posterior spiniform seta on carpus; pereopod 4 with numerous tubercles, carpus wide and ischium with anterodistal projection.

Pleopods setose. Pleopod 2 endopod with appendix masculina subequal to rami. Penes 2 contiguous papillae.

Distribution. Southern NSW, eastern Bass Strait, 868–1730 m depth.

Remarks. Bathygnathia cardiocondyla is easily identified and separated from all other *Bathygnathia*. The raised and ornate appearanee of the cdges of the cephalon and pereonites 1–4 is unique amongst the *Bathygnathia* but similar in some ways to *Bythognathia yucatanensis* Camp.

Bathygnathia opisthopsis sp. nov.

Figures 10–12

Material examined. Holotype. New South Wales, E of Neweastle, (33°03.6′S, 152°48′E), 2632–2698 m, Menzies trawl, W. Ponder and R.T. Springthorpe, 8 Oct 1982 (AM stn U216), AM P42181 (1 male).

Paratype. Type locality, AM P42105 (1 male).

Description. Total length of holotype: 7.67 mm.

Cephalosome pentagonal, as long as wide, lateral margins slightly eonvex. Eycs absent. Frontal border produced as broad rostrum; pointed and raised, with few submarginal setae. Buccal cavity wall clearly visible beyond anterior margin of rostrum. Supraoeular lobe smoothly convex. Cephalosome smooth; with

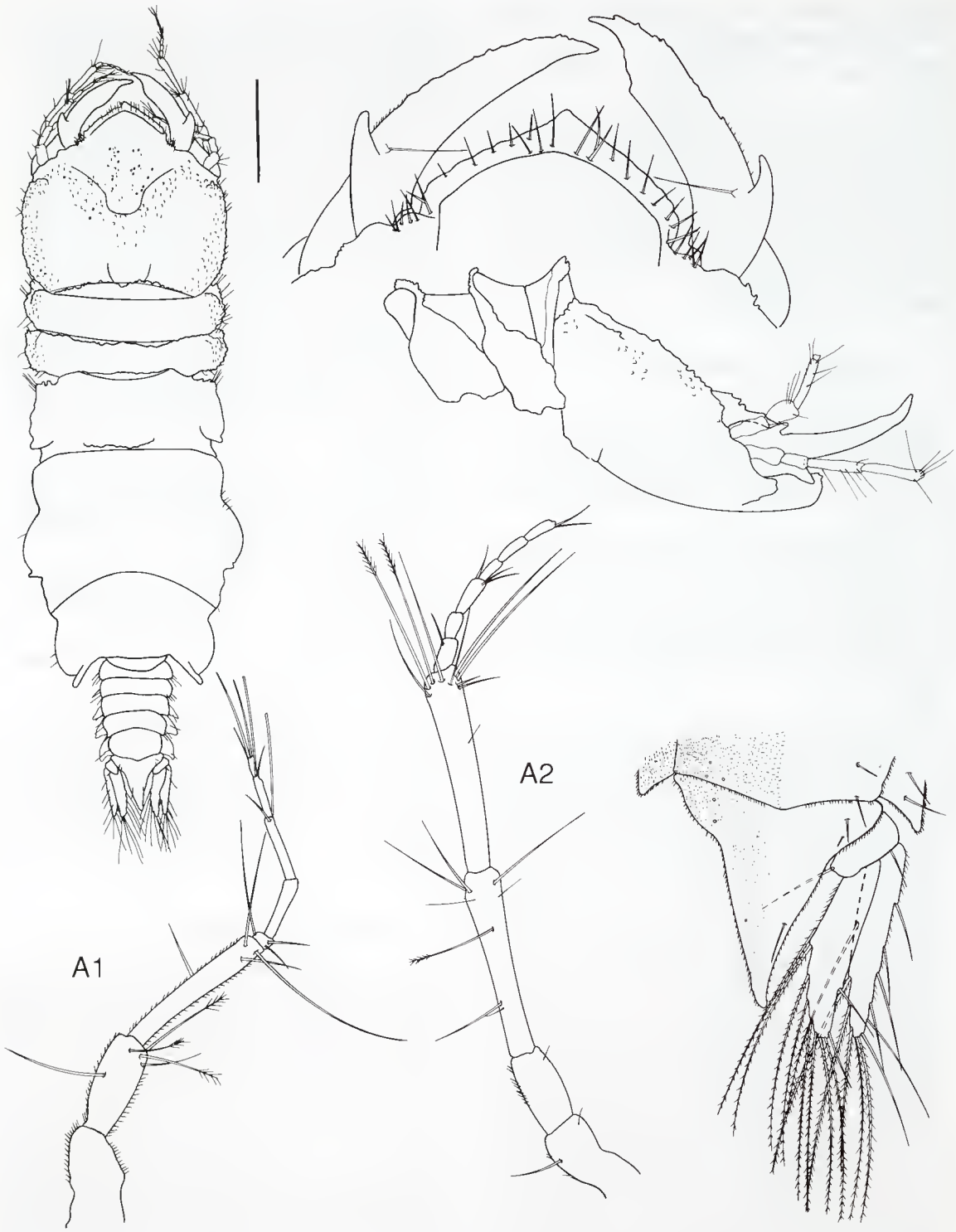

Figure 7. *Bathygnathia cardiocondyla*. Holotype, NMV J8372.

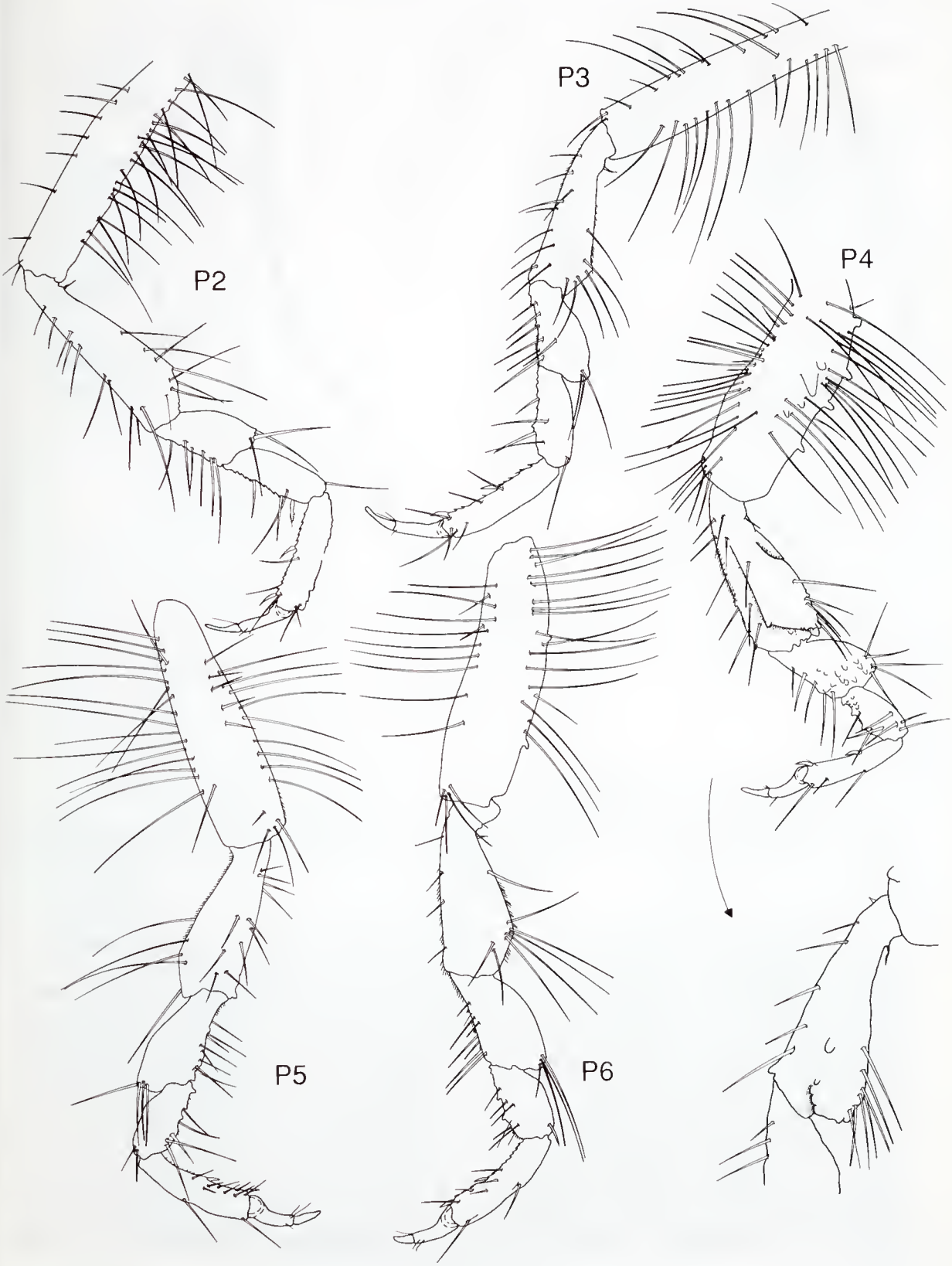

Figure 8. *Bathygnathia cardiocondyla*. Holotype, NMV J8372.

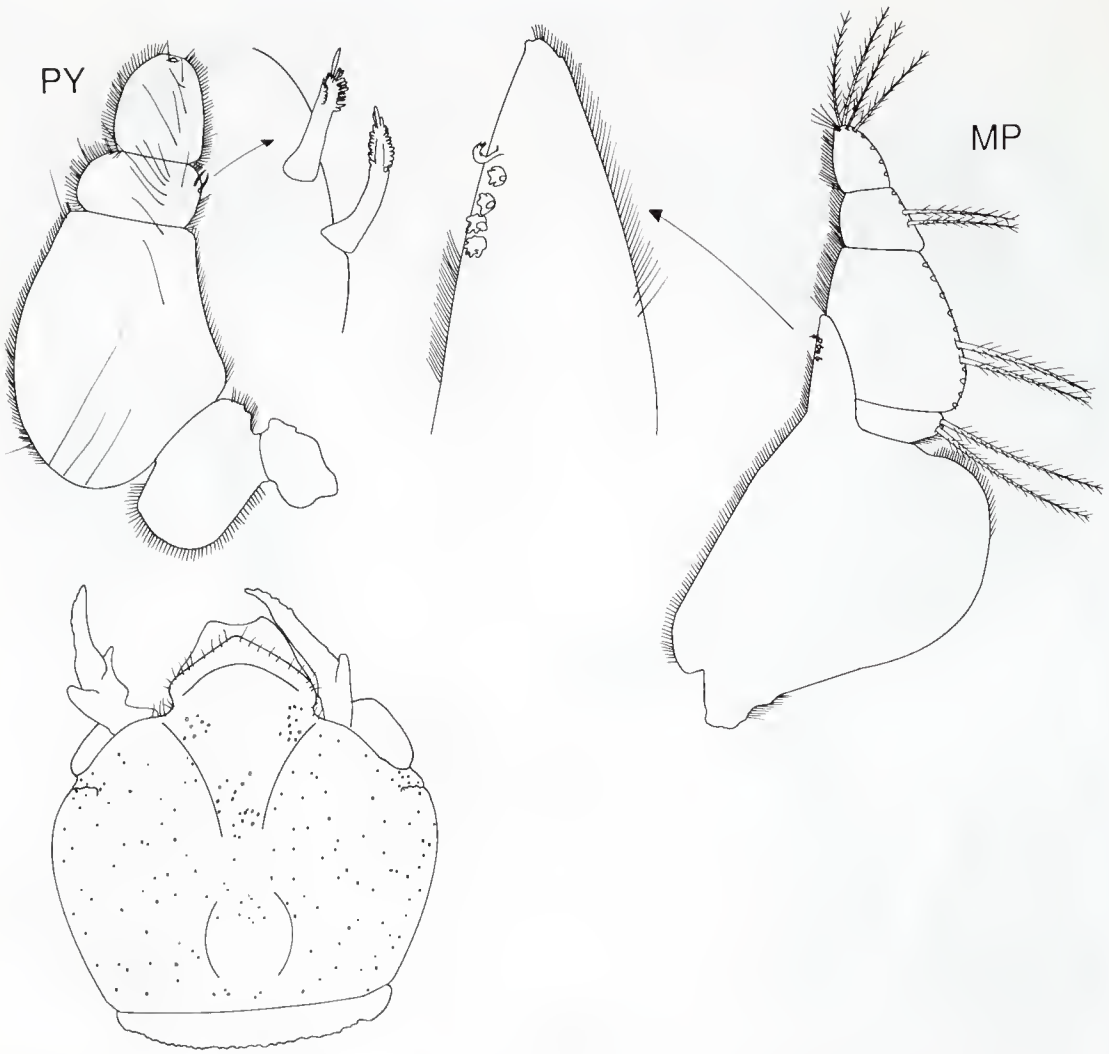

Figure 9. *Bathygnathia cardiocondyla*. Holotype, NMV J8372; Dorsal view of cephalon paratype, AM P42099.

broad but shallow dorsal sulcus extending posteriorly to base of posterior median tubercle. Antenna 1 flagellum of 5 articles, with no aesthetase. Antenna 2 twice as long as antenna 1; flagellum of 8 articles. Mandible half length of cephalosome, cylindrical with tapered apex; armed carina extending to distal apex of mandible; pronounced mandibular incisor and conical internal lobe ventrally, opposite incisor. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, with 3 coupling hooks. Pylopod 5-articled: article 2 with 1 large acrola; article 3 with 2 strong setae on external anterolateral margin; articles 2–3 with few short setae on ventral surface; article 5 minute.

Pereon evenly sided, as wide as cephalosome except pereonite 5 which is slightly wider around base of pereopods. Pereonite 1 narrow, clearly reaching lateral margins of pereon dorsally and visible laterally. Pereonites 2 and 3 much shorter than each of pereonites 4–6, pereonite 5 longest. Pereonite 6 lobuii thin and elongate. Pereonite 7 small, overlapping narrow pleon. Pleonites progressively narrower, pleonal epimera not prominent. Pleotelson damaged; subtriangular, with rounded apex; wider than long; lateral margins sinuous with up to 4 pairs of simple, short setae

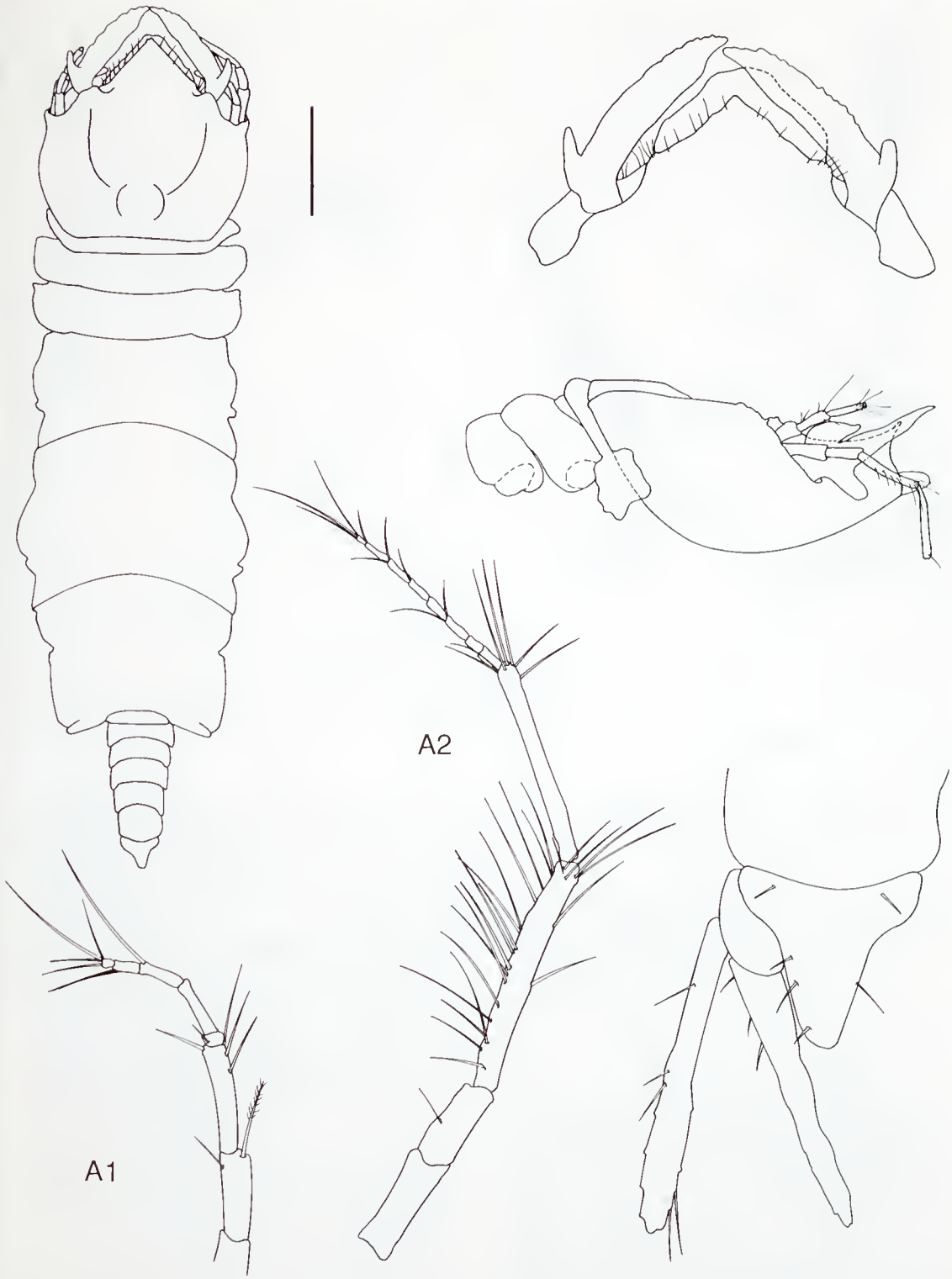

Figure 10. *Bathygnathia opisthopsis*. Holotype, AM P42181.

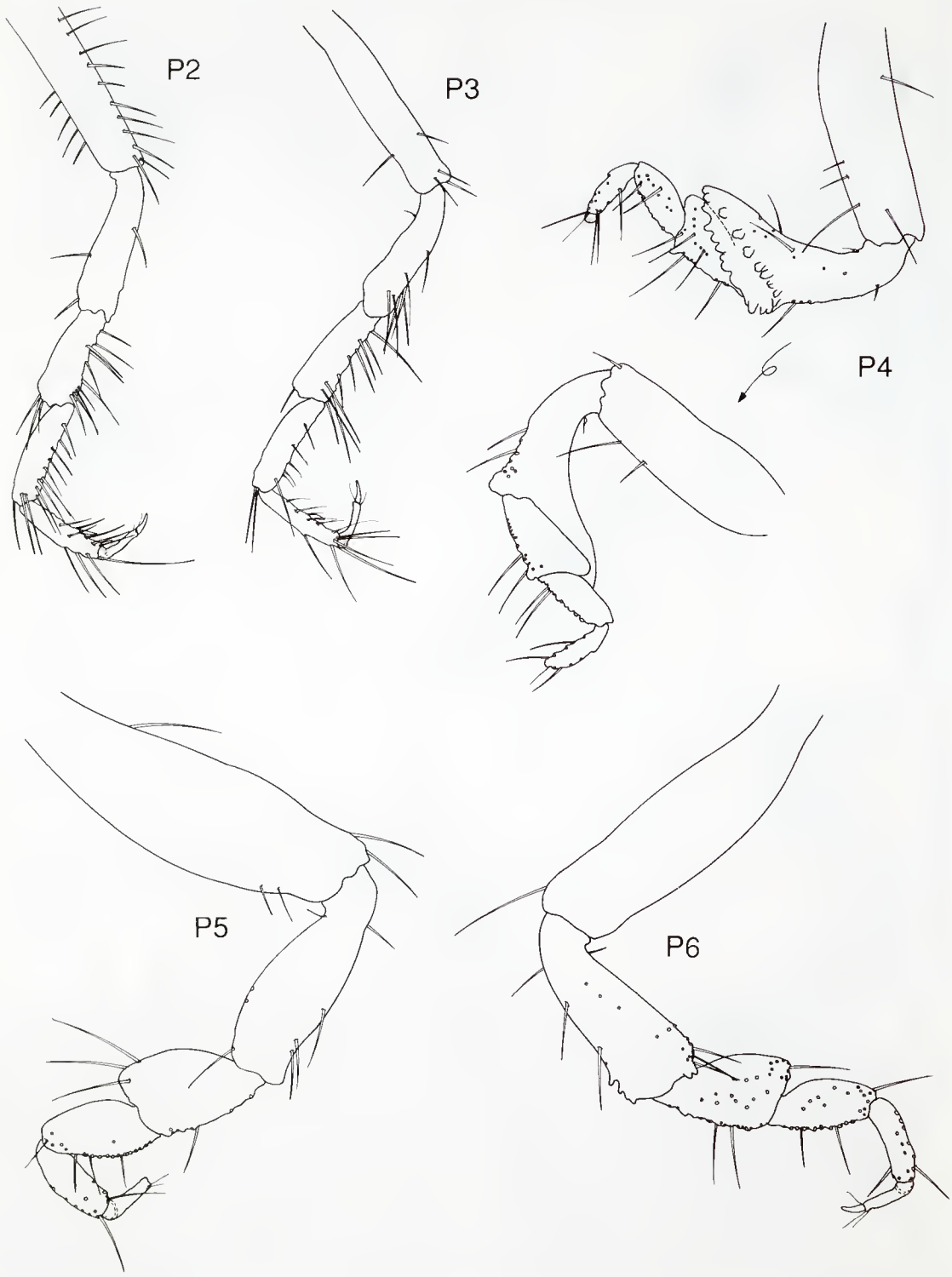

Figure 11. *Bathygnathia opisthopsis*. Holotype, AM P42181; P5 and P6 of paratype, AM P42105.

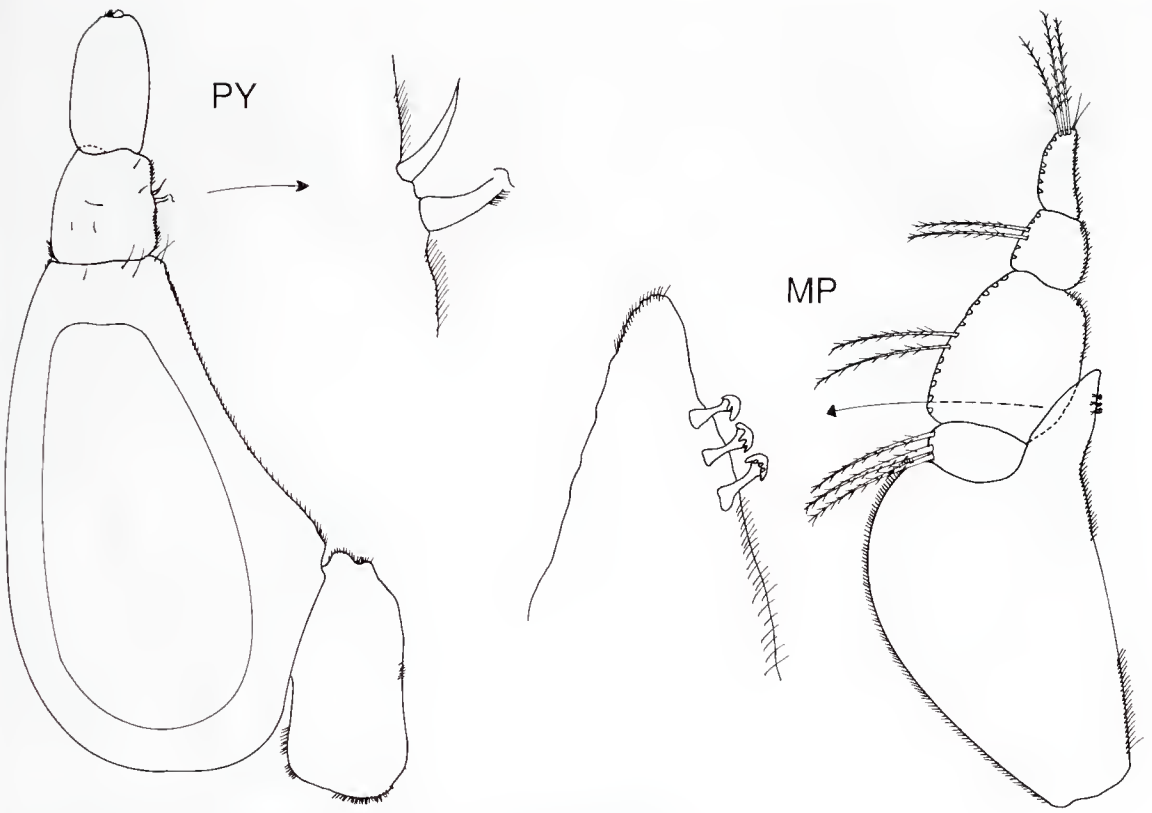

Figure 12. *Bathygnathia opisthopsis*. Holotype, AM P42181.

laterally. Uropodal peduncle without setae; rami subequal, long and narrow, reaching well beyond apex of pleotelson, external margins bearing numerous setae.

Pereopods with dense cover of simple setae particularly distally; pereopods 2 and 3 less stout than pereopods 4–6; ischium of pereopod 4 with very pronounced anterodistal projection, distally flattened with numerous small tubercles.

Pleopods setose. Pleopod 2 endopod with appendix masculina three-quarters or almost as long as rami. Penes 2 contiguous papillae.

Distribution. Southern NSW, 2632–2698 m.

Remarks. Bathygnathia opisthopsis possesses similar body proportions and similar mandibles to those of *B. cardiocondyla* but lacks the raised and ornate margins of the anterior pereonites. Both species are characterised by the weakly armed mandibular carina. *B. opisthopsis* was collected almost 1000 m deeper than any other specimen of *Bathygnathia.*

Bathygnathia tapinoma sp. nov.

Figures 13–15

Material examined. Holotype. New Zealand. Off W coast of South Island (42°15.9′S, 170°1.8′E), 924 m, letter-box dredge, P.K. Probert, 17 Feb 1982 (NZOI stn Q689A), NZOI H-618 (1 male).

Paratype. Type locality, NMV J4753 (2 males).

Other material. Type locality, NMV J4755 (1 female).

Description. Total length of holotype: 5.39 mm.

Cephalosome pentagonal, 1.4 times as long as wide, lateral margins convex. Entire frontal border produced as very wide rostrum with many setae on anterior margin; ventrolateral walls of buccal cavity protruding considerably beyond rostrum. Cephalosome with large, diamond-shaped translucent region on rostrum. Eyes absent. External scissura smoothly rounded. Antenna 1 flagellum of 5 articles, with 3 aesthetascs; antenna 2 longer than antenna 1; flagellum

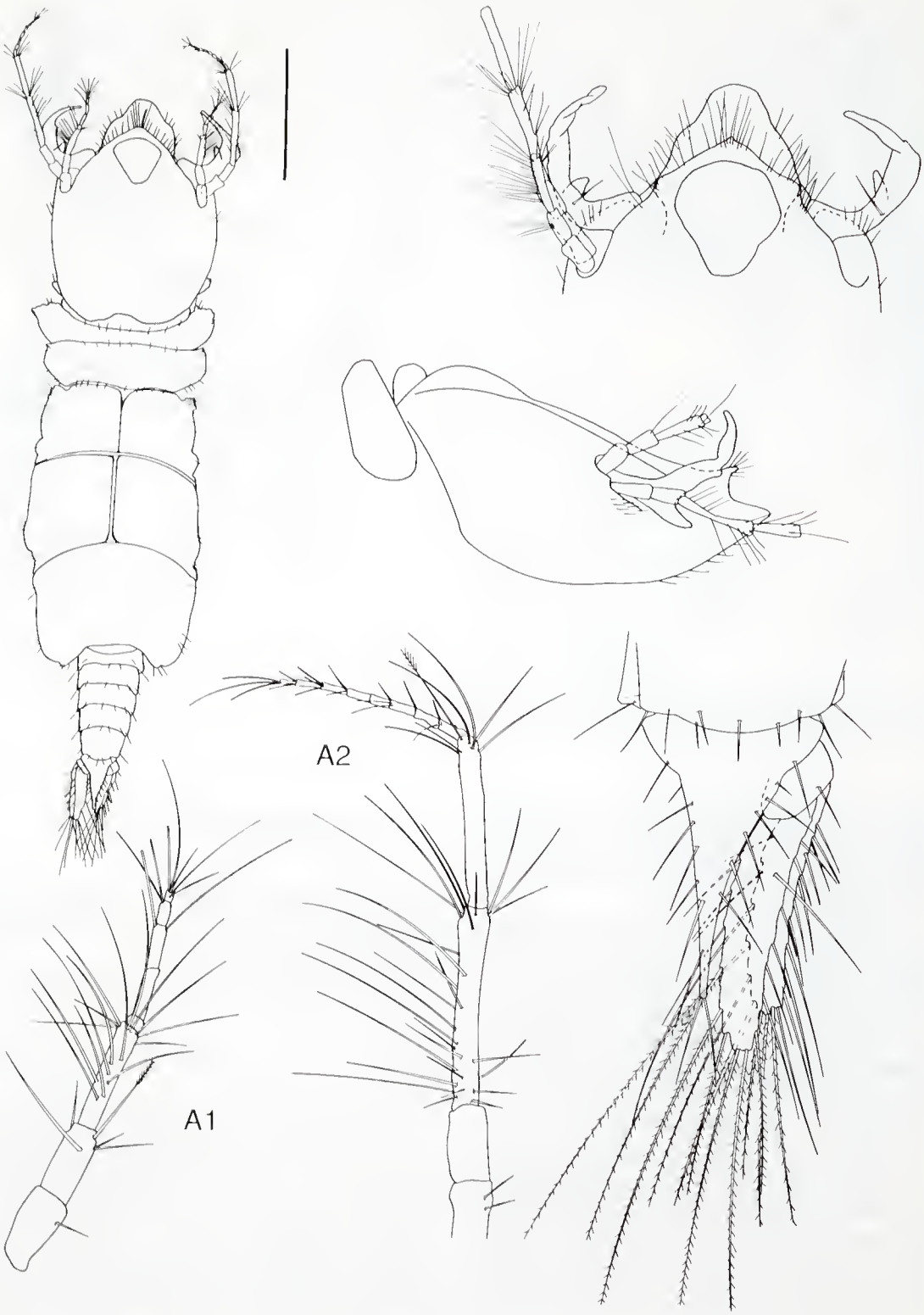

Figure 13. *Bathygnathia tapinoma*, Holotype, NZOI H-618.

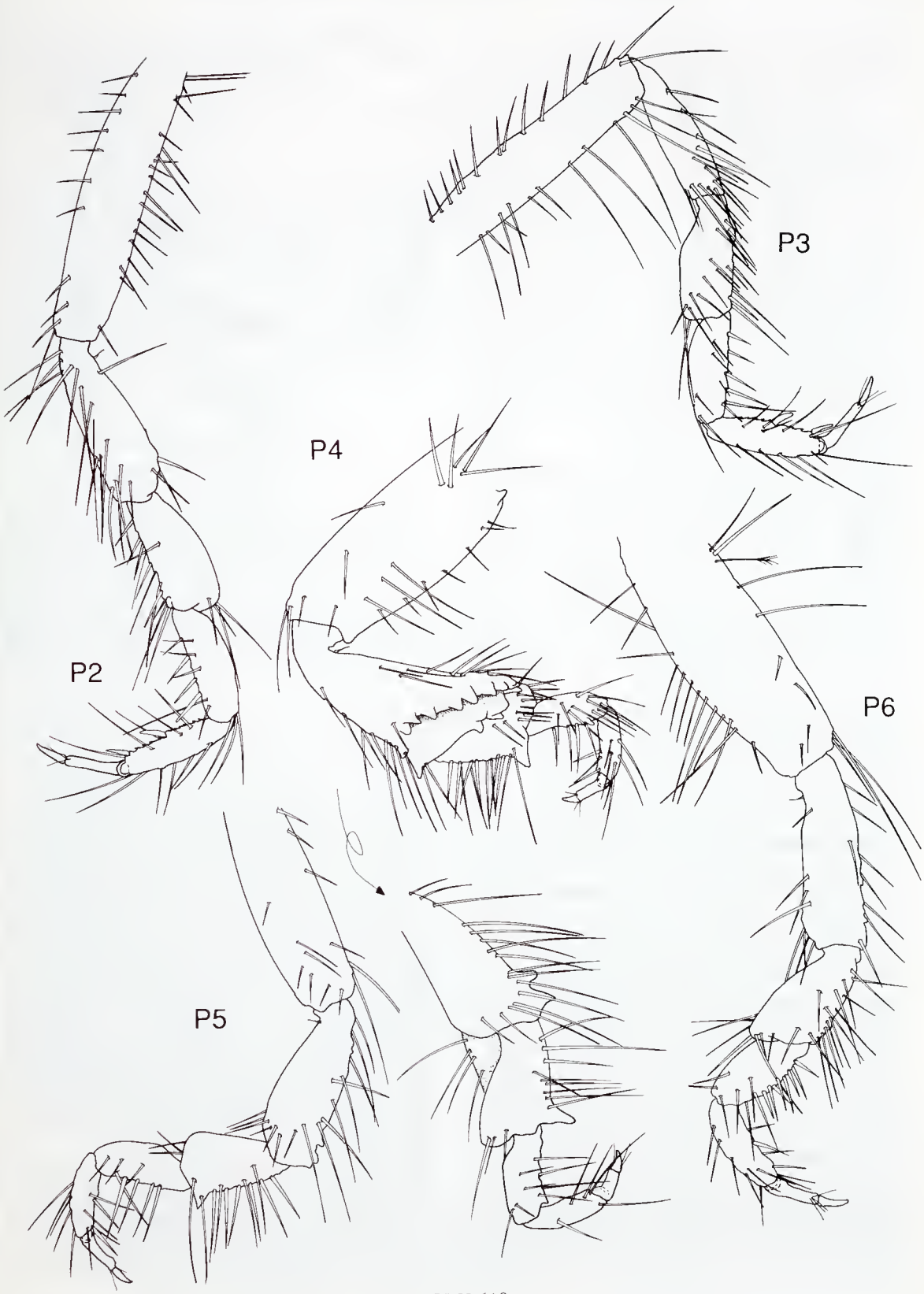

Figure 14. *Bathygnathia tapinoma*. Holotype, NZOI H-618.

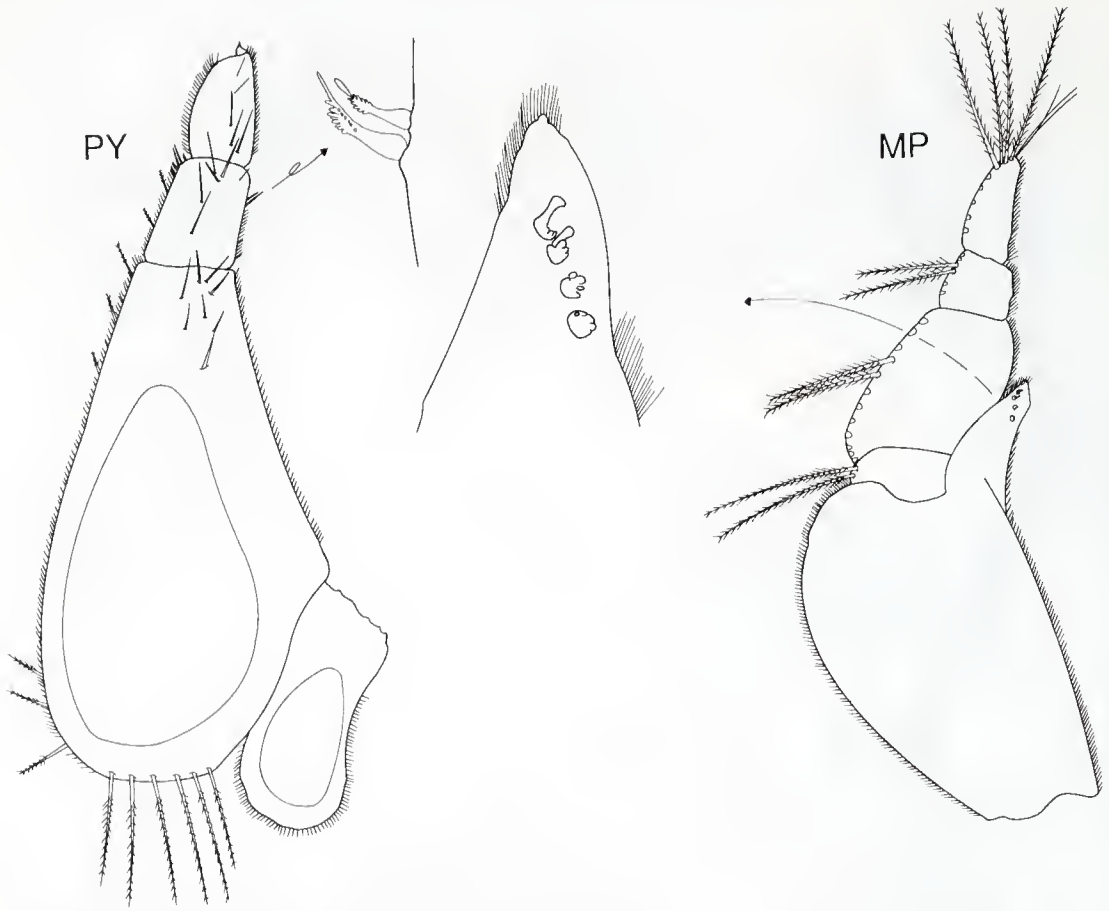

Figure 15. *Bathygnathia tapinoma.* Holotype, NZOI H-618.

of 8 articles. Mandible soft and flexible in preserved specimens; one-third length of cephalosome; distally raised in lateral view; apex curved inwards; cylindrical, with no recognisable blade; a unarmed carina; seta one-third way along; inferior conical internal lobe distal to seta. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, with 4 coupling hooks. Pylopod 5-articled; internal margin with few well-spaced long plumose setae proximally and short plumose setae distally; anteromedianly with numerous simple setae; article 1 elongate, firmly attached to article 2; articles 1 and 2 with arcolae; article 3 with 2 pectinate setae on external anterolateral margin; fifth article minute.

Pereon widest at pereonite 2, slightly wider than cephalosome; pereonites progressively longer. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by cephalon and partially obscured laterally by pereonite 2. Pereonite 3 narrowest, pereonites 4–6 progressively wider. Pereonite 4 with anterior constriction and thin median groove. Pereonite 5 with dorsal sulcus as thin median groove. Pereonite 6 with very small lobuii. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer and narrower, pleonal epimera not prominent. Pleotelson subtriangular, longer than wide; lateral margins straight; with 7–8 pairs of simple setae laterally and pair of seta on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching beyond apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with many posterior setae and dense cover of simple setae; pereopods 2 and 3 less robust than 4 to 6; pereopod 4 basis without quadrate lobe, ischium distally expanded as concave circular cusp with 10 or more tubercles.

Pleopods setose. Pleopod 2 endopod with appendix masculina three-quarters length of rami. Penes 2 contiguous papillae.

Distribution. West coast of South Island of New Zealand, 924 m.

Remarks. Bathygnathia tapinoma is most similar to *B. oedipus* (Stebbing) and both are characterised by the presence of a pronounced distal extension on the ischium of pereopod 4; weak mandibles located closer to the lateral margin on the frontal border than in most other species; and similar pereon and pleotelson dimensions. *B. tapinoma* differs from *B. oedipus* in possessing a wider yet shorter rostrum and a large diamond-shaped translucent region at the base of the rostrum.

Bathygnathia vollenhovia sp. nov.

Figures 16–18

Material examined. Holotype. Tasmania, off Freycinet Peninsula (42°2.20′S, 148°38.70′E), 800 m, coarse shelly sand, WHOI epibenthic sled, M.F. Gomon et al. on ORV *Franklin*, 27 Jul 1986 (stn SLOPE 45), NMV J19120 (1 male).

Other material. New Zealand, off W coast of South Island, (42°15.9′S, 170°1.8′E), 924m, letter-box dredge, P.K. Probert, 17 Feb 1982 (NZOI stn Q689A), NMV J4754 (1 male).

Description. Total length of holotype: 9.66 mm.

Cephalosome pentagonal, 1.4 times as long as wide, lateral margins convex. Rostrum narrow and greatly produced; half length of cephalon; at base approximately one-third width of cephalosome; with many short setae on anterior margin. Ventrolateral walls of buccal cavity protruding anteriorly; cephalon with translucent elliptical region on rostrum (faded in some material). Eyes absent. External scissura smoothly rounded. Supraocular lobe very low, acute. Cephalosome with broad, shallow dorsal sulcus, two-thirds length of cephalon; low, very small posterior median tubercle. Antenna flagellum of antenna 1 of 5 articles, with 4 aesthetases; antenna 2 longer than antenna 1; flagellum of 6 articles. Mandible subequal to length of cephalosome (excluding rostrum); proximal two-thirds slightly curved, distal third with internal margins parallel, forming vice-like structure; with unarmed carina; slight mandibular incisor almost half-way along; lacking seta. Maxilliped 5-articled; external margins of articles 2 to 4 bearing plumose setae; endite clearly reaching article 3, wide, with 5 coupling hooks. Pylopod 5-articled, with many setae medianly on ventral surface; margin of article 2 with several plumose setae; article 3 with 1 pectinate seta on external anterolateral margin; fifth article minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 large, laterally directed forward; reaching lateral margins dorsally and visible as continuous band laterally. Pereonite 2 and 3 subequal, shorter than pereonites 4–6. Pereonite 5 with dorsal sulcus as thin median groove. Pereonite 7 very narrow, overlapping pleon. Pleonite 1 wider than other pleonites, pleonal epimera prominent. Pleotelson subtriangular, as wide as long, lateral margins sinuous with 17–18 pairs of simple setae laterally and 3 setae medianly. Uropodal peduncle with 4 setae; endopod longer than exopod, reaching beyond apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods with dense cover of simple setae and with many strong posterior setae, particularly on carpus; pereopods 4–6 more stout than 2 and 3, with laterally enlarged merus.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 contiguous papillae.

Distribution. Tasman Sea, off west coast of South Island of New Zealand and east coast of Tasmania, 800 m depth.

Remarks. Of the blind species, *Bathygnathia vollenhovia* is most similar to *B. bathybius* (Beddard) and *B. monodi* Cals. All possess a long narrow rostrum of similar proportions. These three species, and *B. curvirostris* Richardson, *B. affinis* Birstein and *B. porca* Kensley, form a complex of species characterised by a most pronounced rostrum and expand merus of some or all of pereopods 2–6. *B. vollenhovia* differs from *B. bathybius* in possessing a more complex mandible characterised by incisors and an opposing straight distal region; and from *B. monodi* in a more complex and rounded mandible, shorter translucent elliptical region confined entirely to the rostrum and cephalon with a posterior tubercle and dorsal sulcus.

Bythognathia Camp

Bythognathia Camp, 1988: 668.

Type species. Bythognathia yucatanensis Camp, 1988 (original designation).

Diagnosis. Eyes absent. Frontal border produced into rostrum, without processes. Mandibles straight, lacking obvious blade. Pereonite 1

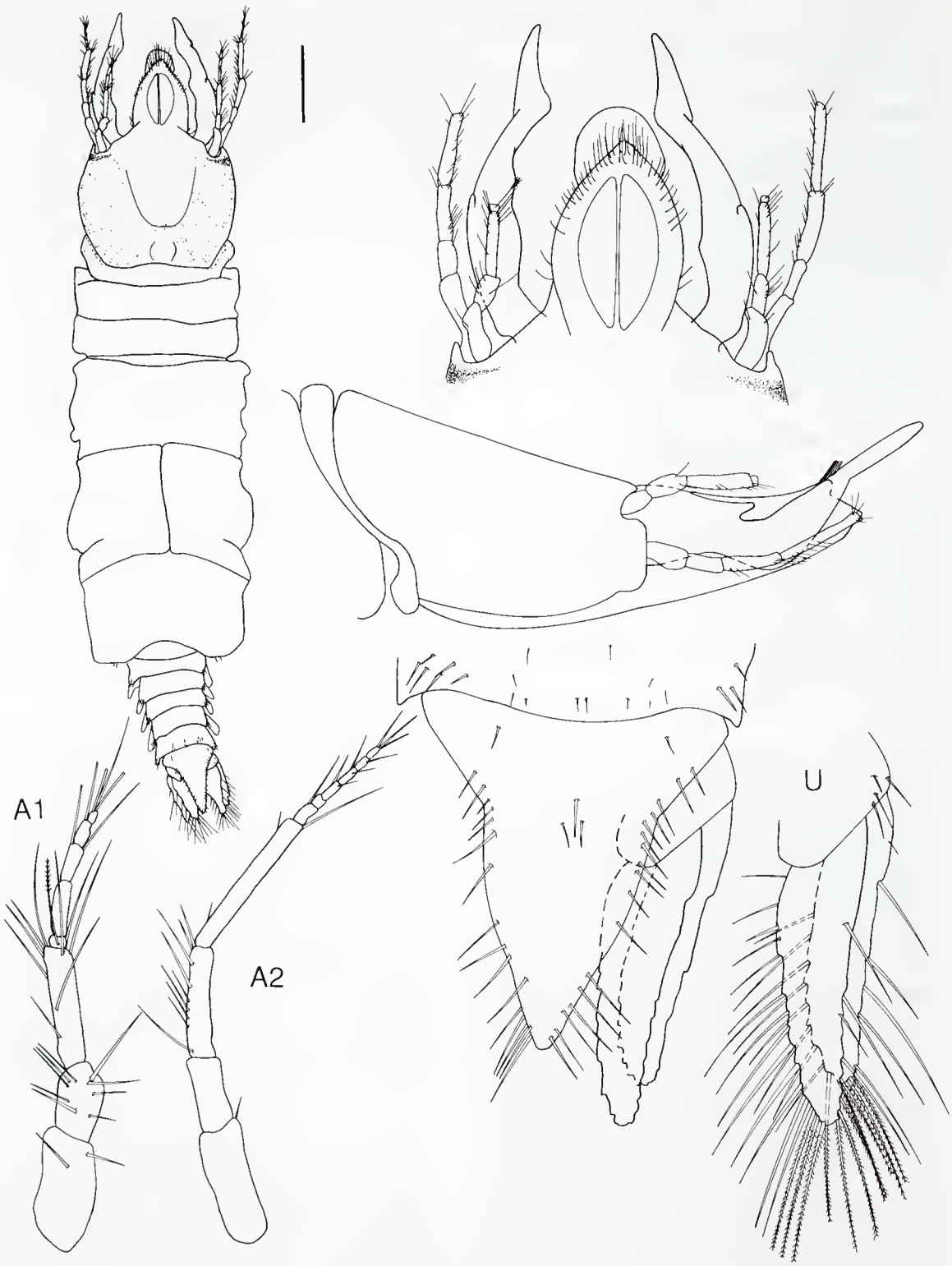

Figure 16. *Bathygnathia vollenhovia*. Holotype, NMV J19120.

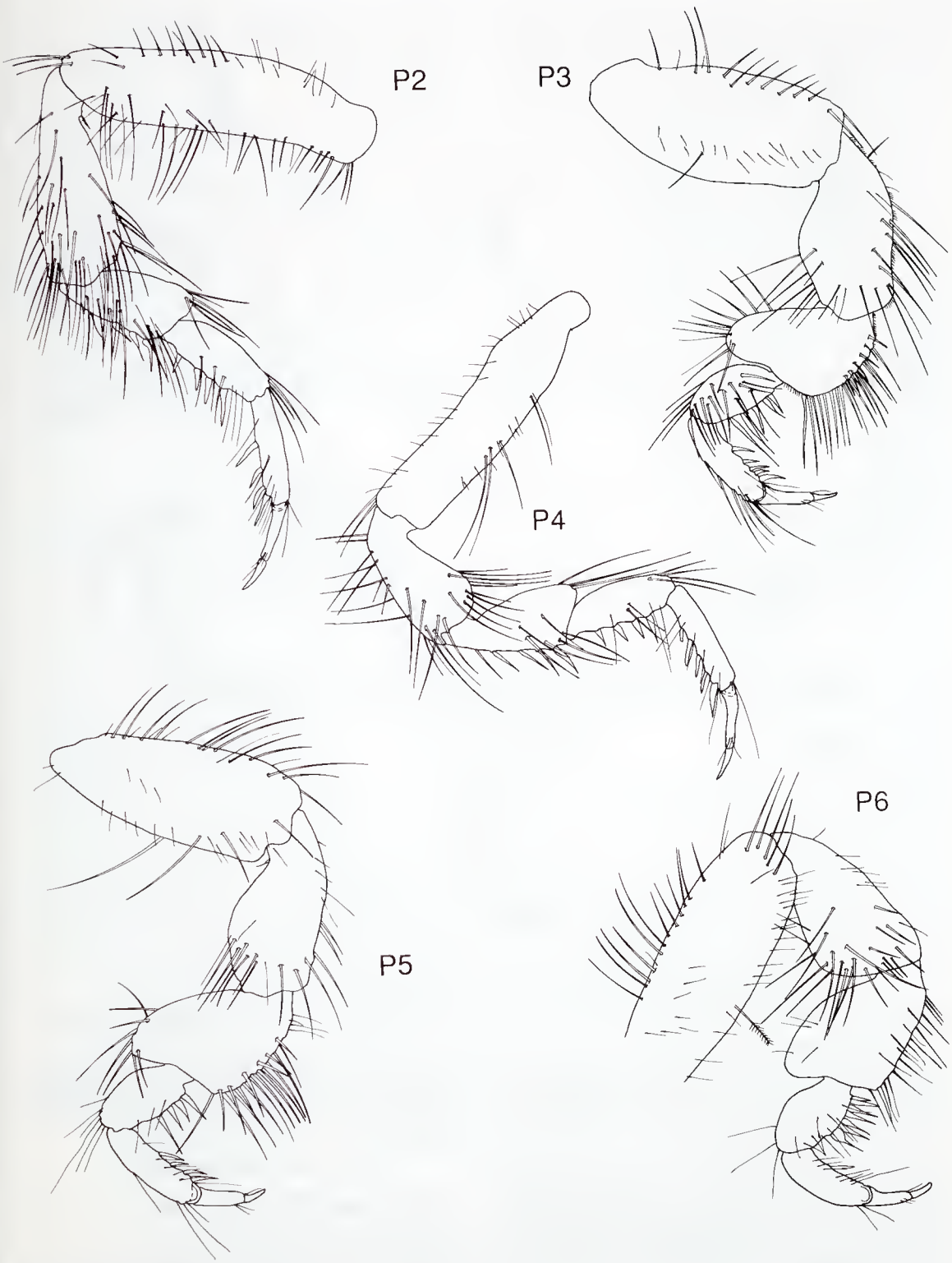

Figure 17. *Bathygnathia vollenhovia*. Holotype, NMV J19120.

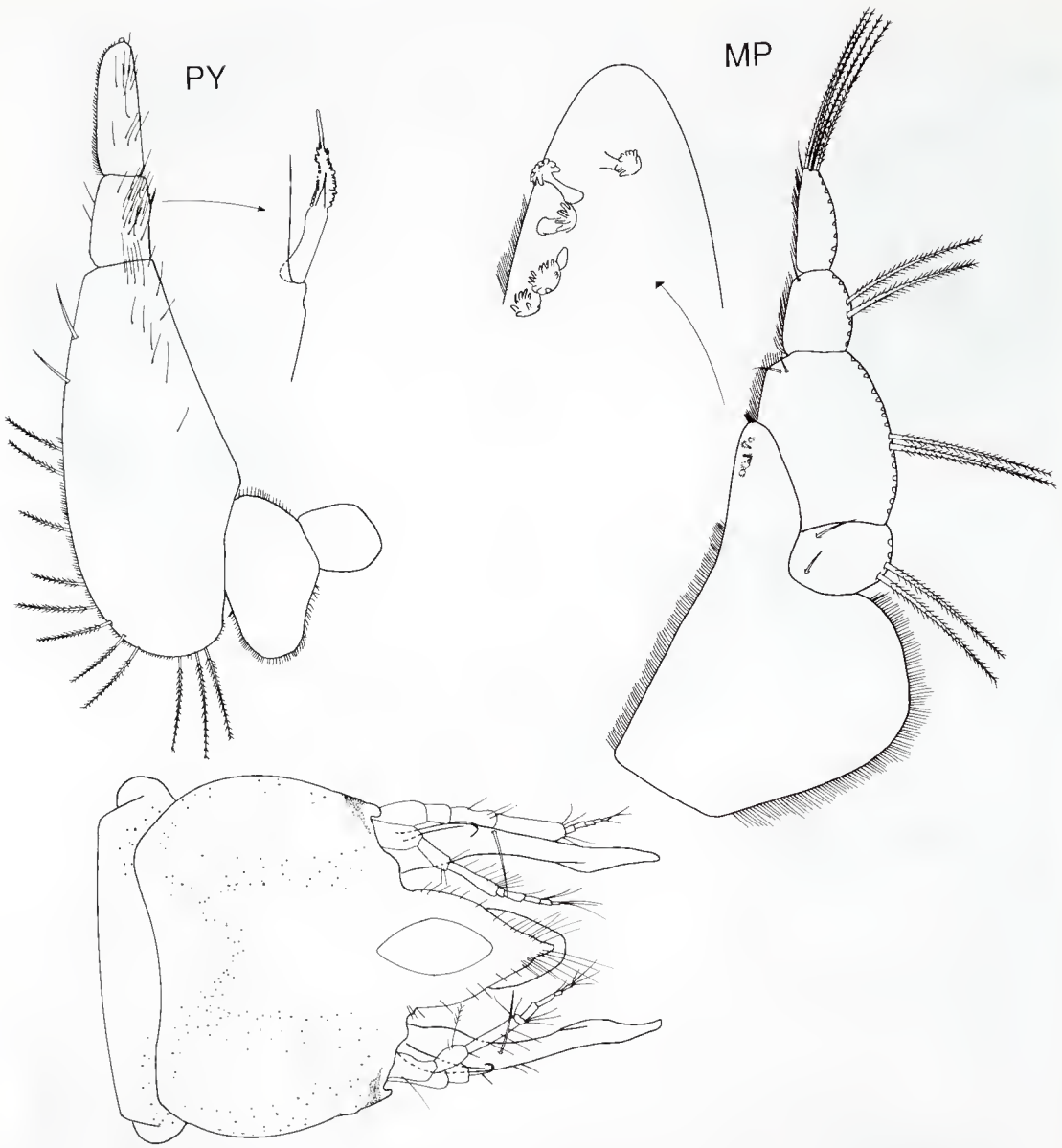

Figure 18. *Bathygnathia vollenhovia.* Holotype, NMV J19120; Dorsal view of cephalon of NMV J4754.

produced, partially obscuring pereonite 2; clearly reaching lateral margins of pereon. Pylopod 6-articled (sixth article fused), not operculate, subchelate and pediform.

Remarks. Bythognathia is a monotypic genus from very deep water in the Caribbean Sea (Camp, 1988). It is characterised by the very large and produced pereonite 1. *Bythognathia* is the only gnathiid with a 6-articled, non-operculate pylopod which is pediform and subchelate. The phylogenetic analysis supports the retention of the generic name. The genus does not occur in Australia.

Caecognathia Dollfus

Caecognathia Dollfus, 1901: 240. — Tattersall, 1906: 61.

Gnathia (*Perignathia*) Monod, 1922: 645 (type species: *Anceus abyssorum* Sars, 1872 or *Gnathia fallax* Monod, 1926. See *Remarks* under *Gnathia*).

Heterognathia Amar and Roman, 1974: 569 (type species: *Heterognathia adeliensis* Amar and Roman, 1974).

not *Gnathia* (*Perignathia*). — Monod, 1926: 554–555.

Type species. *Anceus stygius* Sars, 1877 (original designation).

Diagnosis. Eyes present. Frontal margin of cephalon produced, without frontal processes. Mandibles usually with smooth mandibular blade. Cephalon without paraocular ornamentation or dorsal sulcus. Pereonite 1 immersed in cephalon. Pylopod 2- or 3-articled, operculate, article 1 enlarged, article 3 small or absent.

Remarks. The type species of *Heterognathia*, *H. adelaidensis*, is a juvenile male of the common Antarctic species, *Gnathia calva* Vanhöffen (Wägele, 1987) herein transferred to *Caecognathia*. This genus is therefore a junior synonym of *Caecognathia*. The nomenclatural status of *Perignathia* is uncertain but of little consequence as long as it remains a junior synonym; see *Remarks* under *Gnathia*.

Gnathia and *Caecognathia* are closely related genera formerly synonymised. They share many similarities, particularly the structure of the pylopod but *Caecognathia* is distinguished by a produced frontal border lacking any frontal processes. The genus includes most species of Monod's (1926) Sectio Productae of *Gnathia*.

The only previously described Australian species assigned to this genus are *C. agwillisi* (Seed, 1979) from rocky shores in Victoria (Fig. 2A) and *C. pustulosa* (Hale, 1924) from sponges in South Australia (Fig. 2B and Table 5).

Key to males of Australian species of *Caecognathia*

1. Pleotelson trapeziform, apex broadly truncated ..... *C. agwillisi*
— Pleotelson subtriangular 2
2. Cephalosome elliptical; pereon width evenly increasing posteriorly to pereonite 5; pereonite 6 with marked globular lobuii (see figs 19, 22, 34, 40) 3
— Cephalosome roughly quadrilateral; pereon width not steadily increasing posteriorly; pereonite 6 without lobuii or at most with simple, rounded lobuii only 6
3. Rostrum produced ..... *C. leptanilla*
— Rostrum not produced 4
4. Pereonite 6 with pronounced suture midway along lateral margin ..... *C. diacamma*
— Pereonite 6 without suture 5
5. Pereonite 1 barely reaching lateral margins of body; frontal border smoothly rounded with rounded external scissura ..... *C. brachyponera*
— Pereonite 1 clearly reaching lateral margins of body, divided into 3 regions by posterior margin of cephalon; frontal border with a slight median indentation and very shallow external scissura ..... *C. trachymesopus*
6. Cephalon with 3 furrows, 2 mesiolateral and 1 medially; pylopod 2-articled 7
— Cephalon without furrows; pylopod 3-articled 9
7. Mandibles with internal quadrate lobe; pereonite 4 with posterior bilobed projection ..... *C. paratrechia*
— Mandibles lacking internal lobe; pereonite 4 with anterior spine 8
8. Body not setose; mandibles without mandibular setae, blade a smooth arc; cephalon without low tubercle, spine on peronite 4 pronounced ..... *C. pustulosa*

— Body setose, especially anteriorly; mandibles with mandibular setae, blade slightly asssymetrical, produced; posterior cephalon with small tubercle .. ..*C. huberia*

9. Mandibles with armed carina; small opaque spines on cephalon, visible in lateral view; frontal border produced as a rostrum; pereopod 4 basis not produced distally ..... *C. dolichoderus*

— Mandibles cylindrical, without armed carina; no spines on cephalon; frontal border not produced as a rostrum; pereopod 4 basis expanded distally ... . *C. gnamptogerys*

Caecognathia branchyponera sp. nov.

Figures 19–21

Material examined. Holotype. New South Wales, 44 km E of Nowra (34°55.79′S, 151°08.06′E), 429 m, muddy coarse shell, WHOI epibenthic sled, G.C.B. Poore et al. on RV *Franklin*, 22 Oct 1988 (stn SLOPE 56), NMV J27575 (1 male).

Paratypes. Type locality, NMV J19126 (6 males).

Other material. Type locality, NMV J29889 (4 females). Vic. S of Point Hicks (38°17.70′S, 149°11.30′E), 400 m, coarse sand, gravel, mud, many sponges, WHOI epibenthic sled, M.F. Gomon et al. on RV *Franklin*, 24 Jul 1986 (stn SLOPE 40), NMV J19125 (80 specimens).

Description. Total length: 3.09 mm.

Cephalosome elliptical, 1.2 times as long as wide, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border slightly produced, rounded; with 5 submarginal setae each side of mid-dorsal line. External scissura smoothly rounded. Supraocular lobe smoothly convex. Antennae stout, subequal; flagellum of antenna 1 of 5 articles, without aesthetascs; flagellum of antenna 2 of 3 articles. Mandible strongly curved, one-third length of cephalosome; with unarmed carina; smooth double-scalloped blade on distal two-thirds, distal scallop twice as long as proximal scallop; basal neck ventrally smoothly arced, dorsally covered by pronounced crisma. Erisma with dense covering of fine setae on external margin. Maxilliped 5-articled; palp thin and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled; internal margin of plumose setae; article 1 with 4 plumose setae on ventral surface; article 2 conical, proximal margin completely joined to article 1, with 3 setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pereonite 5, 1.75 times as wide as cephalosome; margins with numerous setae. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 5 and 6 each twice as long as pereonites 2–4; posterior border of pereonite 6 markedly concave with distinct gobular lobuii. Pereonite 7 very narrow, overlapping pleon. Pleon with pleonites subequal, epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins slightly sinuous; with 3 pairs of plumose setae laterally and pair of setae on distal apex. Uropodal peduncle with 1 plumose seta on internodistal margin; rami subequal, not reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with moderate cover of plumose setae, particularly on basis and few, pronounced lateral projections on anterior face of ischium to carpus.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Eastern Bass Strait, eastern NSW, 400–429 m.

Remarks. Caecognathia branchyponera belongs to a complex of species characterised by a roughly elliptical cephalosome; simple mandibles; pear-shaped pereon; presence of globular lobuii; and distinct pylopods (article 2 is not circular). The three species *C. leptanilla*, *C. trachymesopus* and *C. diacamma* also belong to this complex.

C. branchyponera most closely resembles *C. trachymesopus* though is distinguishable by the smaller pereonite 1 which is not divided into three regions; a flatter frontal border with evenly spread small setae, a deeper external scissura and no median indentation.

Caecognathia diacamma sp. nov.

Figures 22–24

Material examined. Holotype. Victoria, western Bass Strait, 26 km SW of Cape Otway (39°01.0′S,

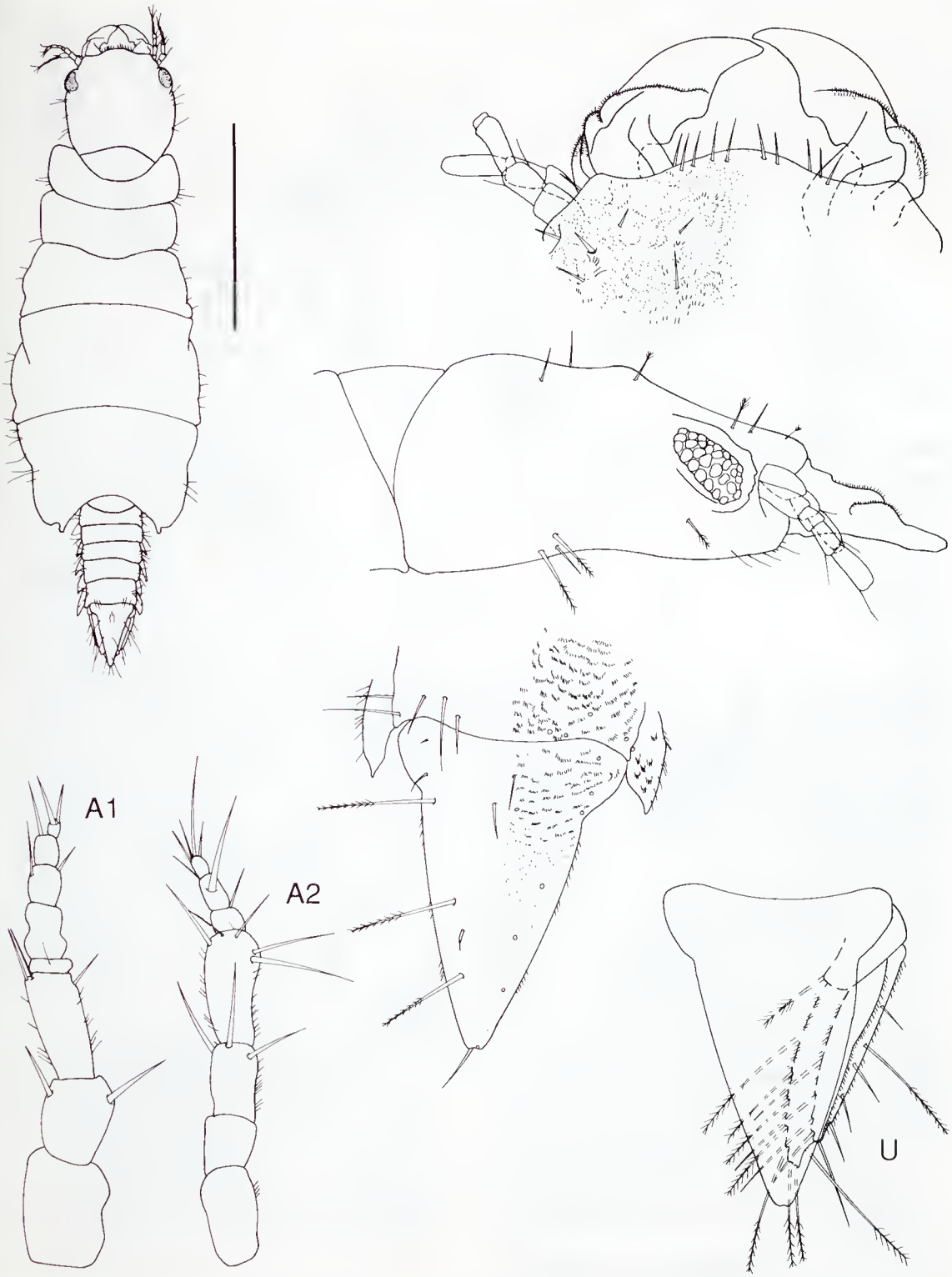

Figure 19. *Caecognathia branchyponera*. Holotype, NMV J27575.

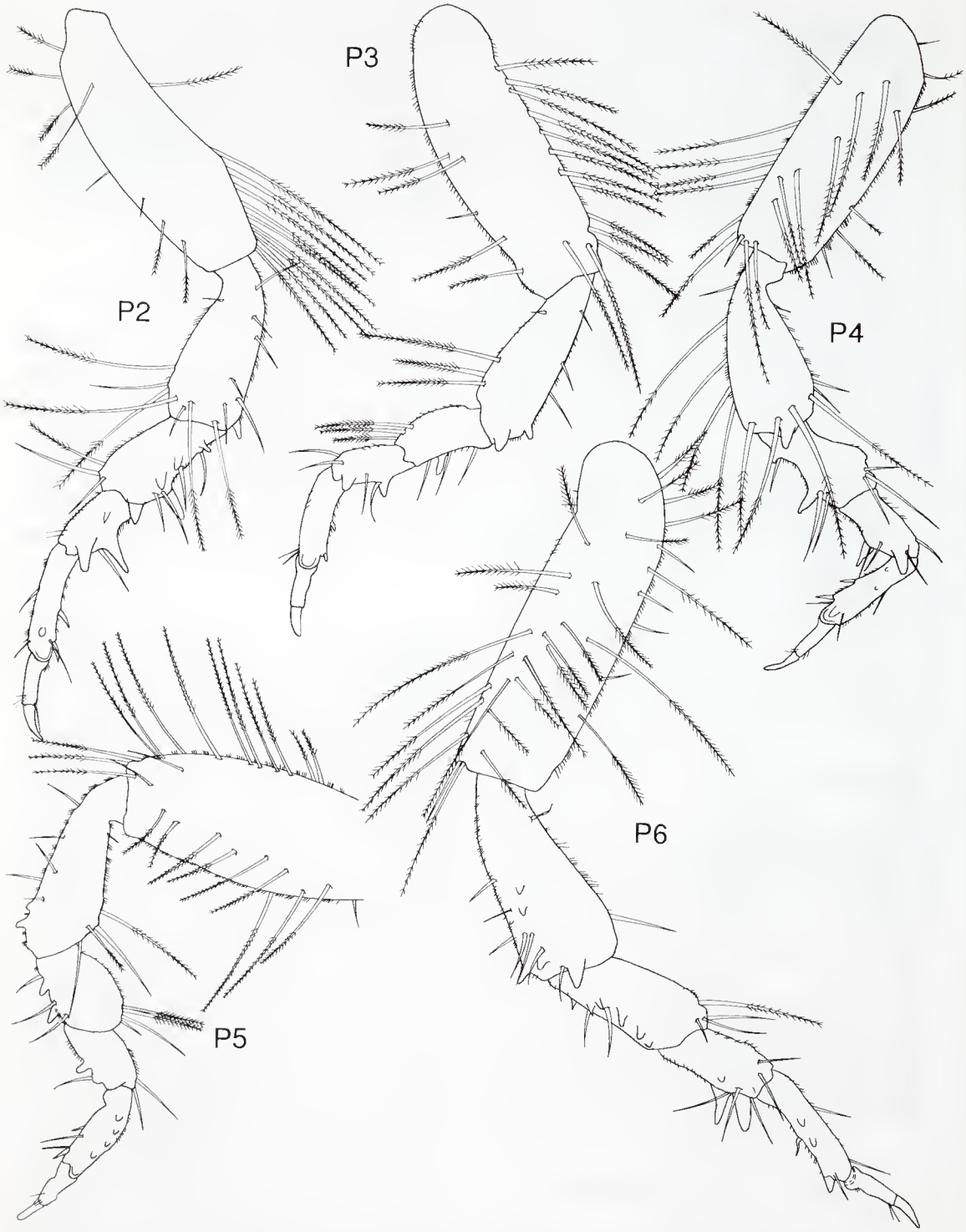

Figure 20. *Caecognathia branchyponera*. Holotype, NMV J27575.

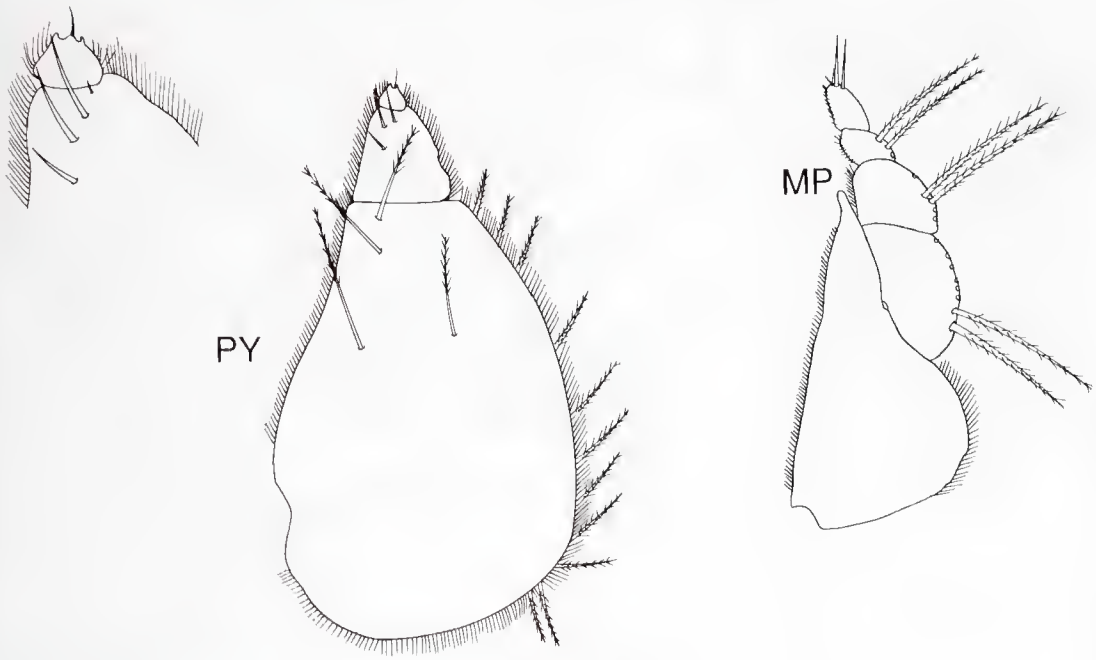

Figure 21. *Caecognathia branchyponera*. Holotype, NMV J27575.

143°22.1′E), 84 m, medium sand, WHOI epibenthic sled, M.F. Gomon et al. on RV *Hai Kung*, 31 Jan 1981 (stn BSS 120), NMV J27569 (1 male).

Paratypes. Tasmania, western Bass Strait, 59 km WNW of Cape Farewell, King I. (39°28′S, 143°17′E), 103 m, coarse sand, Smith-McIntyre grab, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 81), NMV J8316 (3 males).

Victoria. Various collectors, 1980–1981. Western Bass Strait, 30 km SSW of Warrnambool (38°38.2′S, 142°35.0′E), 59 m, WHOI epibenthic sled (stn BSS 188), NMV J8321 (2 males). 51 km SSW of Cape Otway (39°16′S, 143°17′E), 90 m, medium sand, Smith-McIntyre grab (stn BSS 73), NMV J8320 (1 male). 35 km SSW of Cape Otway (39°06′S, 143°21′E), 59 m, coarse sand, Smith-McIntyre grab (stn BSS 57), NMV J8317 (2 males). 26 km SW of Cape Otway (39°01.0′S, 143°22.1′E), 84 m, medium sand, WHOI epibenthic sled (stn BSS 120), NMV J8313 (7 males). 25 km S of Cape Otway (39°06.7′S, 143°28.7′E), 92 m, fine sand, WHOI epibenthic sled (stn BSS 119), NMV J8312 (4 males). 11 km SSW of Cape Otway (38°58′S, 143°29′E), 67 m, medium sand, Smith-McIntyre grab (stn BSS 51), NMV J8319 (1 male). 15 km S of Cape Otway (39°00′S, 143°32′E), 79 m, medium sand (stn BSS 50, NMV J8318, (1 male). 25 km S of Cape Otway (39°06.0′S, 143°35.8′E), 95 m, fine sand, WHOI epibenthic sled (stn BSS 118), NMV J8315 (4 males), NMV J8314 (2 males).

Description. Total length of holotype: 5.29 mm.

Pale colour. Cephalosome elliptical; posterior margin only slightly curved, broad; cephalosome 1.3 times as long as wide, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border slightly produced, rounded with slight median projection; 10 submaginal setae of differing sizes on each side of median projection. External scissura absent. Supraocular lobe smoothly convex. Antennae subequal; antenna 1 down-turned in lateral view, flagellum of 5 articles, long, only marginally shorter than peduncle, without aesthetases; flagellum of antenna 2 of 6 articles. Mandible strongly curved, one-third length of cephalosome; with unarmed carina; smooth blade on distal two-thirds; basal neck smoothly arced; erisma pronounced. Maxilliped 5-articled, palp thin and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled, with dense internal margin of plumose setae; article 1 with 75–80 plumose setae on ventral surface; article 2 conical, posterior margin completely joined to article 1, with 7 simple setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pcronite 5, 1.5 times as wide as cephalosome, margins with numerous fine, short setae. Pereonite 1 dorsally reaching lateral margins and

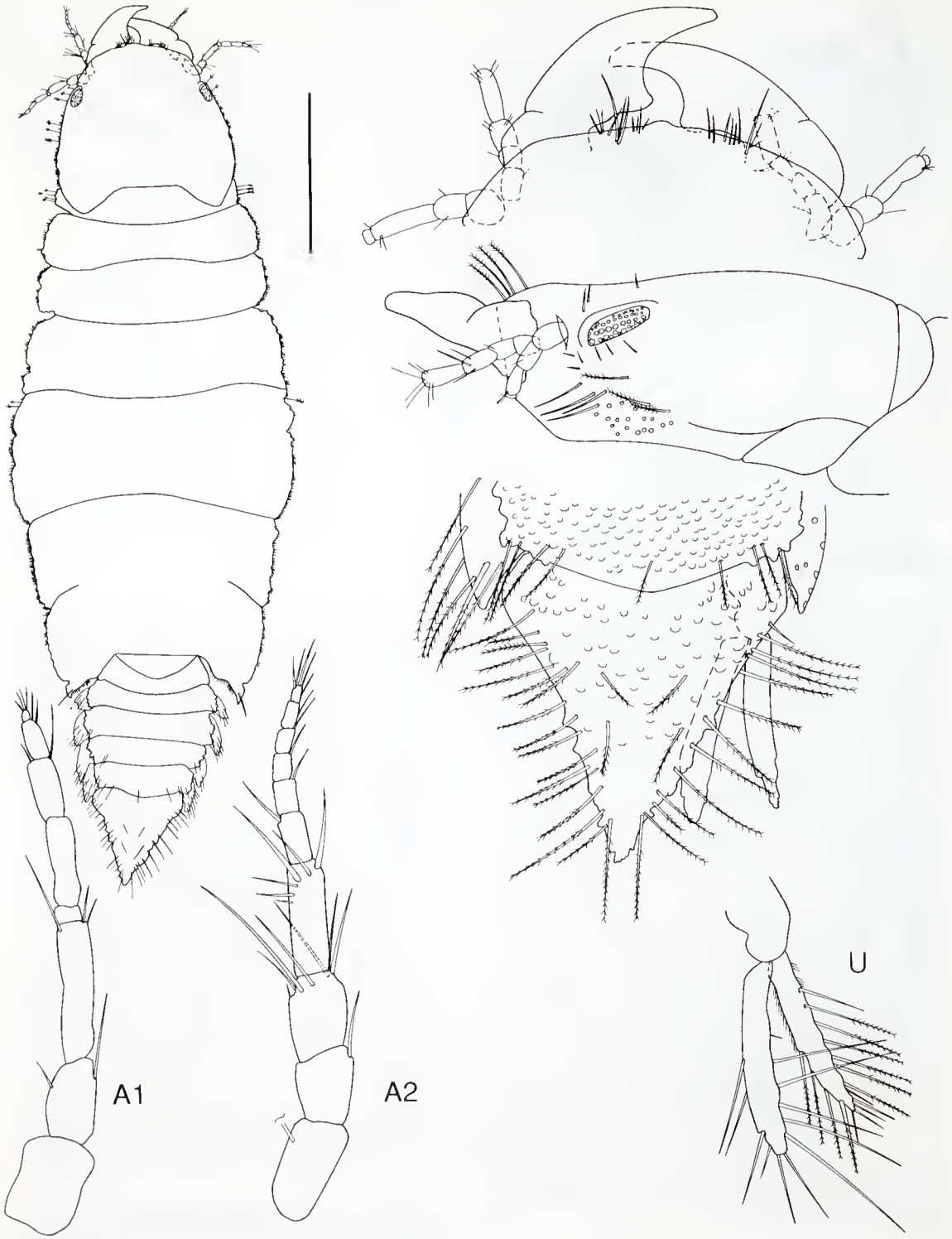

Figure 22. *Caecognathia diacamma*. Holotype, NMV J27569.

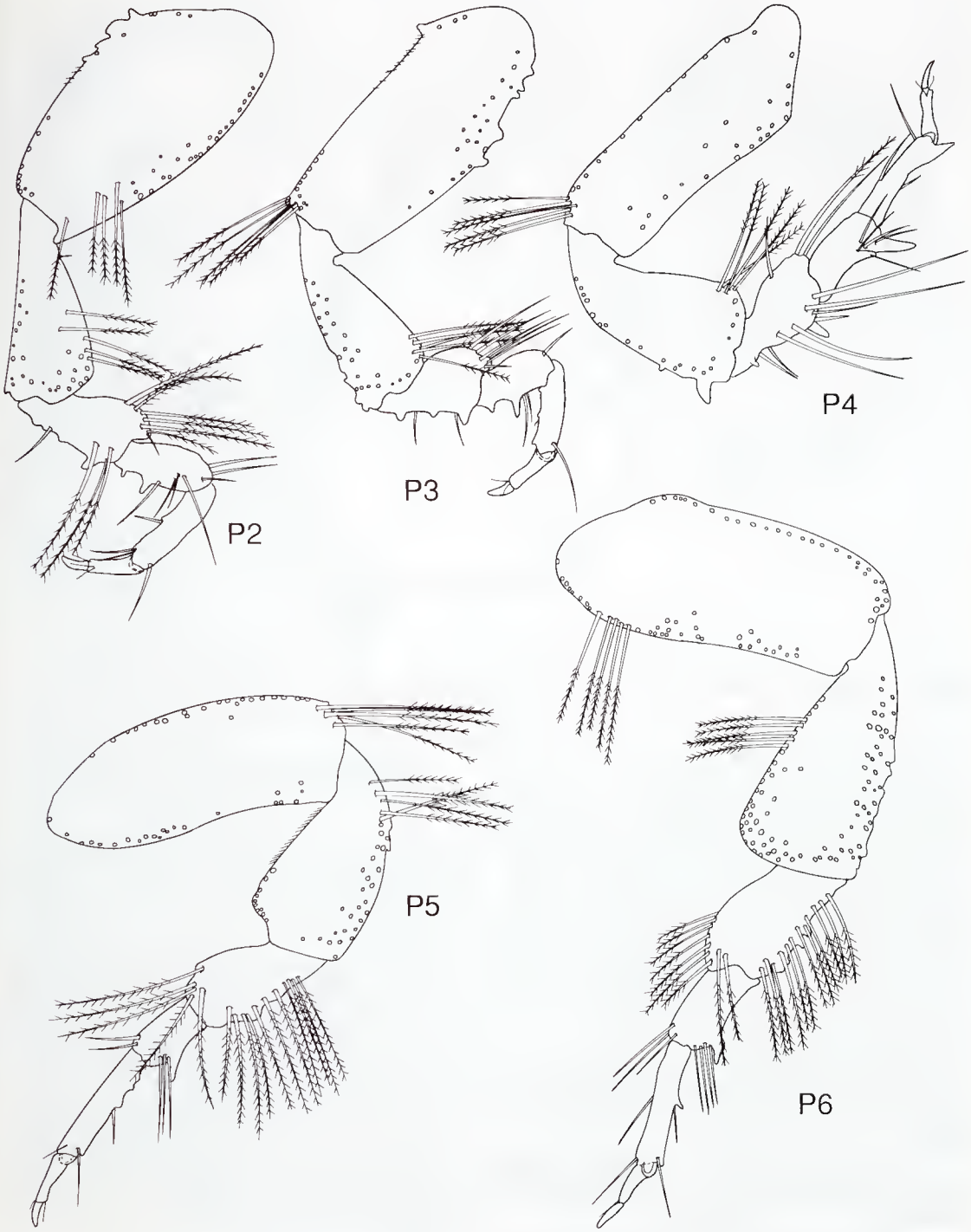

Figure 23. *Caecognathia diacamma*. Holotype, NMV J27569.

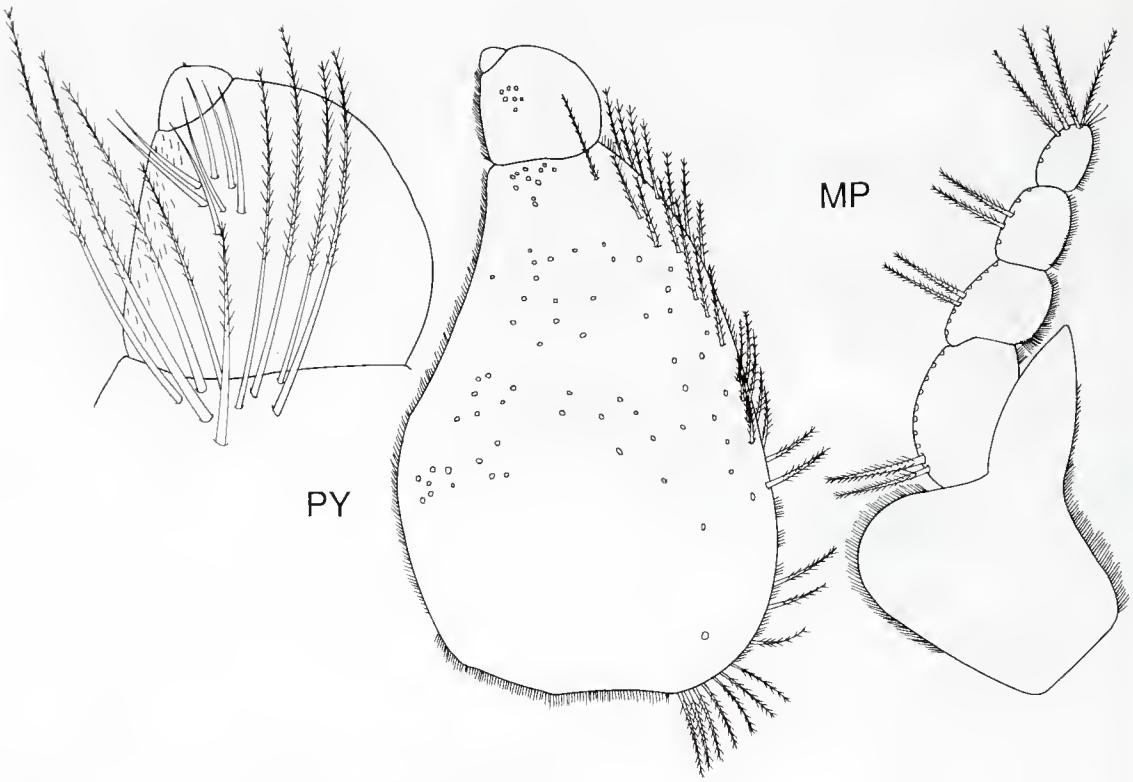

Figure 24. *Caecognathia diacamma*. Holotype, NMV J27569.

partially obscured laterally by pereonite 2. Pereonite 6 with pronounced globular lobuii and suture midway on lateral margins. Pereonite 7 very narrow, overlapping pleon. Pleon broad with irregular lateral borders; pleonites 1 and 5 narrower than others; epimera prominent. Pleotelson subtriangular, as wide as long, with numerous tubercules and 12–17 pairs of plumose setae laterally and 2 medianly. Uropod peduncle without setae; rami subequal, not reaching apex of pleotelson; exopod bearing numerous plumose setae.

Pereopods with dense cover of plumose setae; with few lateral projections on anterior faces of ischium to carpus; pereopod 4 smaller than others.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Western Bass Strait, 59–103 m.

Remarks. Caecognathia diacamma is characterised by the distinct suture on the lateral margins of pereonite 6.

Caecognathia dolichoderus sp. nov.

Figures 25–27

Material examined. Holotype. Tasmania, eastern Bass Strait, 63 km E of North Point, Flinders I. (39°44.8′S, 148°40.6′E), 124 m, muddy sand, Smith-McIntyre grab, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 167), NMV J27561 (1 male).

Paratypes. Most collected using WHOI epibenthic sled by R.S. Wilson on RV *Tangaroa*, Nov 1981. Tas. Eastern Bass Strait, 100 km NE of North Point, Flinders I. (38°52.6′S, 148°25.2′E), 130 m, fine sand (stn BSS 170), NMV J8333 (3 males). 85 km NE of North Point, Flinders I. (39°02.4′S, 148°30.6′E), 120 m, muddy sand (stn BSS 169), NMV J8335 (4 males). 60 km E of North Point, Flinders I. (39°41.7′S, 148°39.5′E), 115 m, muddy sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 27 Mar 1979 (stn BSS 32), NMV J8336 (2). 63 km E of North Point, Flinders I. (39°44.8′S, 148°40.6′E), 124 m, muddy sand, Smith-McIntyre grab (stn BSS 167), NMV J8334 (1 male).

Description. Total length of holotype: 3.15 mm.

Cephalosome rectangular with pronounced

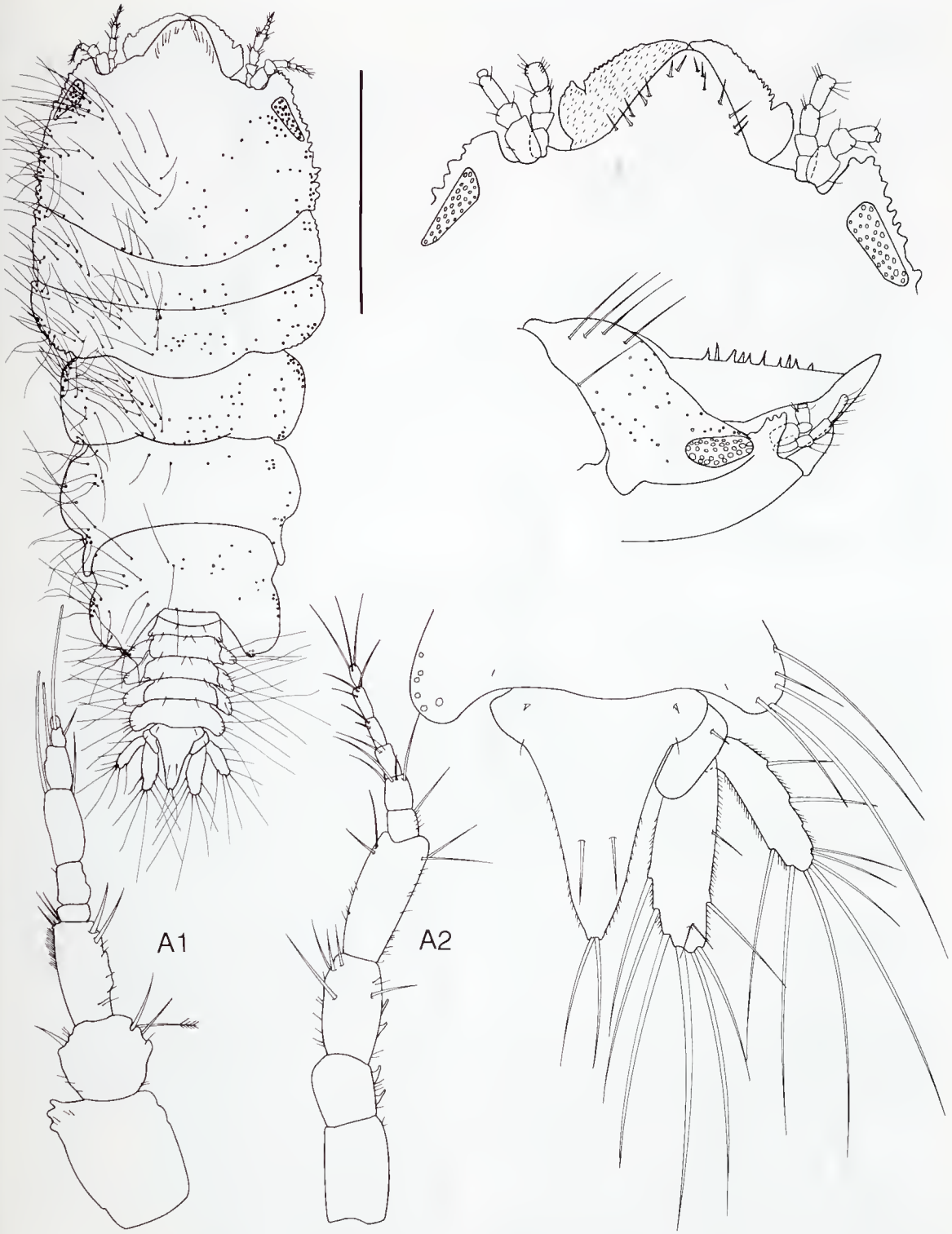

Figure 25. *Caecognathia dolichoderus*. Holotype, NMV J27561.

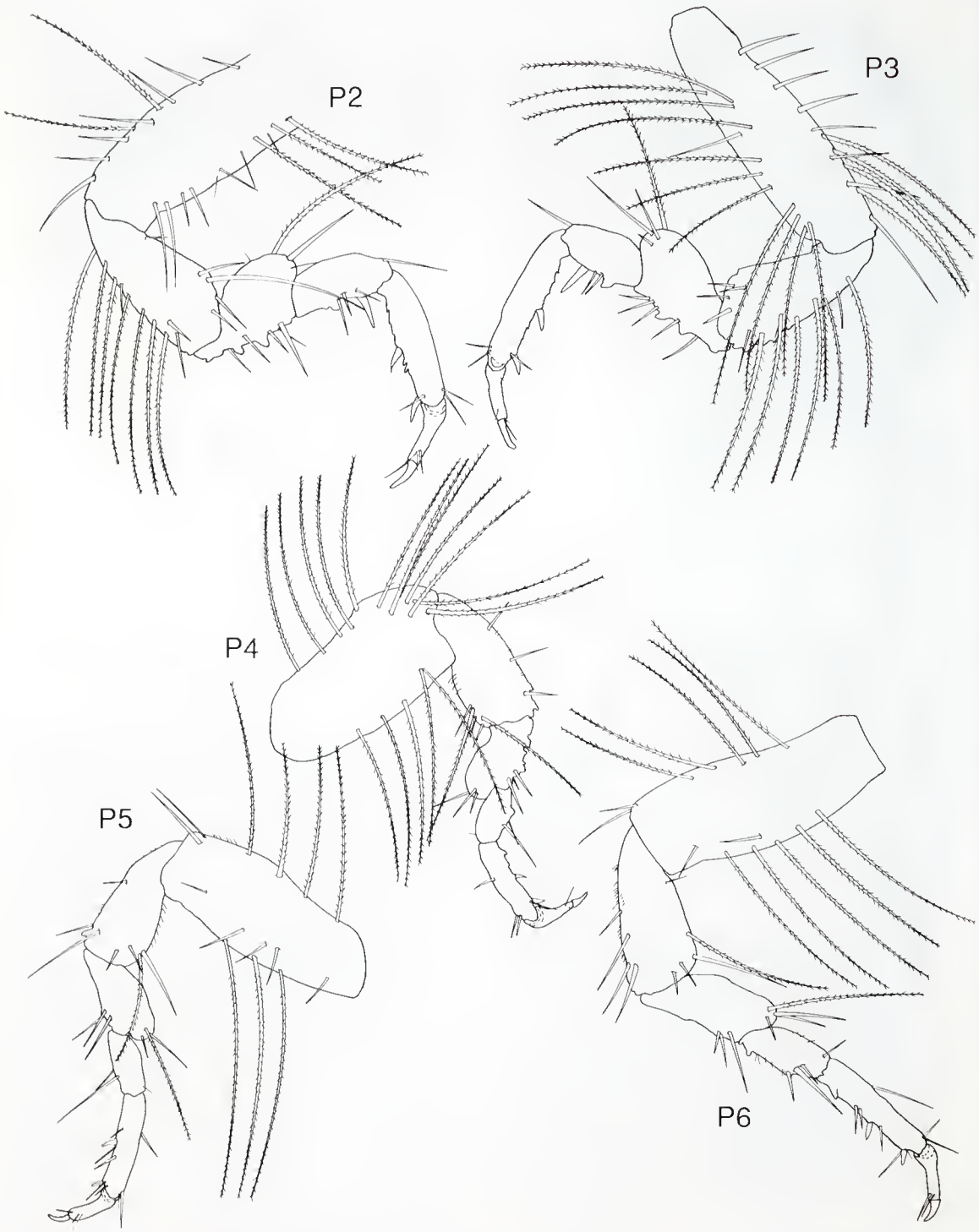

Figure 26. *Caecognathia dolichoderus*. Holotype, NMV J27561.

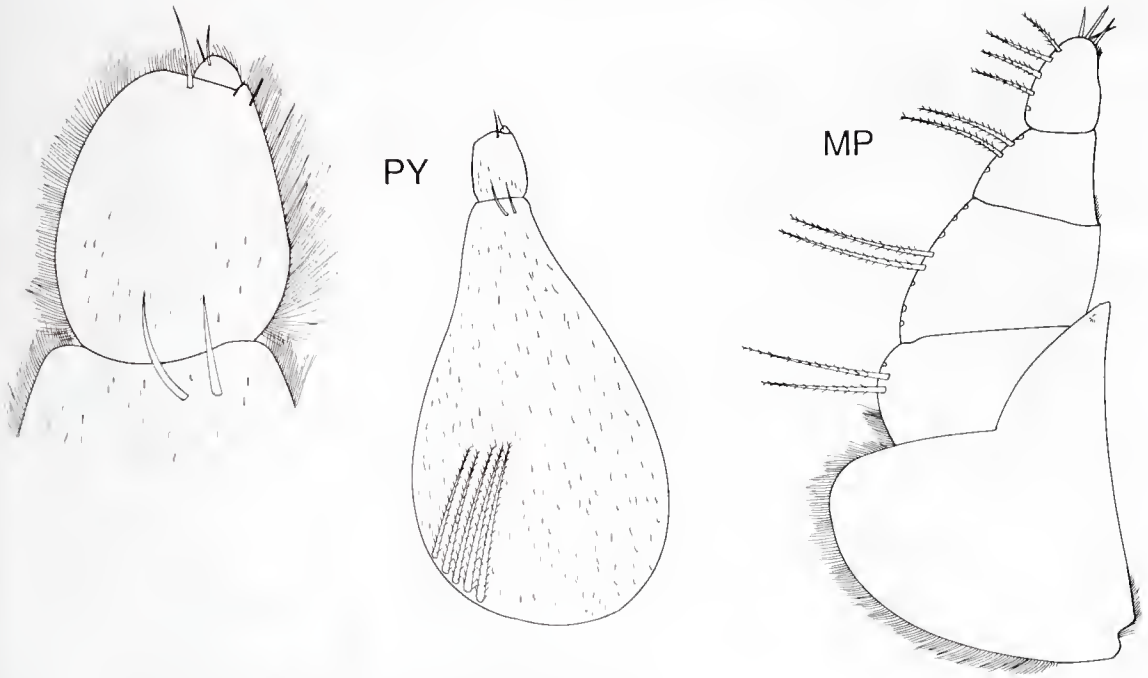

Figure 27. *Caecognathia dolichoderus*. Holotype, NMV J27561.

rostrum, 1.15 times as wide as long, lateral margins convex and irregular. Eyes well developed, lateral and sessile. Frontal border produced as rostrum, smoothly rounded with 14 setae spread submarginally. External scissura rounded. Supraocular lobe not pronounced. Cephalosome with many small spines anteriorly, visible in lateral view. Antennae stout, subequal; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 6 articles. Mandible one-third length of cephalosome with sparse covering of small fine setae; armed carina; pronounced mandibular incisor; mandible tightly closing around rostrum. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide, with 1 coupling hook. Pylopod 3-articled, internal margin lacking long setae; article 1 with 2 setae on ventral surface distally and 5 plumose setae at basis; article 2 with 1 seta on ventral surface; article 3 minute.

Pereon dorsoventrally flattened; widest anteriorly, as wide as cephalosome; covered with numerous long simple setae. Pereonite 1 dorsally fused with cephalosome and not visible laterally. Pereonites 2 and 3 subequal, pereonites 4–6 narrower and longer than 2 and 3; pereonite 6 with small, rounded lobuli. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer and wider, epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins straight; with 2 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching apex of pleotelson margins; rami bearing long simple setae.

Pereopods with moderate cover of large plumose setae, particularly on basis and ischium; elsewhere few, short simple setae. Pereopods 2 and 3 with few acute projections on lateral faces of merus–carpus.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Eastern Bass Strait, 115–130 m.

Remarks. Caecognathia dolichoderus does not closely resemble any previously described species. It is characterised by flat mandibles with a large incisor and very well armed carina, which fit snugly around the rostrum.

Caecognathia gnamptogenys sp. nov.

Figures 28–30

Material examined. Holotype. Victoria, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on RV *Franklin*, 23 Jul 1986 (stn SLOPE 32), NMV J19116 (1 male).

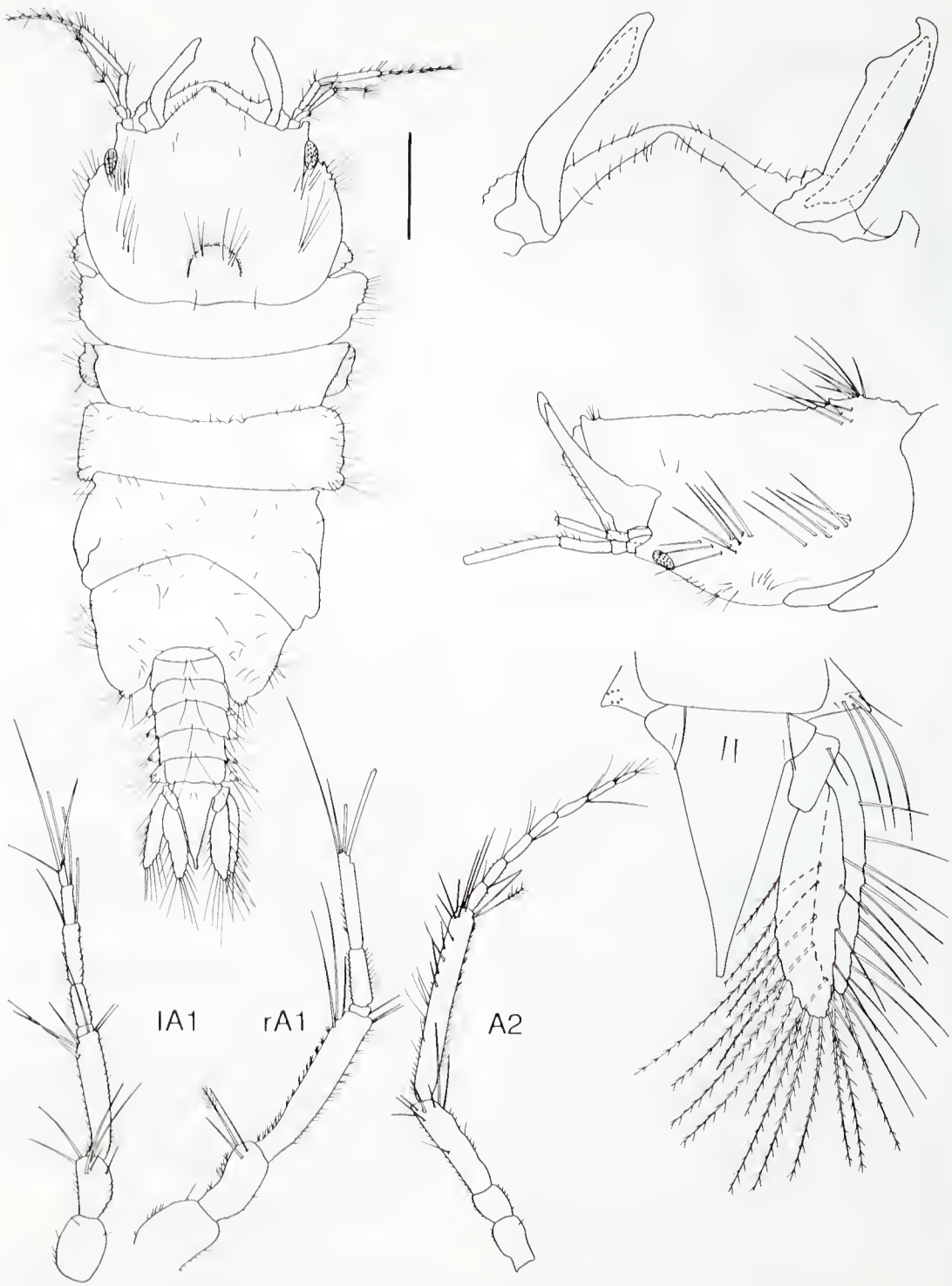

Figure 28. *Caecognathia gnamptogenys*. Holotype, NMV J19116.

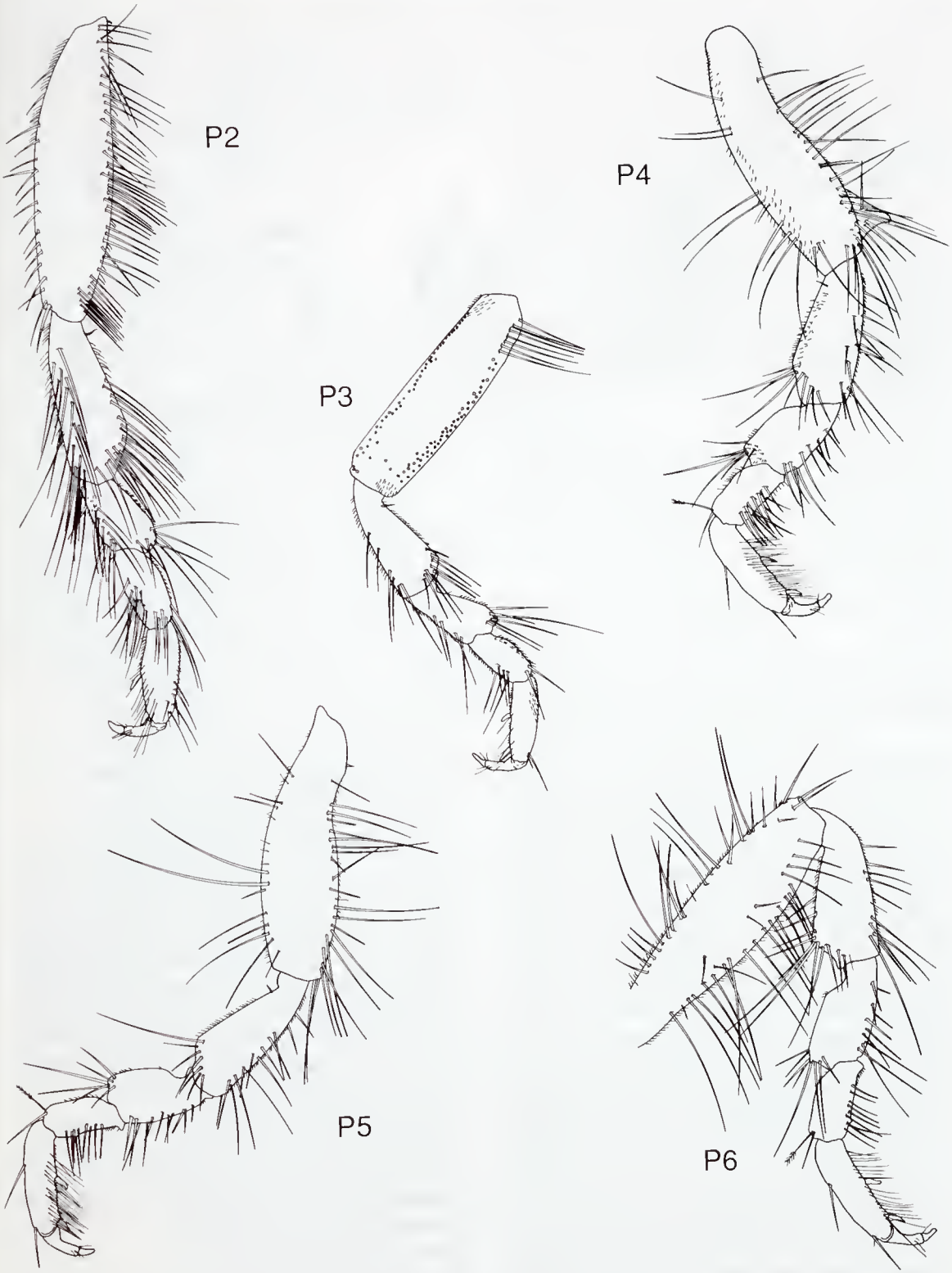

Figure 29. *Caecognathia gnamptogenys*. Holotype, NMV J19116.

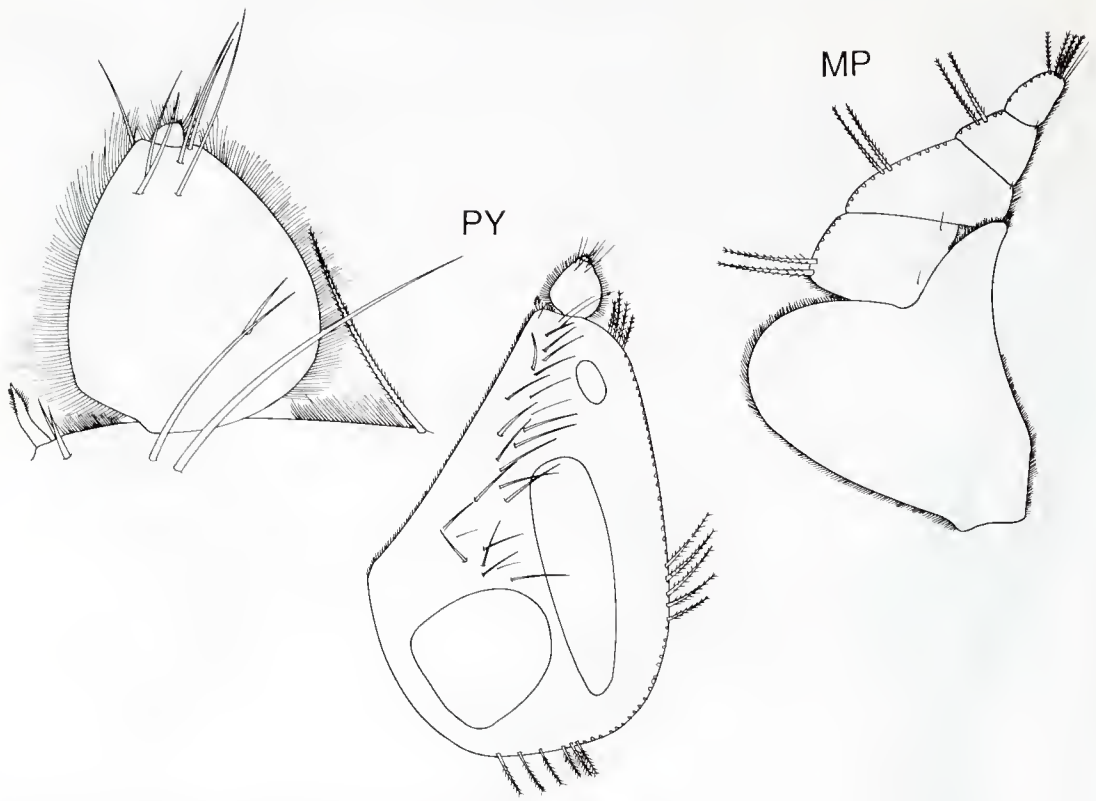

Figure 30. *Caecognathia gnamptogenys*. Holotype, NMV J19116.

Description. Total length of holotype: 7.4 mm.

Cephalosome quasipentagonal, lateral margins posterior to eyes rounded, frontal margin rounded. Eyes ventrolateral. Frontal border produced, conical, with 12 setae submarginally each side in 2 rows of 6: 1 row on rounded ventral buccal wall extension; other row on frontal border. Lamina dentata visible. External scissura very shallow. Supraocular lobe very low, acute. Cephalosome with low, posterior median tubercle with 6–7 long setae. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 7 articles (right antenna 1 flagellum of only 3 articles and 1 aesthetasc, terminal article as long as 3 and 4 articles of left flagellum). Mandible straight, raised in lateral view, one-third length of cephalosome; cylindrical, lacking obvious blade; with unarmed carina. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, with internal margin of plumose setae; article 1 with 3 areolae, second areola very elongate, with 27 setae on ventral surface medianly; article 2 with 7 setae on ventral surface distally; article 3 minute.

Pereon widest anteriorly, wider than cephalosome, covered with numerous simple setae. Pereonite 1 dorsally fused with cephalosome, visible as 2 small regions laterally on cephalosome. Pereonite 3 with ventrolateral extensions, pereonites 5 and 6 together as long as 2 to 4 together. Pereonite 7 very narrow, overlapping pleon. Pleonites subequal, pleonal epimera prominent. Pleotelson elongate, 1.5 times as long as wide, with 2 pairs of simple setae. Uropodal peduncle with 1 seta; rami subequal, reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods with dense cover of simple setae. Percopod 3 smaller than others; basis of pereopod 4 with distal conical projection.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

Distribution. Eastern slope of Bass Strait, 1000 m.

Remarks. Caecognathia gnamptogenys is characterised by the distal expansion of the basis of percopod 4; eyes situated more ventrolaterally than in other species; and short and simple mandibles. *C. serrata* (Richardson) from the Atlantic Ocean shares similar features but possesses a greatly produced frontal border.

Caecognathia huberia sp. nov.

Figures 31–33

Material examined. Holotype. Victoria, western Bass Strait. 50 km SSW of Warrnambool (38°49.5′S, 142°35.4′E), 89 m, coarse sand, R.S. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 190), NMV J27565 (1 male).

Paratypes. Tasmania, western Bass Strait, 59 km W of Stokes Point, King I. (40°07′S, 143°14′E), 185 m, sandy mud, Smith-McIntyre grab, G.C.B. Poore on HMAS *Kimbla*, 11 Oct 1980 (stn BSS 104), NMV J8364 (1 male).

Victoria, western Bass Strait, 50 km SSW of Warrnambool (38°49.5′S, 142°35.4′E), 89 m, coarse sand, R.S. Wilson on RV *Tangaroa*, 21 Nov 1981 (stn BSS 190), NMV J8363 (3 males). 5 km S of Point Reginald (38°48.0′S, 143°14.5′E), 47 m, hard rocky bottom, R.S. Wilson on RV *Tangaroa*, 20 Nov 1981 (stn BSS 185), NMV J8362 (2 males). Eastern Bass Strait, 11.7 km W of Pt Ricardo (37°49.89′S, 148°30.13′E), 27 m, coarse sand, Smith-McIntyre grab, N. Coleman on RV *Sarda* (stn MSL-EG 105), NMV J24635 (3 males); (stn MSL-EG 78) NMV J24634 (1 male). 7.3 km SSW of Cape Conran (37°52.65′S, 148°42.15′E), 49 m, coarse sand, Smith-McIntyre grab, N. Coleman on RV *Sarda*, Feb 1991 (stn MSL-EG 116), NMV J24636 (1 male).

Description. Total length of holotype: 2.99 mm.

Eyes well developed, lateral and sessile. Frontal border produced medianly, truncated, with 2 slight lateral depressions near internal margin of mandible; 6 short setae medianly and 4 longer setae laterally. External scissura deep, smoothly rounded. Supraocular lobe not pronounced. Cephalosome and pereon with numerous granules and long simple setae; with anterior, mesial furrow and shallower, oblique posterior mesolateral furrows and low, posterior median tubercle. Antennae stout, down-turned; antenna 1 longer than antenna 2, flagellum of 4 articles, with 3 aesthetases; flagellum of antenna 2 of 4 articles, shorter than article 4 of peduncle. Mandible curved inward, one-third length of cephalosome, slightly asymmetrical; with unarmed carina; pronounced mandibular incisor one-third to half way along; short setae near incisor; smooth arc-shaped blade on distal half with long irregular basal neck proximally giving blade produced and irregular appearance. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3, with 2 coupling hooks. Pylopod 2-articled, article 2 small; internal margin of fine short setae; article 1 operculate, with 4 setae distally on ventral surface; article 2 with 6 setae on ventral surface.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites progressively longer. Pereonite 4 with slight anterior constriction; small, anteriorly directed median spine and smoothly rounded median extension of posterior margin. Pereonite 5 with dorsal sulcus and areae laterales. Pereonite 6 with lobi laterales and rounded lobuli. Pereonite 7 very narrow, overlapping pleon. Pleon progressively narrower, with numerous large setae; pleonal epimera prominent. Pleotelson subtriangular, wider than long, with pair of simple setae medianly and pair of setae on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching beyond the apex of pleotelson; rami margins with a few long simple setae.

Pereopods subequal, with few simple setae; few lateral projections, mainly on carpus and merus; tubercles on basis of pereopod 3 and basis-merus of pereopod 6.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Bass Strait, 27–185 m.

Remarks. Caecognathia huberia belongs to a complex of south-eastern Australian species most easily recognised by the mesial and oblique posterior grooves on the cephalon. The other species in this complex are *C. pustulosa* (Hale), *C. agwillisi* (Seed) and *C. paratrechia*. *C. huberia* is very similar to *C. pustulosa* (Hale) but differs by being hirsute, particularly anteriorly; possessing a smaller anterior spine on pereonite 4; possessing a distinct posterior extension on peronite 4; smoothly rounded external scissura; and mandibles with a more complex blade and pronounced incisors.

Caecognathia leptanilla sp. nov.

Figures 34–36

Material examined. Holotype. Tasmania, central Bass Strait, 25 km SW of Cape Frankland, Flinders I., (40°09.4′S, 147°32.6′E), 51 m, shelly sand, WHOI epi-

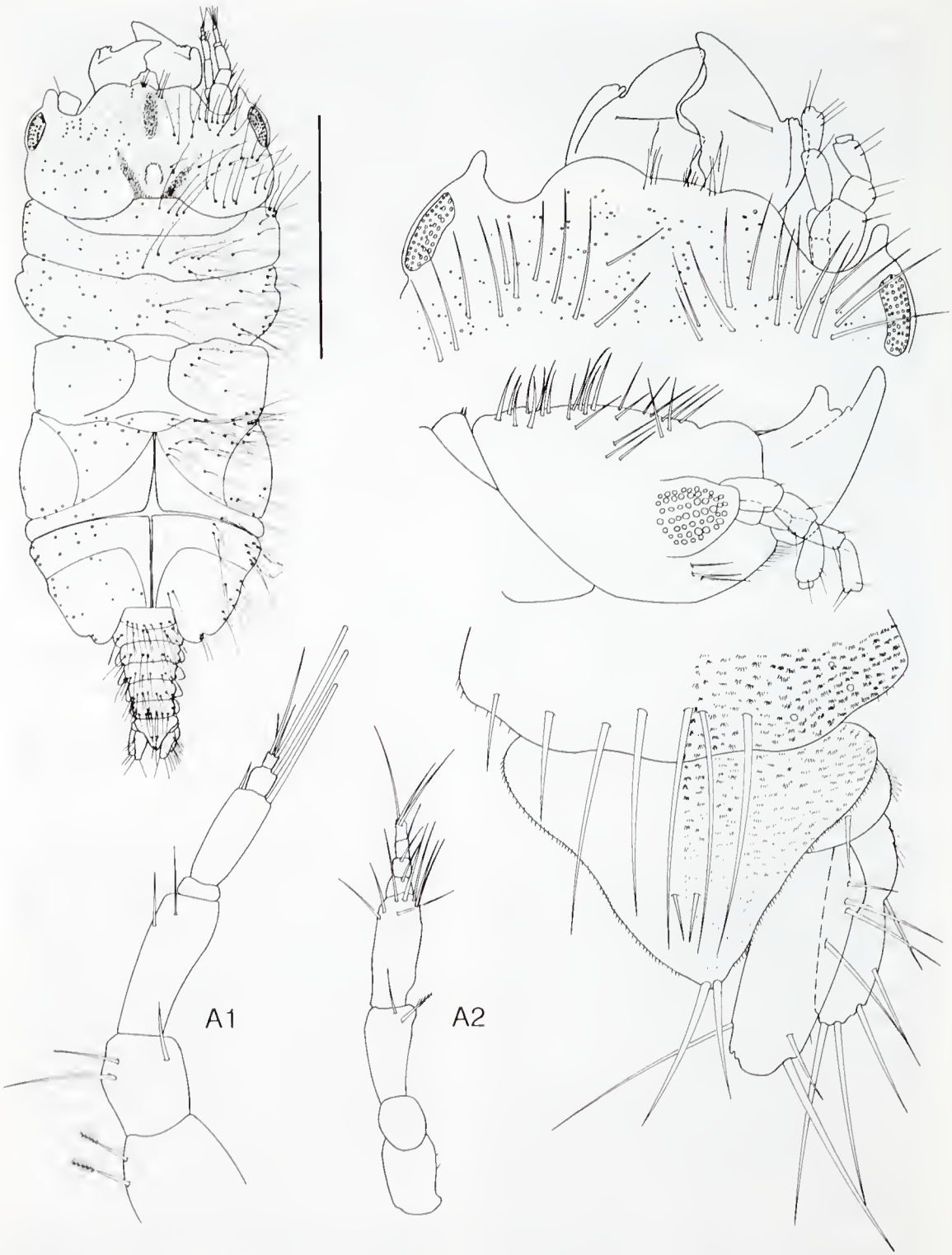

Figure 31. *Caecognathia huberia*. Holotype, NMV J27565.

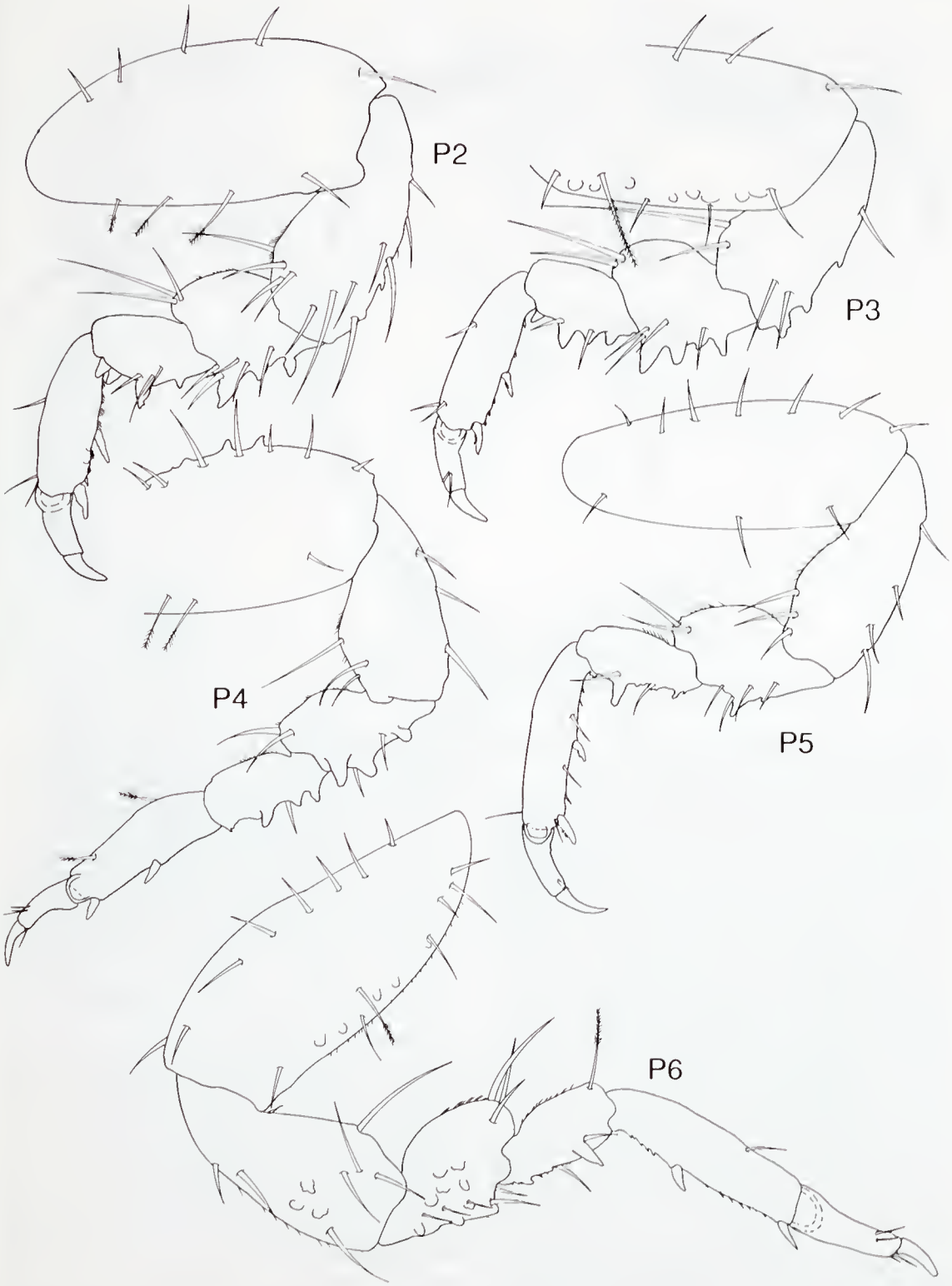

Figure 32. *Caecognathia huberia*. Holotype, NMV J27565.

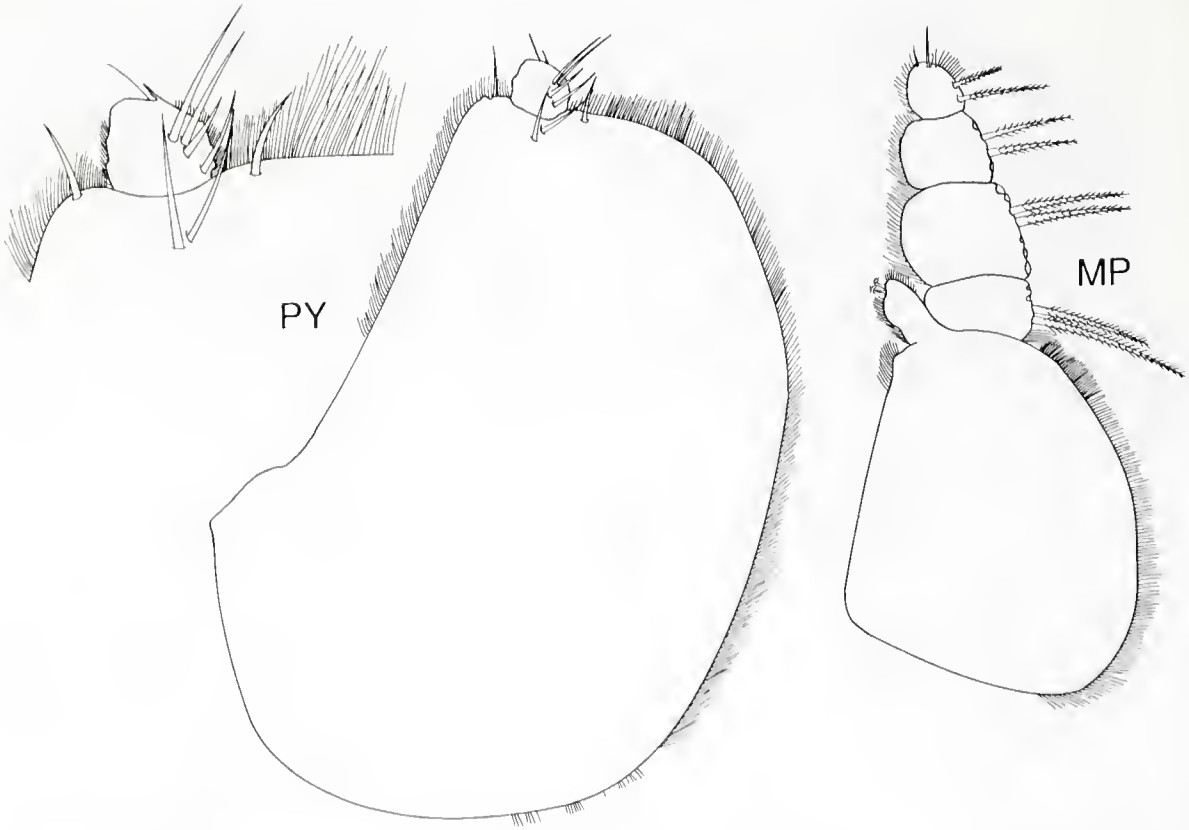

Figure 33. *Caecognathia huberia*. Holotype, NMV J27565.

benthic sled, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 162), NMV J27562 (1 male).

Paratypes. Most collected by R.S. Wilson on RV *Tangaroa* using WHOI epibenthic sled, Nov 1981. Tasmania, western Bass Strait, 70 km W of Cape Farewell, King I., (39°38.2′S, 143°07.2′E), 127 m, mainly sand (stn BSS 195) NMV J8340 (1 male). Central Bass Strait, 44 km NE of Cape Wickham, King I. (39°22.0′S, 144°18.3′E), 60 m, coarse sand (stn BSS 203), NMV J8348 (1 male). 33 km S of Deal I. (39°48.3′S, 147°19.2′E), 60 m, muddy sand, Smith-McIntyre grab (stn BSS 161) NMV J8347 (1 male). 25 km SW of Cape Frankland, Flinders I. (40°09.4′S, 147°32.6′E), 51 m, shelly sand (stn BSS 162), NMV J8339 (4 males). Eastern Bass Strait, 20 km SSW of Babel I. (40°06.8′S, 148°24.3′E), 22 m, coarse shell, Smith-McIntyre grab (stn BSS 166), NMV J8344 (3 males). 37 km NNE of Eddystone Point (40°40.7′S, 148°36.9′E), 67 m, muddy sand (stn BSS 164), NMV J8338 (1 male).

Victoria. Western Bass Strait, 80 km WSW of Cape Otway (39°59′S, 142°37′E), 94 m, coarse sand, G.C.B. Poore on HMAS *Kimbla*, 9 Oct 1980 (stn BSS 62), NMV J8343 (1 male). 57 km SSW of Cape Otway (39°17′S, 143°14′E), 90 m, coarse carbonate sand, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 72) NMV J8349 (1 male). Central Bass Strait, 6 km S of Cape Schanck (38°33.4′S, 144°54.9′E), 55 m, medium sand (stn BSS 154), NMV J8560 (1 male). 38 km SW of Cape Paterson (38°56.4′S, 145°16.6′E), 70 m, fine sand (stn BSS 155), NMV J8341 (4 males), J35492 (1 male). Eastern Bass Strait, 8 km S of Wilsons Promontory (39°12.9′S, 146°27.3′E), 65 m, medium sand (stn BSS 180), NMV J8345 (1 male). 43 km SE of Port Albert (38°53.7′S, 147°06.5′E), 58 m, coarse shell (stn BSS 177), NMV J8342 (2 males). 50 km SE of Port Albert (38°54.3′S, 147°13.4′E), 58 m, coarse shell, Smith-McIntyre grab (stn BSS 176), NMV J8346 (1 male).

Other material. 27 lots from 27–800 m depth in eastern Bass Strait and Tasmania, NMV collections.

Description. Total length of holotype: 5.08 mm.

Cephalosome roughly elliptical, 1.3 times as long as wide, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border produced dorsally into rostrum; smoothly rounded, with 10 submarginal setae of uniform size each side of mid-dorsal line. External scissura absent. Supraocular lobe smoothly convex. Antennae subequal, downturned in lateral view; flagellum of antenna 1 of 5 articles, with 3 aesthetases; flagellum of antenna 2 of 6 articles. Mandible strongly curved, one-third length of cephalosome; with unarmed carina; smooth blade. Maxilliped 5-articled, palp thin

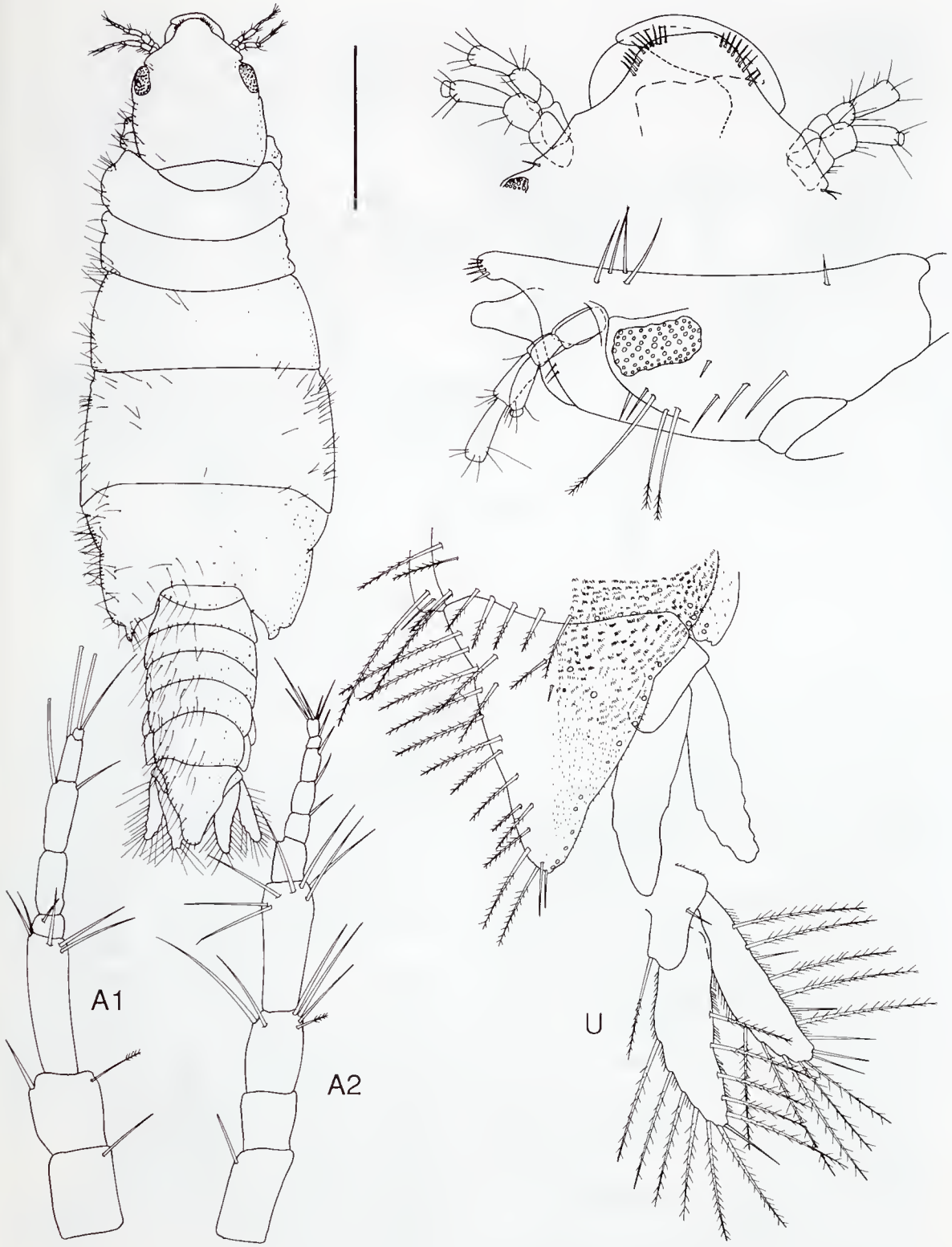

Figure 34. *Caecognathia leptanilla.* Holotype, NMV J27562.

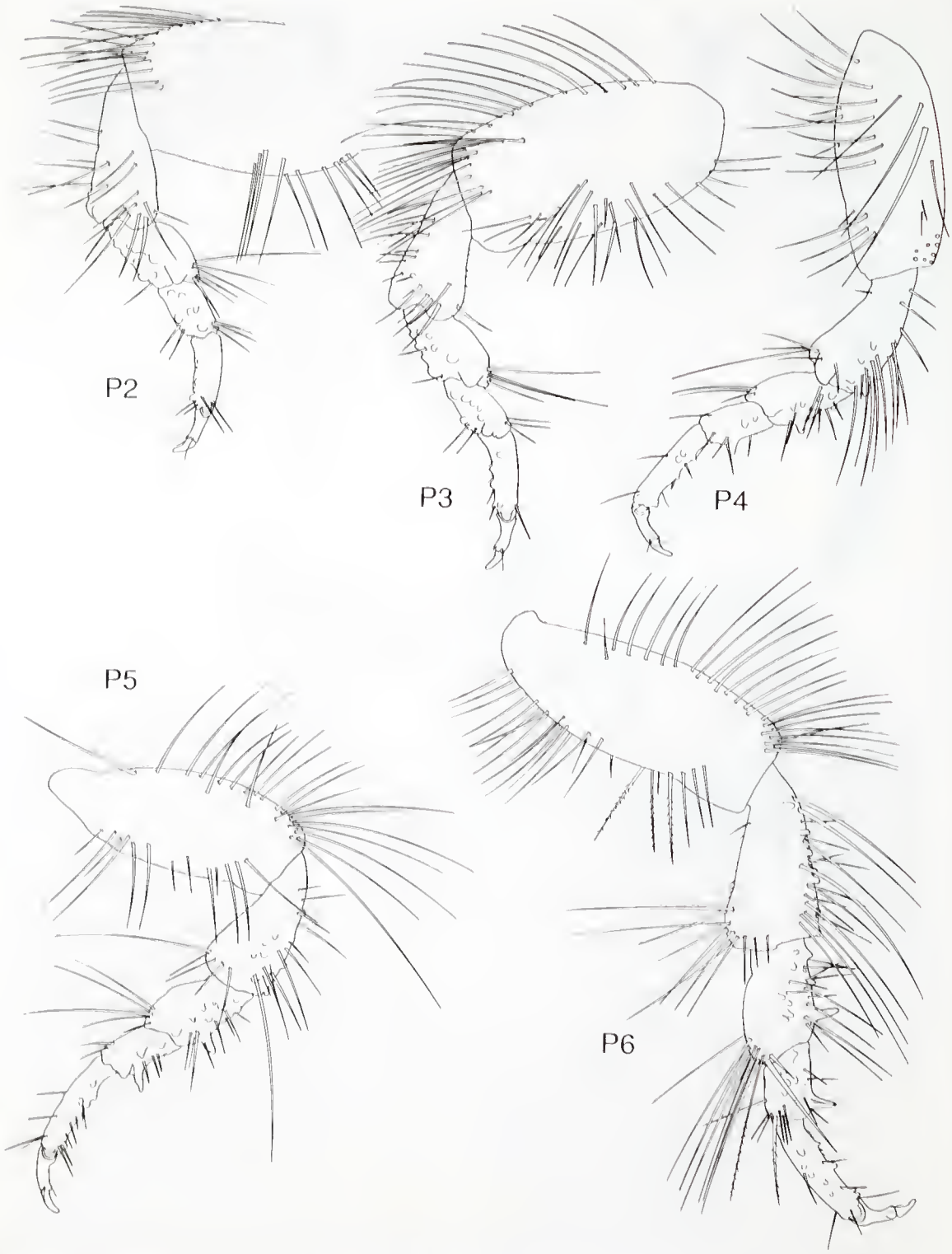

Figure 35. *Caecognathia leptanilla*. Holotype, NMV J27562.

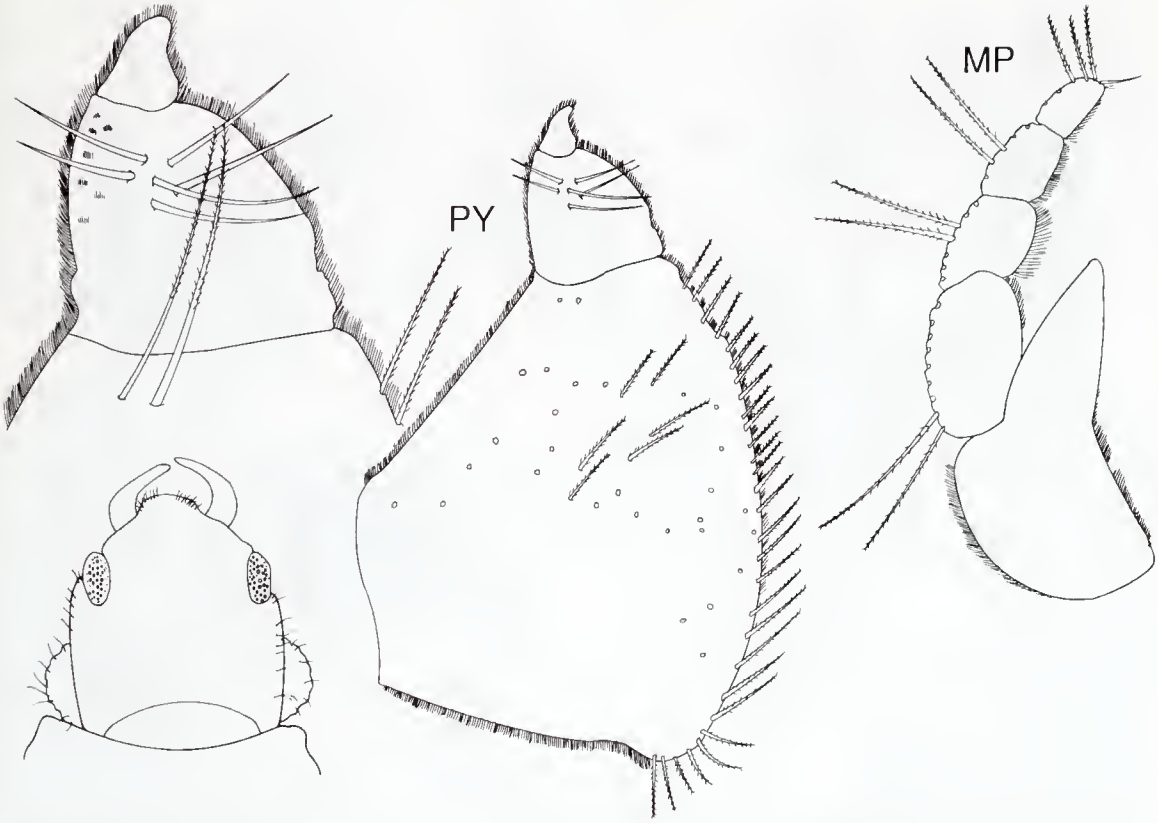

Figure 36. *Caecognathia leptanilla*. Holotype, NMV J27562; Dorsal view of cephalon of paratype, NMV J35492.

and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Palpod 3-articled, internal margin of plumose setae; article 1 with about 35 plumose setae on ventral surface; article 2 conical, proximal margin completely joined to article 1, with 6 setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pereonite 5, twice as wide as cephalosome; covered with fine, short setae. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by posterior margin of cephalosome and partially obscured laterally by pereonite 2. Pereonites progressively longer, except pereonite 2 and 3 subequal. Pereonite 6 posterior border markedly indented; lobuli pronounced, globular. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively longer; pleon tapered, pleonites 1 and 5 narrower than others; pleonal epimera prominent on pleonites 4 and 5. Pleotelson subtriangular, as wide as long, lateral margins slightly sinuous; with 15 pairs of plumose setae laterally and pair of setae on distal apex. Uropodal peduncle with 2 setae; rami subequal, reaching apex of pleotelson, bearing numerous plumose setae.

Pereopods with dense cover of simple setae, particularly on basis; with few lateral projections on anterior faces of ischium to carpus. Pereopods 2 and 3 with broad basis.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Bass Strait and eastern Tasmania. 27–800 m.

Remarks. C. leptanilla is characterised by its produced rostrum.

Caecognathia paratrechia sp. nov.

Figures 37–39

Material examined. Holotype. South Australia, Pearson I., E side in bay (33°57.30′S, 134°15.70′E), 20 m, bryozoans, sponges etc. on shaded surface, SCUBA,

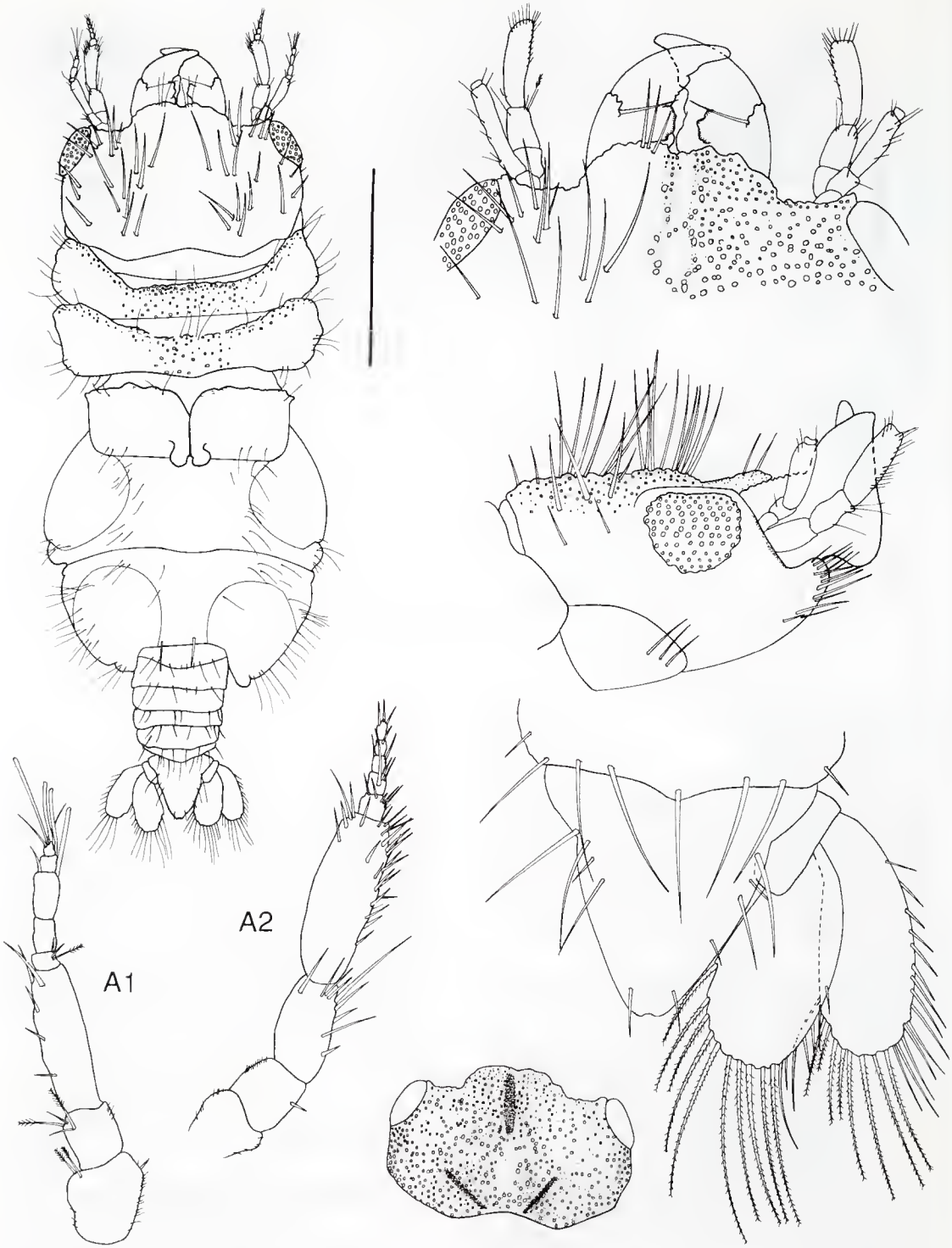

Figure 37. *Caecognathia paratrechia*. Holotype, NMV J27578.

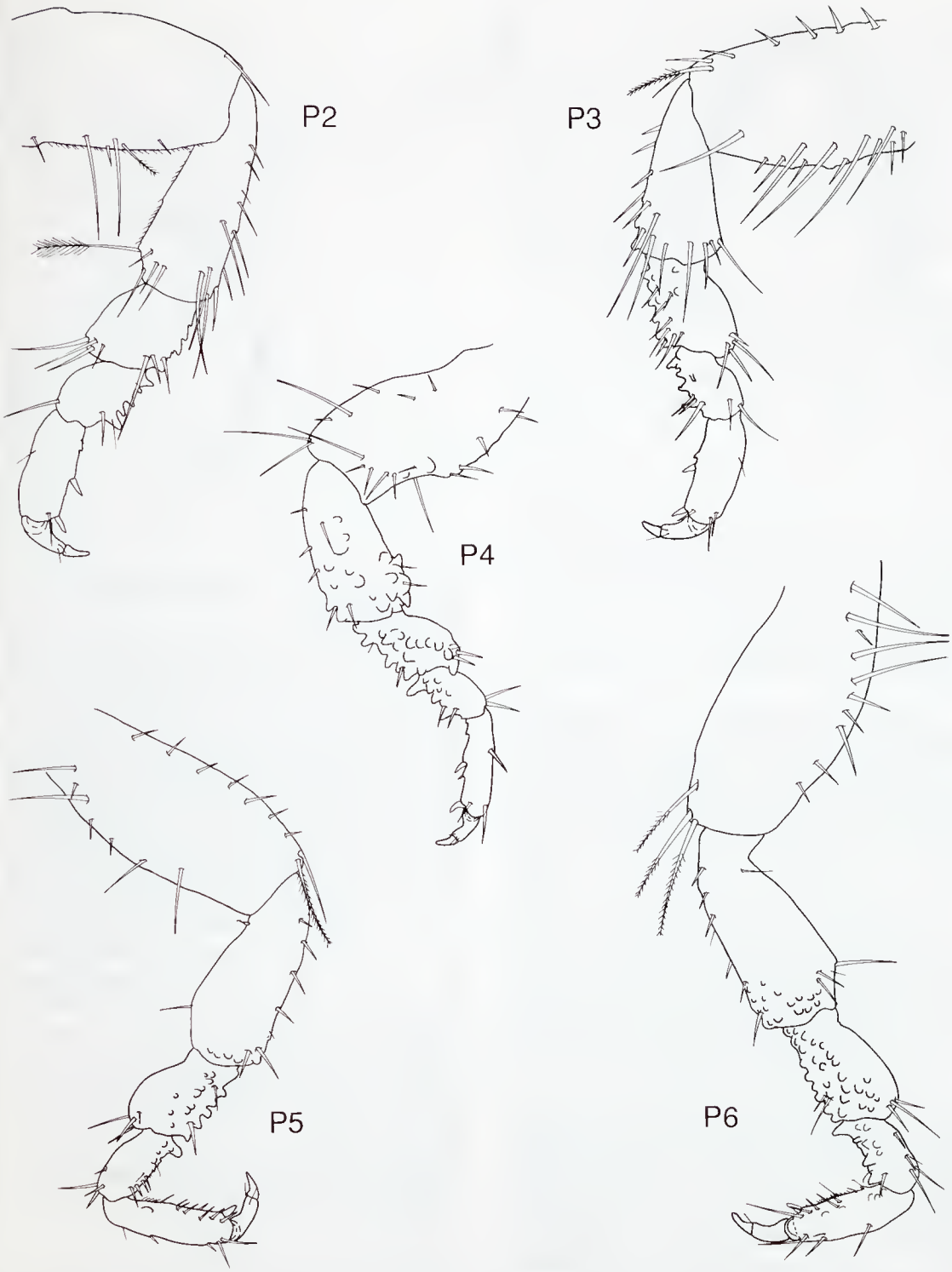

Figure 38. *Caecognathia paratrechia*. Holotype, NMV J27578.

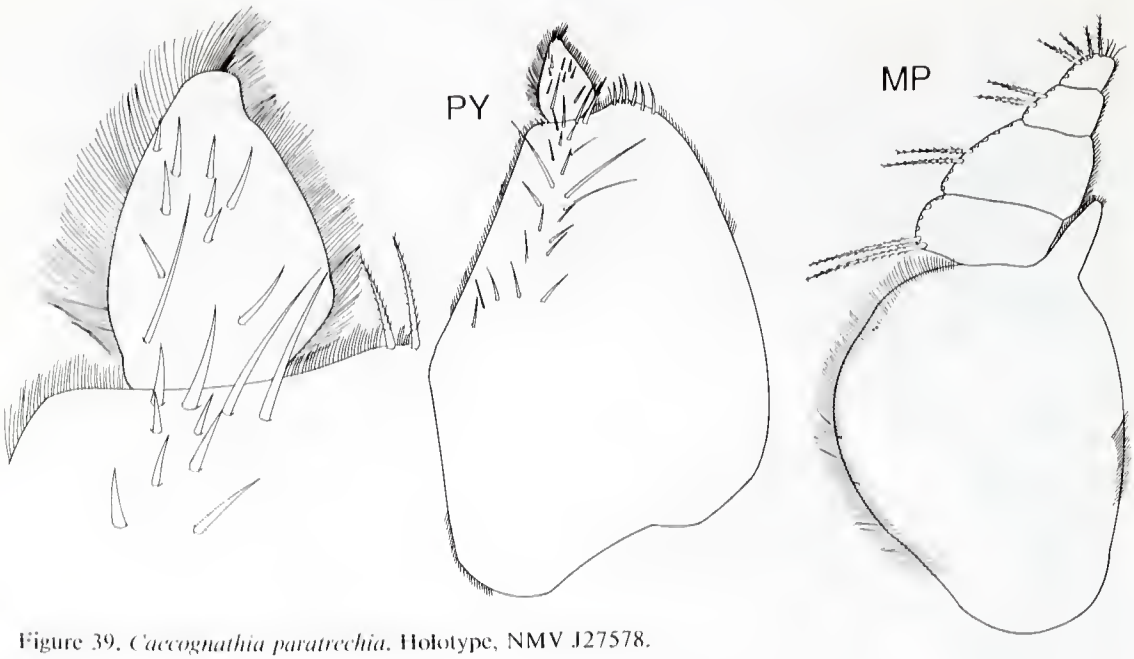

Figure 39. *Caecognathia paratrechia*. Holotype, NMV J27578.

G.C.B. Poore, 17 Apr 1985 (stn SA 55), NMV J27578 (1 male).

Description. Total length of holotype: 3.67 mm.

Cephalosome rectangular, 1.5 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border produced medianly, rounded with irregular border and median indentation; 3 long submarginal setae each side of median indentation. External scissura rounded. Supraocular lobe smoothly convex. Cephalosome with many long simple setae and numerous granules; with mesial furrow and shallower, oblique posterior mesiolateral furrows. Antennae subequal; flagellum of antenna 1 of 5 articles, with 4 aesthetases, article 3 of peduncle longer than flagellum or peduncle articles 1 and 2 together; flagellum of antenna 2 of 5 articles, flagellum short, shorter than distal article of peduncle. Mandible scoop-shaped, strongly curved, one-third length of cephalosome; with unarmed carina; armed mandibular incisor one-third way along; slightly crenulate blade; setae at base of incisor and prominent quadrate internal lobe at base of mandible. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, narrow. Pylopod 2-articled, internal margin of fine short setae with 6–7 plumose setae on anteromesial margin; article 1 operculate with 23 setae on ventral surface medianly; article 2 conical, with 9–10 setae on ventral surface.

Pereon widest posteriorly at pereonites 5 and 6, 1.2 times as wide as cephalosome; covered with numerous simple setae. Pereonite 1 dorsally reaching lateral margins and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal, as wide as cephalon. Pereonite 4 narrow; with anterior constriction; thin median groove and posteriorly directed, bilobed extension of posterior border of pereonite 4. Pereonite 5 and 6 rounded, similar to praniza but not fused. Pereonite 5 with arcae laterales. Pereonite 6 with lobi laterales and rounded lobuli. Pereonite 7 not visible. Pleotelson subtriangular, as wide as long; lateral margins sinuous; with 5 pairs of simple setae laterally. Uropodal peduncle without setae; rami rounded, subequal, reaching just beyond apex of pleotelson, bearing numerous plumose setae distally.

Pereopods with few simple setae; with many tubercles on ischium, merus and carpus, particularly on pereopod 4; pereopod 4 smaller than other pereopods.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. SA, rocky habitats, 20 m.

Remarks. *C. paratrechia* is characterised by the quadrate mandibular lobe and bilobed posterior projection on pereonite 4.

Caecognathia trachymesopus sp. nov.

Figures 40–42

Material examined. Holotype. Tasmania, central Bass Strait, 20 km NNE of North Point (40°32.0′S, 145°23′E), 44 m, muddy shell grit, Smith-McIntyre grab, M.F. Gomon and G.C.B. Poore on FV *Sarda*, 4 Nov 1980 (stn BSS 116), NMV J27571 (1 male).

Paratypes. Collected by M.F. Gomon and G.C.B. Poore on FV *Sarda*, 1980, unless otherwise noted. Tasmania, western Bass Strait, 55 km W of Stokes Point, King I. (40°06′S, 143°16′E), 187 m, fine sand, Smith-McIntyre grab, G.C.B. Poore on HMAS *Kimbla*, 11 Oct 1980 (stn BSS 101), NMV J8310 (1 male). Central Bass Strait, 23 km E of Cape Rochon, Three Hummock I. (40°22.2′S, 145°17′E), 40 m, mainly sand, WHOI epibenthic sled (stn BSS 112), NMV J7799 (2), NMV J7798 (2). 20 km NNE of North Point (40°32.0′S, 145°23′E), 44 m, muddy shell grit, Smith-McIntyre grab (stn BSS 116), NMV J7796 (8). (40°23.8′S, 145°32′E), 66 m, muddy sand, Smith-McIntyre grab (stn BSS 113), NMV J7797 (2). 33 km S of Deal I., (39°48.3′S, 147°19.3′E), 60 m, muddy sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 161), NMV J8304 (1).

Victoria. Western Bass Strait, 25 km WSW of Cape Otway (38°55′S, 143°25′E), 67 m, medium sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 8 Oct 1980 (stn BSS 53), NMV J8309 (1). Central Bass Strait, 60 km SW of Cape Schanck, (39°00.2′S, 144°33.9′E), 74 m, sandy shell, R.S. Wilson on RV *Tangaroa*, 23 Nov 1981 (stn BSS 202), NMV J8307 (2). Eastern Bass Strait, 40 km SSW of Lakes Entrance, Victoria (38°18.0′S, 147°37.0′E), 55 m, muddy fine shell, M.F. Gomon and R.S. Wilson on FV *Silver Gull*, 31 Jul 1983 (stn BSS 209), NMV J8301 (4). Eastern Bass Strait, between Lake Tyers and Pt Ricardo, 21–45 m, sandy sediments, Sep 1990, MSL-EG stns, 10 lots: NMV J24637 (1), NMV J24693 (3), NMV J24638 (1), NMV J24695 (3), NMV J26358 (1), NMV J26359 (2), NMV J26360 (1), NMV J24694 (1), NMV J24640 (1), NMV J24691 (3).

Other material. 11 lots from Bass Strait, 27–293 m depth, NMV collections.

Description. Total length of holotype: 3.23 mm.

Brown. Cephalosome elliptical, 1.3 times as long as wide, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border slightly produced, rounded with small median indentation; with 9 submarginal setae each side of indentation, setae generally decreasing in size laterally. External scissura very shallow. Supraocular lobe smoothly convex. Antennae down-turned; antenna 1 slightly longer than antenna 2; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 4 articles. Mandible strongly curved, half length of cephalosome; with unarmed carina; smooth blade on distal half; basal neck smooth except for 1 rounded, posteriorly directed projection giving an uneven double-scalloped effect; erisma pronounced, covering base of mandible. Maxilliped 5-articled, palp thin and elongate; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, wide. Pylopod 3-articled, internal margin of plumose setae; article 1 with 24 setae on ventral surface; article 2 conical, posterior margin completely joined to article 1, with 5 setae on ventral surface; article 3 minute.

Pereon width increasing posteriorly; widest at pereonite 5, twice as wide as cephalosome; margins with numerous plumose setae. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by posterior margin of cephalosome and partially obscured laterally by pereonite 2. Pereonites progressively longer; pereonite 6 posterior border markedly indented; lobuli pronounced, globular. Pereonite 7 very narrow, overlapping pleon. Pleon with pleonites subequal, pleonite 5 slightly longer than others. Pleotelson subtriangular, as wide as long; lateral margins sinuous; with 8 pairs of plumose setae laterally and pair of setae on distal apex. Uropodal peduncle with 2 setae; endopod longer than exopod, not reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Basis to carpus of pereopods with dense cover of plumose setae, particularly on basis; with few lateral projections on anterior face of ischium to carpus.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Bass Strait, 27–293 m.

Remarks. Caecognathia trachymesopus is similar to *C. diacamma* but is differentiated by the less produced frontal border, narrower and longer cephalosome, more complex mandible and the lack of lateral sutures on pereonite 6.

Elaphognathia Monod

Gnathia (*Elaphognathia*) Monod, 1926: 558–560. — Gurjanova, 1936: 256–257. — Bacescu, 1960: 107–112. — Cals, 1973: 295, 305. — Holdich and Harrison, 1980: 218.

Type species. Anceus ferox Haswell, 1885 (herein designated).

Diagnosis. Eyes present. Frontal margin of cephalon transverse, deeply excavated; with

Figure 40. *Caecognathia trachymesopus*, Holotype, NMV J27571.

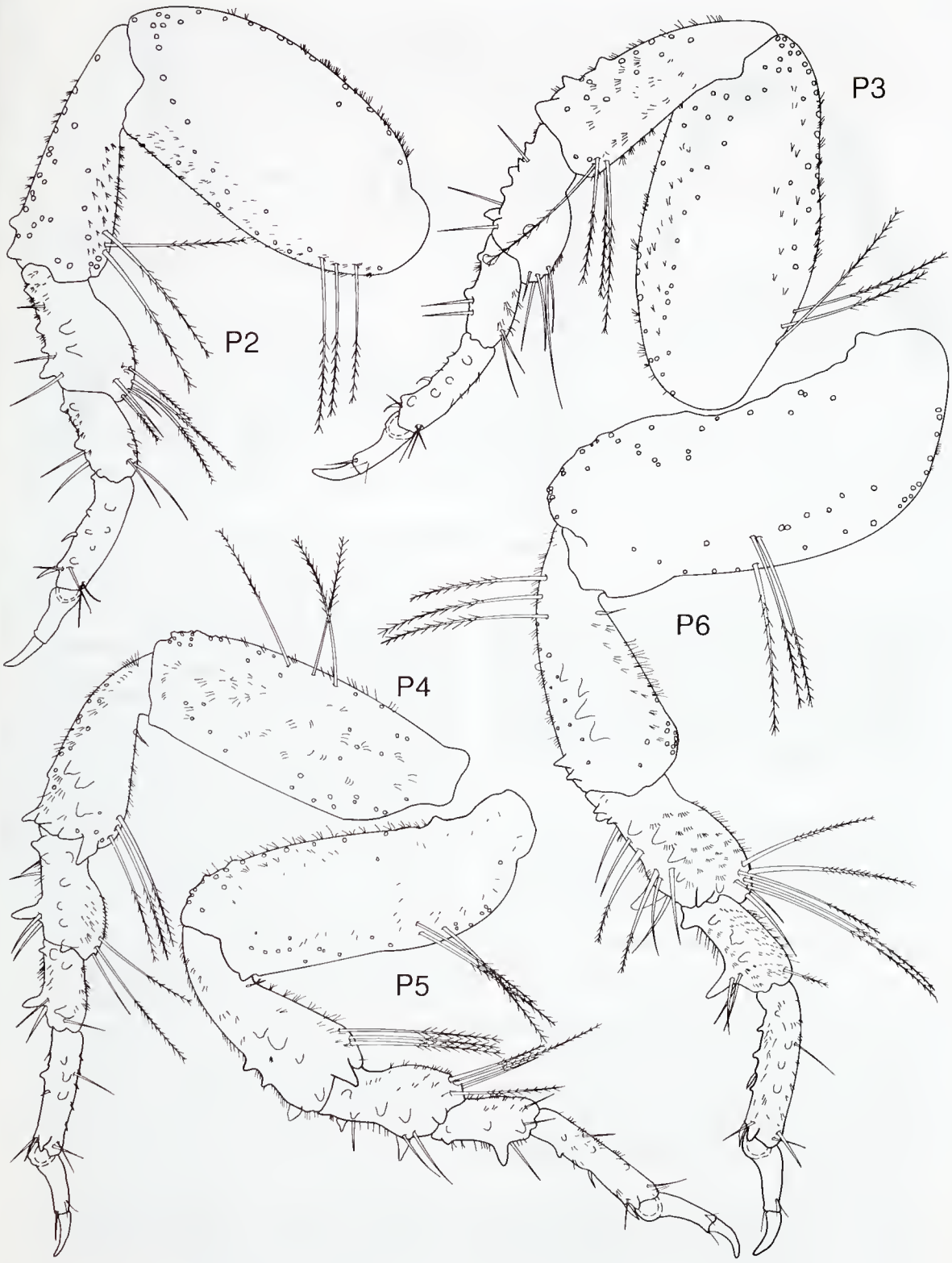

Figure 41. *Caecognathia trachymesopus*. Holotype, NMV J27571.

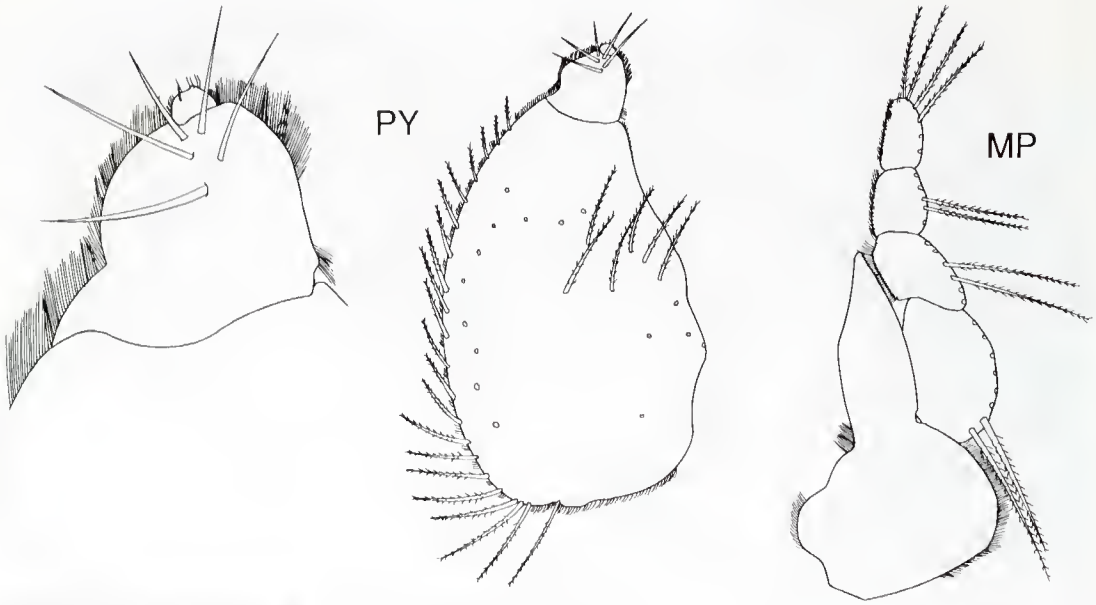

Figure 42. *Caecognathia trachymesopus*. Holotype, NMV J27571.

frontal processes which may be emarginate. Mandibles long, cylindrical; often lacking mandibular blade though may poeess numerous specialised structures. Pereonite 1 immersed in cephalon. Pylopod 2- or 3-articled; operculate, article 1 enlarged, generally with dense external margin of plumose setae; article 3 small or absent.

Remarks. The subgenus *Elaphognathia* was erected by Monod (1926) for four species but none was selected as type species, then or since. As the first described *Elaphognathia*, Haswell's Australian species is designated here and the name elevated to generic rank.

Species of *Elaphognathia* are most easily recognised by the excavate frontal border and the elongate mandibles lacking any dentate blade.

The genus was described as Indopacific by Gurjanova (1936) and Bacescu (1960) and Tethyan in origin by Cals (1973). There are 13 species distributed through the Indo-West Pacific and Mediterranean. Of the five species known from Australia, one is newly described. The other four are briefly illustrated (see figs 2N–Q).

Key to males of Australian species of *Elaphognathia*

1. Supraocular lobe extended dorsally as crest, pereonites 5–6 fused as in pranzia stage ..... *E. rimifrons*

— Supraocular lobe not extended dorsally as crest, pereonites 5–6 not fused 2

2. Mandibles almost twice as long as cephalon, pereonite 1 obvious, pylopods without aerolae 3

— Mandibles as long as cephalon, pereonite 1 not visible, pylopods with aerolae 4

3. Mandibles with conical internal lobe at base, without small internal notch behind tip; mediofrontal process with 3 setae either side of median notch and not produced beyond base of mandibles ..... *E. froygattella*

— Mandibles with large quadrate internal lobe at base and small internal notch behind tip; mediofrontal process produced beyond base of mandibles with 2 acute lateral projections, no setae ..... *E. bifurcilla*

4. Mandibles cylindrical, with 2–3 apical cusps; cephalon without low median tubercle; pylopod 3-articled, with 2 plumose setae on anterior margin of article 1 (NB: specimens can lack the slight median projection found at the base of the rounded excavation of the frontal border, a characteristic used in previous keys) ..... *E. ferox*

— Mandibles with small blade, lacking apical cusps; cephalon with low median tubercle; pylopod 2-articled, article 1 with many plumose setae on margin ..... *E. forceps*

Elaphognathia froygattella sp. nov.

Figures 43–45

Material examined. Holotype. Victoria, western Bass Strait, 35 km SSW of Cape Otway (39°07.0'S, 143°14.6'E), 84 m, coarse sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 20 Nov 1981 (stn BSS 183), NMV J27568 (1 male).

Paratypes. Type locality, NMV J8374 (2 males).

Description. Total length of holotype: 5.09 mm.

Cephalosome rectangular, twice as wide as long, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border deeply excavated mid-dorsally; mediofrontal process inferior, ventral to excavation, conical with large median notch, with 6 setae spread across base of notch; superior frontolateral process acute, directed anterolaterally, located at base of mandible, with 4 evenly spread setae on both margins. Inferior frontolateral process acute. External scissura very shallow. Supraocular lobe very low, acute. Antenna 1 directed ventrally in lateral view; flagellum of 5 articles, with 4 aesthetascs. Antenna 2 twice as long as antenna 1; flagellum of 7 articles. Mandible straight, twice as long as cephalosome; cylindrical, with no obvious blade; with unarmed carina and 2 conical internal lobes; distal lobe, one-third way along, directed anteriorly; proximal lobe, at base of mandible, directed posteriorly. Maxilliped 5-articled, endite clearly reaching article 3; palp broad with articles 2–5 wider than long, external margins bearing plumose setae. Pylopod 3-articled; article 1 with 4 setae on ventral surface medianly, distal internal margin bearing plumose setae; article 2 circular with 3 setae on ventral surface distally; article 3 minute.

Pereon evenly sided, as wide as cephalosome, margins with numerous setae. Pereonite 1 barely reaching lateral margins dorsally, partially obscured laterally by pereonite 2; pereonites 2 and 3 subequal, 4 wider than 5 and 6. Pereonite 7 not visible. Pleon broad, epimera prominent. Pleonites 2–4 subequal, pleonite 5 shorter than others. Pleotelson subtriangular, wider than long, lateral margins sinuous; with 3–5 pairs of simple setae. Uropodal peduncle with 3 setae; rami subequal, reaching beyond the apex of pleotelson, bearing numerous plumose setae distally.

Pereopods progressively longer, with dense cover of simple setae. Pereopod 6 with one anterior spiniform seta on merus,

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Western Bass Strait, 84 m.

Remarks. Elaphognathia froygattella is most similar to *E. bifurcilla* Holdich and Harrison from North Queensland, particularly in overall body proportions; the great length of the mandibles and their more lateral attachment. *E. froygattella* differs from *E. bifurcilla* in the smaller emarginate mediofrontal process, absence of an internal notch near the tip of the mandible and the different internal mandibular lobe.

Euneognathia Stebbing

Euneognathia Stebbing, 1893: 338. — Monod, 1926: 312–313 (and other authors).

Type species. Anceus gigas Beddard, 1886 (monotypy).

Diagnosis. Eyes present. Frontal margin of cephalon not produced; transverse, with frontal processes. Mandibles with blade and pseudoblade. Cephalon with paraocular ornamentation. Pereonite 1 immersed in cephalon. Posterior margin of pereonite 6 deeply excavated for pleon. Pylopod 5-articled; not operculate, with dense external margin of plumose setae.

Remarks. Euneognathia is a monotypic genus found around Antarctica (Schultz, 1978). It is the only genus of Gnathiidae with the combination of frontal processes and a 5-articled, non-operculate pylopod. *Euneognathia gigas* is a very large species, males being greater than 10 mm long. The species' status as member of a

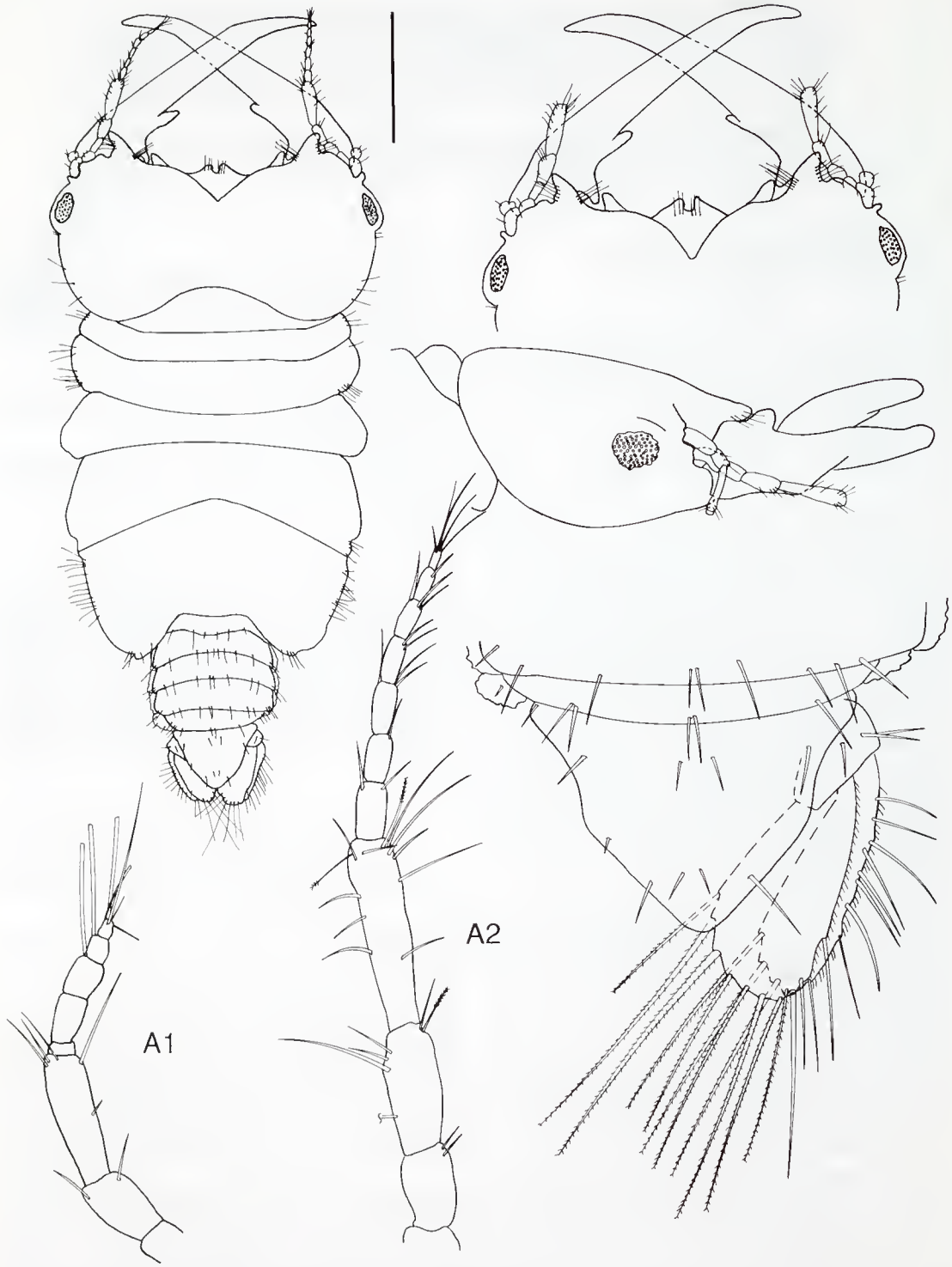

Figure 43. *Elaphognathia froygattella*. Holotype, NMV J27568.

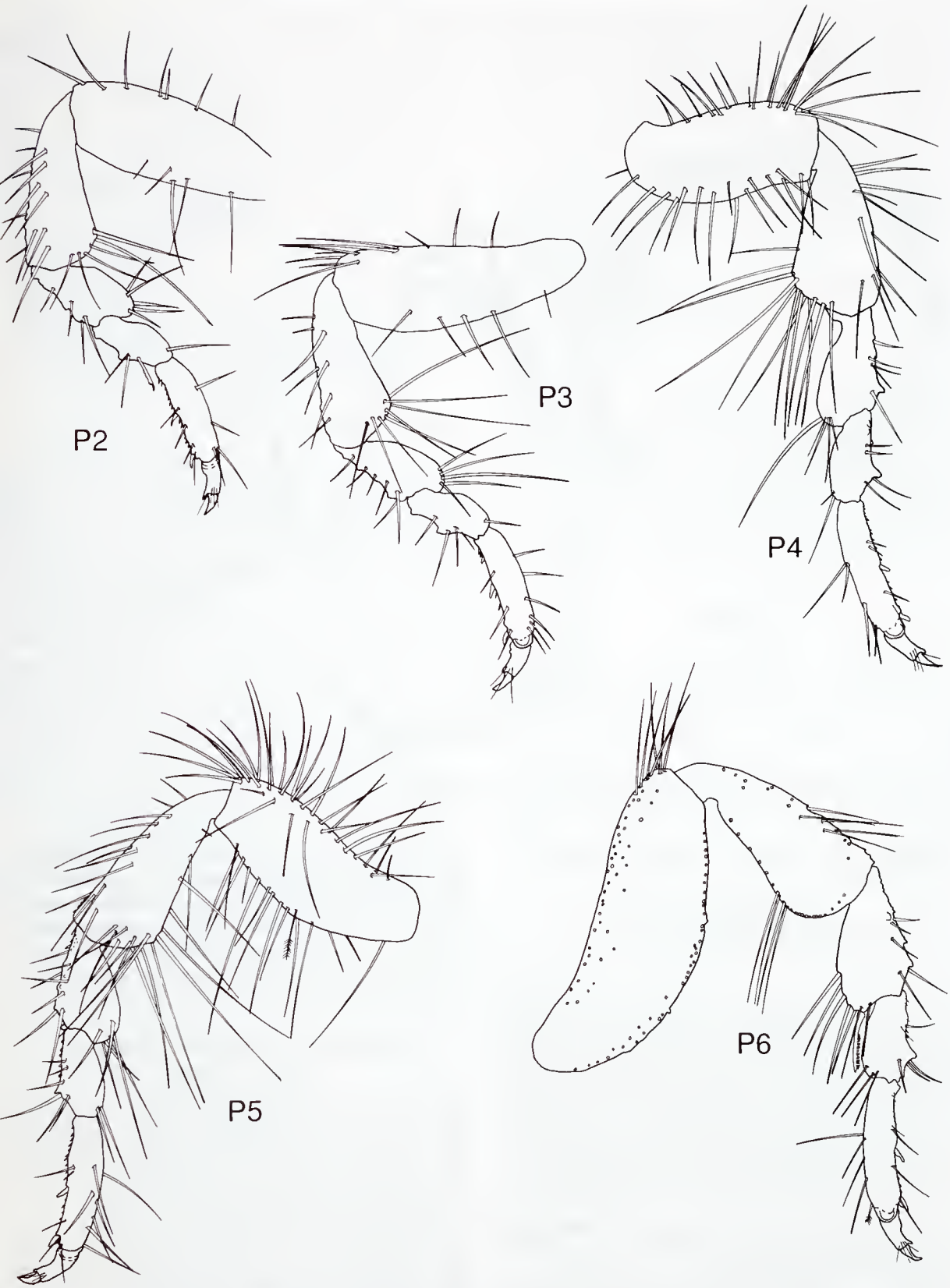

Figure 44. *Elaphognathia froygattella*. Holotype, NMV J27568.

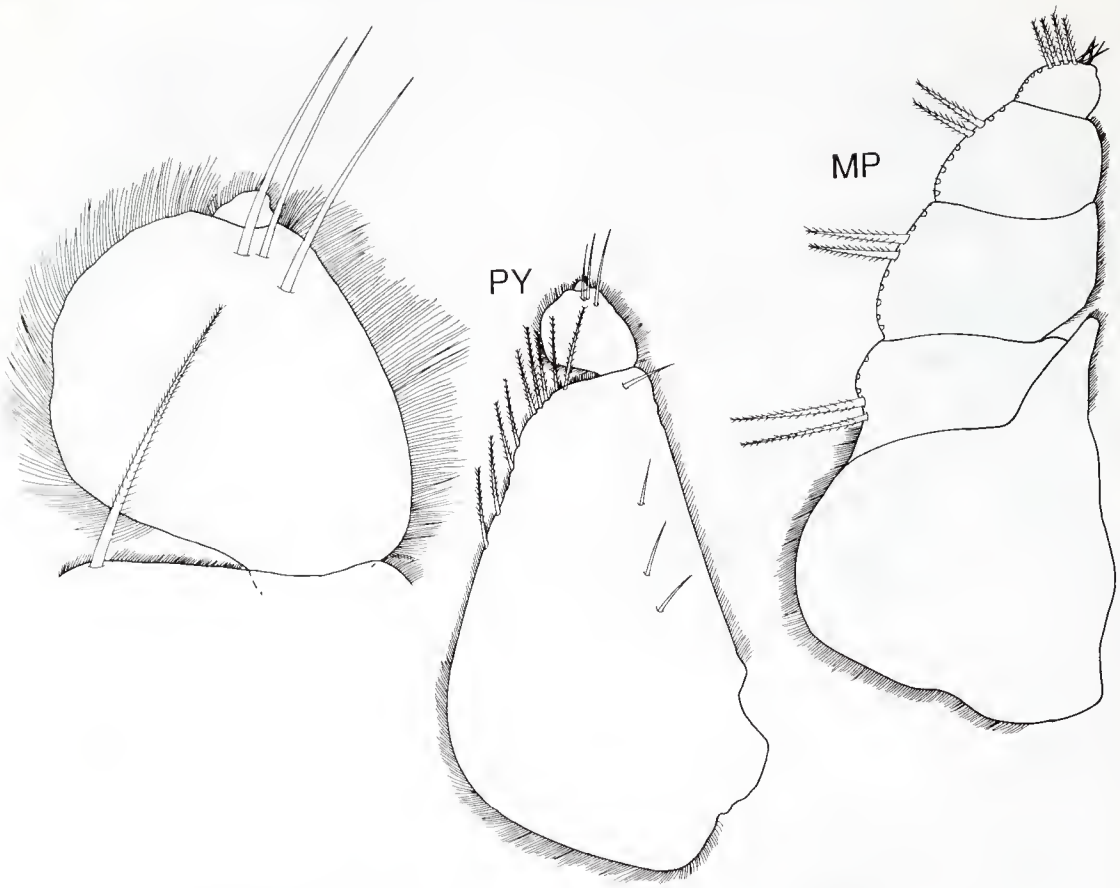

Figure 45. *Elaphognathia froygattella.* Holotype, NMV J27568.

monotypic genus is supported by the phylogenetic analysis.

Gibbagnathia gen. nov.

Type species. Gibbagnathia europalothrix sp. nov.

Diagnosis. Eyes present. Frontal border slightly produced. Mandibles simple, lacking distinct blade. Antenna 1 with stout peduncle. Mouthparts small; pylopod pediform and maxilliped of 2 articles. Pereon rectangular, with numerous setae and small granules; pereonite 3 with large anteriorly directed projection; pereonite 7 visible. Pleon wide, with prominent epimera.

Etymology. From *gibba* (Latin), meaning a hump, referring to the dorsal prominence on pereonite 3 and *Gnathia.*

Remarks. Gibbagnathia is a monotypic genus confined to Bass Strait, the only species being *G. europalothrix.* It is most easily distinguished from other Gnathiidae by the large anteriorly directed projection orginating dorsally from pereonite 3. *Gibbagnathia* and *Thaumastognathia* both have reduced maxillipeds and small, pediform pylopods but differ largely in the shape of the pereon and mandibles.

Gibbagnathia europalothrix sp. nov.

Figures 46, 47

Material examined. Holotype. Tasmania, eastern Bass Strait, 30 km N of North Point, Flinders I., (39°26.3′S, 147°48.7′E), 49 m, medium sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 17 Nov 1981 (stn BSS 173), NMV J8366 (1 male).

Paratypes. Tasmania, western Bass Strait, 48 km NNW of Cape Farewell, King I. (39°22′S, 143°28′E), 104 m, medium sand, carbonate, G.C.B. Poore on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 78), NMV J8369 (2). 47 km NW of Cape Farewell, King I. (39°20′S, 143°34′E), 95 m, coarse sand, carbonate, G.C.B. Poore

on HMAS *Kimbla*, 10 Oct 1980 (stn BSS 77), NMV J8368 (1 male). Central Bass Strait, 44 km NE of Cape Wickham, King I. (39°22.0'S, 144°18.3'E), 60 m, coarse sand, R.S. Wilson on RV *Tangaroa*, 23 Nov 1981 (stn BSS 203), NMV J8365 (1 male). Eastern Bass Strait, 30 km N of North Point, Flinders I., (39°26.3'S, 147°48.7'E), 49 m, medium sand, Smith-McIntyre grab, R.S. Wilson on RV *Tangaroa*, 17 Nov 1981 (stn BSS 173), NMV J8367 (1 male).

Victoria. Western Bass Strait, 30 km SSW of Warrnambool, (38°38.2'S, 142°35.0'E), 59 m, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 20 Nov 1981 (stn BSS 188), NMV J8370 (1 male). Eastern Bass Strait, 19.1 km W of Pt Ricardo (37°50.57'S, 148°25.02'E), 36 m, sand-shell, Smith-McIntyre grab, Marine Science Laboratories on FV *Sarda*, 26 Sep 1990 (stn MSL-EG 43), NMV J24633 (1 male).

Description. Total length of holotype: 2.03 mm.

Cephalosome rectangular, 2.4 times as wide as long, lateral margins straight. Cephalosome and anterior pereon covered with numerous setae. Eyes well developed, lateral and sessile, not easily visible dorsally. Frontal border slightly produced medianly, with 6 setae submarginally, in 2 clumps of 3. Lamina dentata visible, external scissura very shallow. Supraocular lobe not pronounced dorsally, raised in lateral view as distinct projection. Antennae stout, antenna 2 longer than antenna 1; flagellum of antenna 1 of 4 articles, with 3 aesthetascs, peduncle articles slightly rounded; flagellum of antenna 2 of 5 articles. Mandible located on median projection; close set, straight; half length of cephalosome; dorsoventrally flattened; thin and flexible in preserved specimens without obvious blade or features, raised in lateral view. Maxilliped very reduced, of 2 articles with 4 setae distally. Pylopod thin, elongate, 4-articled, all with seta, terminal article minute.

Pereon evenly sided, as wide as cephalosome, covered with numerous simple setae except for pereonite 5. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 2 slightly produced anterolaterally. Pereonite 3 with large, distinct anteriorly directed, bilobed projection partially overhanging pereonites 1 and 2. Pereonite 4 with narrow anterior constriction. Pereonite 6 posterior border deeply concave, with large extensions lateral to pleon. Pereonite 7 very narrow, overlapping pleon. Pleon wide except pleonite 1 which is constrained by pereonite 6; pleonite 2 three-quarters width of pereon; pleonites 3–5 decreasing in width posteriorly. Pleotelson subtriangular, wider than long, lateral margins sinuous with 1 pair of simple setae laterally and pair of setae on distal apex. Uropodal peduncle without setae; endopod twice as long as exopod, reaching beyond apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods with moderate cover of plumose and simple setae, plumose setae confined mainly to basis and ischium; pereopods 2 and 6, larger than pereopods 3–5, with setae scales on ischium.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes fused as 1 small papilla.

Distribution. Bass Strait, 36–104 m depth.

Remarks. G. europalothrix has similar mouthparts to species of *Thaumatognathia* but differs by possessing a rectangular pereon with a deeply concave posterior border, straight pleon with pronounced epimera and straight mandibles without a distinct blade. *G. europalothrix* is most easily identified by the very large anteriorly directed projection on pereonite 3.

Gnathia Leach

Gnathia Leach, 1814: 386, 402. — Monod, 1926: 326–329 (part) and numerous other authors.

Anceus Risso, 1816: 8 (type species: *Anceus forficularius* Risso, 1816).

Praniza Latreille, 1817: 54 (type species: *Oniscus marinus* Slabber, 1778).

Zuphea Risso, 1826: 104 (type species: *Zuphea spariicola* Risso, 1826).

Gnathia (*Gnathia*) s.s. — Monod, 1926: 329 (part).

Gnathia (*Perignathia*). — Monod, 1926: 554–555 (not *Perignathia* Monod, 1922).

Type species. Gnathia termitoides Leach, 1814 (= *Cancer maxillaris* Montagu, 1804) (monotypy)

Diagnosis. Eyes usually present. Frontal margin of cephalon generally transverse, with frontal processes. Mandibles usually with dentate mandibular blade and mandibular incisor. Cephalon may possess paraocular ornamentation and/or a dorsal sulcus. Pereonite 1 immersed in cephalon. Pylopod 2- or 3-articled; opereulate, article 1 enlarged, generally with dense external margin of plumose setae; article 3 small or absent.

Remarks. The genera *Anceus*, *Praniza*, and *Zuphea*, are all based on European gnathiid larval stages whose specific identities are impossible to confirm (Monod, 1926). They have therefore traditionally been treated as junior

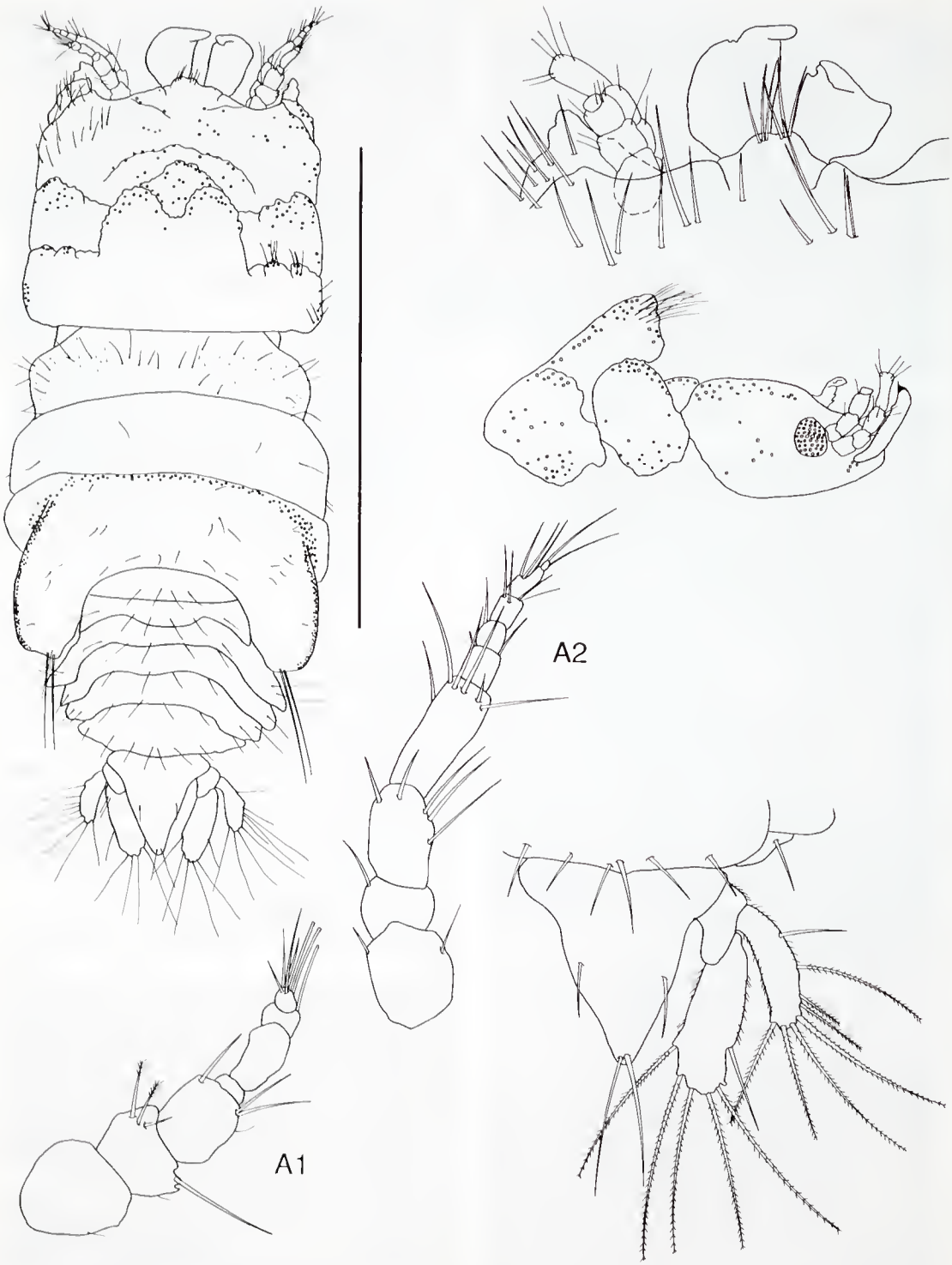

Figure 46. *Gibbagnathia europalothrix*. Holotype, NMV J8366.

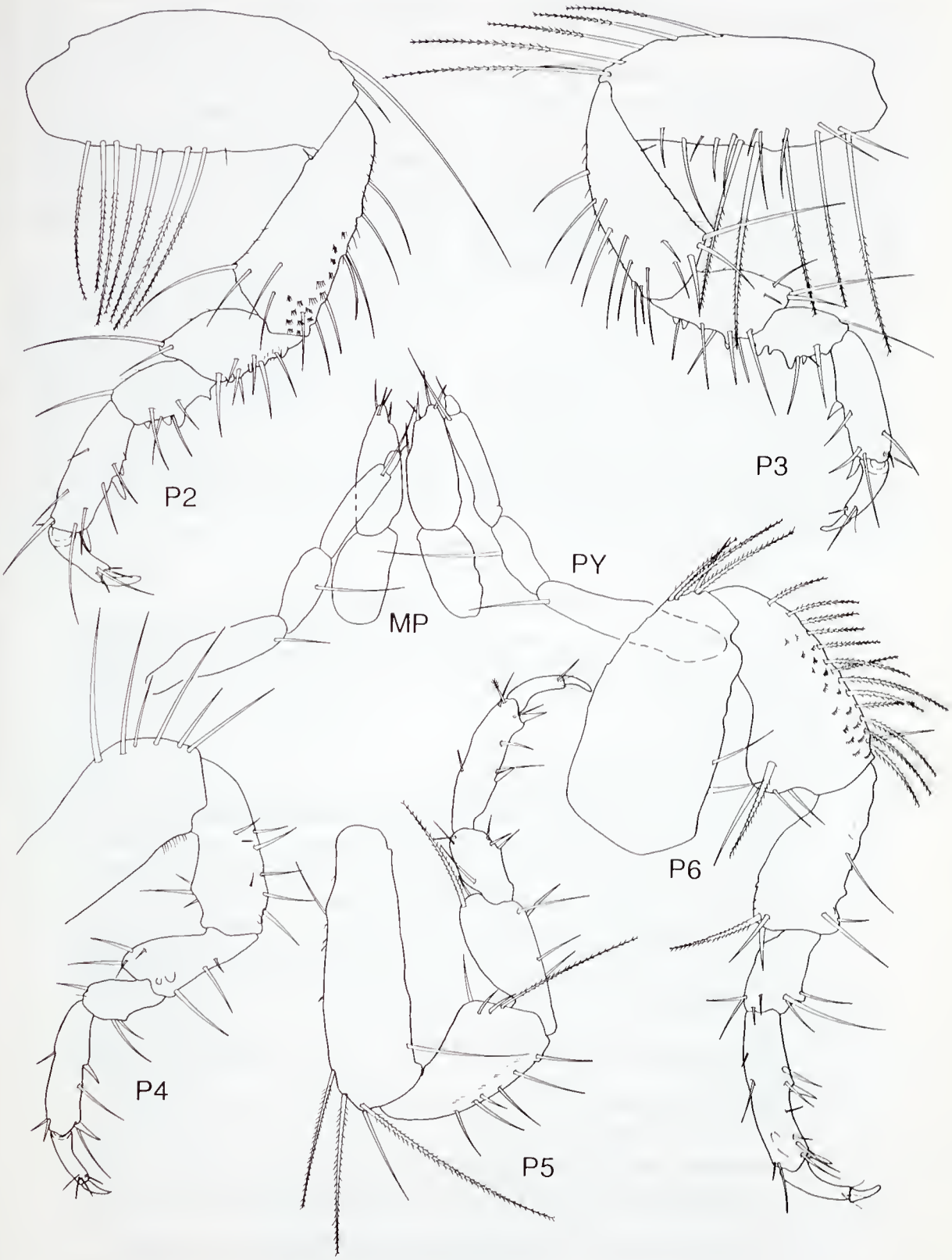

Figure 47. *Gibbagnathia europalothrix*. Holotype, NMV J8366.

synonyms of *Gnathia* and, in the case of *Praniza*, as the name for the larval stage of all gnathiids.

Our concept of *Gnathia* is narrower than that of Monod (1926). A fifth generic name treated as a junior synonym by him, *Caecognathia* Dollfus, 1901, is herein revived for a monophyletic group of species once placed in *Gnathia* but now considered the sister taxon of *Gnathia* + *Elaphognathia*. Wägele (1987) proposed that *Heterognathia* Amar and Roman, 1974 is a junior synonym of *Gnathia* but with the restriction of the generic concept it becomes a junior synonym of *Caecognathia* instead.

Elaphognathia Monod, 1926, hitherto a subgenus, is elevated to generic rank.

Perignathia Monod, 1922 is problematical name. It was erected as a genus for *Anceus abyssorum* Sars, a species we believe to be a member of *Caecognathia* Dollfus and could therefore be its junior synonym. Later, Monod (1926) admitted that the material on which he based his generic diagnosis was not Sars' species and he reidentified it as *Gnathia fallax* Monod, 1926, a member of *Gnathia* s.s. The type species is therefore subject to dispute and can only be decided by reference to the ICZN. As long as the name is viewed as a junior synonym its type species is of little consequence. Monod (1926) further complicated the issue by excluding both potential type species from *Perignathia* and using it as a subgeneric name for another, *Gnathia triospathiona* Boone, 1918. If this species were to warrant generic or subgeneric status it would require a new generic name but our analysis suggests that this is not so.

Gnathia is the largest genus in the family whose species are recognised by the possession of a broad 2- or 3-articled pylopod, presence of frontal processes, a straight frontal border, and non-elongate mandibles with dentate blade. We are unable to find a unifying synapomorphy of *Gnathia* but treat it as a paraphyletic taxon formed by the exclusion of species of the monophyletic *Elaphognathia* from a larger clade. Eleven species from Australia have already been described (see Table 5) and are briefly figured (see fig. 2).

Key to males of species of *Gnathia* from Australia

1. Cephalon with a very large tubercle in anterior midline and 2 smaller tubercles near base of the mandibles. Paraocular ornamentation a single tubercle anterior to oblique ridge of 3 small tubercles ..... *G. mulieraria*

— Cephalon not so 2

2. Penes fused and produced 3

— Penes not fused and produced 4

3. Penes very large, directed posteriorly; mediofrontal process sharply conical; pylopod 2-articled with 3 areolae on article 1 ..... *G. falcipenis*

— Penes small, directed anteriorly; mediofrontal process rounded with 2 setae each side; pylopod 3-articled, with 2 areolae ..... *G. epopostruma*

4. Dorsum dived by shallow grooves marked by lines of chromatophores; paraocular ornamentation as a mediolateral ridge, eyes overhanging in lateral view ..... *G. cornuta*

— Cephalon not so 5

5. Pleopods unequal, anterior pair naked, 2–3 times the size of the 3 setose posterior pairs ..... *G. variobranchia*

— Pleopods subequal 6

6. Paraocular ornamentation present 7

— Paraocular ornamentation absent 13

7. Pylopod lacking internal margin of plumose setae, length greater than twice width 8

— Pylopod with internal margin of plumose setae, length about twice the width 9

8. Superior frontolateral process large and circular, lacking setae; mandibular blade slightly crenulate ..... *G. prolasius*

— Superior frontolateral processes small and conical, with many setae; mandibular blade smooth ..... *G. stigmacros*

9. Inferior frontal border relatively straight, crenulate ..... *G. meticola*

— Frontal border with mediofrontal process 10

10. Paraocular ornamentation extremely pronounced, particularly in lateral view; frontal border produced; maxillipedal endite narrow . *G. notostigma*

— Paraocular ornamentation not extremely produced; frontal border at most only slightly produced; maxillipedal endite broad 11

11. Mandibles slightly asymmetrical, lacking incisor, less than half length of cephalon; mediofrontal process superior; pereon without anterior constriction on peronite 4 ..... *G. calamitosa*

— Mandibles symmetrical, with incisors, greater than half length of cephalon; mediofrontal process inferior; pereon with anterior constriction on peronite 4 12

12. Cephalon and anterior pereon with granules; mandibles with pseudoblade; pylopod with areolae; mediofrontal process conical with many notches on lateral margins ..... *G. campontus*

— Cephalon and pereon without granules; mandibles lacking pseudoblade; pylopod with areolae; mediofrontal process truncate; dorsal sulcus on peronite 5 ..... *G. biorbis*

13. Mandibles without incisors 14

— Mandibles with incisors 17

14. Frontal border produced 15

— Frontal border not produced 16

15. Mandibles with dorsal lobe; frontal border lacking setae . *G. rhytidoponera*

— Mandibles without dorsal lobe; frontal border with 8–9 setae in row, each side of mediofrontal process ..... *G. halei*

16. Peronite 1 not visible; mandibles inflected upwards at 90°; mediofrontal process bifid; sparsely setose ..... *G. mystrium*

— Peronite 1 visible; mandibles not inflected; mediofrontal process trifid; heavily setose ..... *G. iridomyrmex*

17. Mediofrontal border smooth ..... *G. asperifrons*

— Mediofrontal border of cephalosome, between mandibles, markedly toothed or notched 18

18. Mediofrontal process trifid, half length of superior frontolateral process ..... *G. calmani*

— Mediofrontal process a single projection, as long as superior frontolateral processes 19

19. Mandible with mandibular seta, lacking pseudoblade; pleopods without setae; dorsally setose; pereon without granules; cephalon rectangular ..... *G. odontomachus*

— Mandible lacking mandibular seta, with pseudoblade; pleopods setose; not dorsally setose; cephalon and anterior pereon with granules; cephalon quadrate ..... *G. latidens*

Gnathia camponotus sp. nov.

Figures 48–50

Material examined. Holotype. Tasmania, eastern Bass Strait, 100 km NE of North Point, Flinders I. (38°52.6′S, 148°25.2′E), 130 m, fine sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 15 Nov 1981 (stn BSS 170), NMV J27566 (1 male).

Paratypes. Type locality, NMV J8322 (20 males). 37 km NNE of Eddystone Point (40°40.7′S, 148°36.9′E), 67 m, muddy sand, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 14 Nov 1981 (stn BSS 164), NMV J8327 (3 males). 70 km ENE of North Point, Flinders I. (39°28.4′S, 148°41.8′E), 110 m, coarse sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 28 Mar 1979 (stn BSS 35), NMV J8331 (1).

Victoria, eastern Bass Strait, 43 km SE of Port Albert (38°53.7′S, 147°06.5′E), 58 m, coarse shell, Smith-McIntyre grab, R.S. Wilson on RV *Tangaroa*, 18 Nov 1981 (stn BSS 177), NMV J8323 (3). 50 km SE of Port Albert (38°54.3′S, 147°13.4′E), 58 m, coarse shell, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 18 Nov 1981 (stn BSS 176), NMV J8330 (3). 40 km SSW of Lakes Entrance (38°18.0′S, 147°37.0′E), 55 m, muddy fine shell, WHOI epibenthic sled, M.F. Gomon and R.S. Wilson on FV *Silver Gull*, 31 Jul 1983 (stn BSS 209), NMV J8328 (3).

Other material. Bass Strait, 44–115 m, NMV J8325 (1); NMV J8324 (7); NMV J8332 (4), NMV J8329 (2); NMV J8326 (2).

Description. Total length of holotype: 3.36 mm.

Cephalosome quadrate, lateral margins convex. Numerous very fine granules on cephalosome and anterior pereon. Eyes well developed, lateral and sessile. Frontal border transverse; mediofrontal process inferior, conical with marked notches and 2 long setae laterally; superior frontolateral process smoothly conical, half length of mediofrontal process. Lamina dentata visible. External scissura very shallow. Supraocular lobe not pronounced, ventral accessory supraocular less rounded. Cephalosome with broad dorsal sulcus; paraocular tubercles and setae; with small posterior median tubercle at base of sulcus; with translucent elliptical region anteromedianly, above buccal cavity. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 2 aesthetases; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; with unarmed carina; slight mandibular incisor halfway along; ventral dentate blade on distally half, with smooth pseudoblade dorsally; internal lobe on proximal half a long crenulate lamina; basal neck short. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 areolae along internal margin, with 13 setae distally on ventral surface and along external margin; article 2 with 4 setae distally on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 dorsally reaching lateral margins, divided into 3 regions by posterior margin of cephalosome and partially obscured laterally by pereonite 2 and cephalon. Pereonites 2 and 3 subequal; 4 with anterior constriction; 5 and 6 together longer than others together. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively narrower after pleonite 2, pleonal epimera prominent on pleonites 4 and 5. Pleotelson subtriangular, as wide as long, with 2 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 3 setae; rami subequal, reaching apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods of typical gnathiid form with few simple setae.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

Distribution. Bass Strait, 55–130 m depth.

Remarks. This species most closely resembles *G. latidens* (Beddard) from north-eastern Australia. These two species are characterised by an inferior conical mediofrontal process which is wider than long and a smaller superior frontolateral processes.

G. camponotus differs from *G. latidens* in possessing a regularly notched mediofrontal process, a small tubercle on the posterior cephalon and paraocular ornamentation.

Gnathia epopostruma sp. nov.

Figures 51–53

Material examined. Holotype. Victoria, western Bass Strait, 44 km SW of Cape Otway (39°06.3′S, 142°55.6′E), 81 m, medium sand, R.S. Wilson et al. on RV *Tangaroa*, 21 Nov 1981 (stn BSS 192), NMV J8373 (1 male).

Description. Total length of holotype: 3.83 mm.

Specimen damaged, missing left mandible and slightly deformed. Cephalosome quadrate, lateral margins straight. Eyes well developed, lateral and sessile. Frontal border produced; mediofrontal process superior, rounded with 2 setae laterally; superior frontolateral process conical, with 4–5 setae on external margin. External scissura very shallow. Supraocular lobe

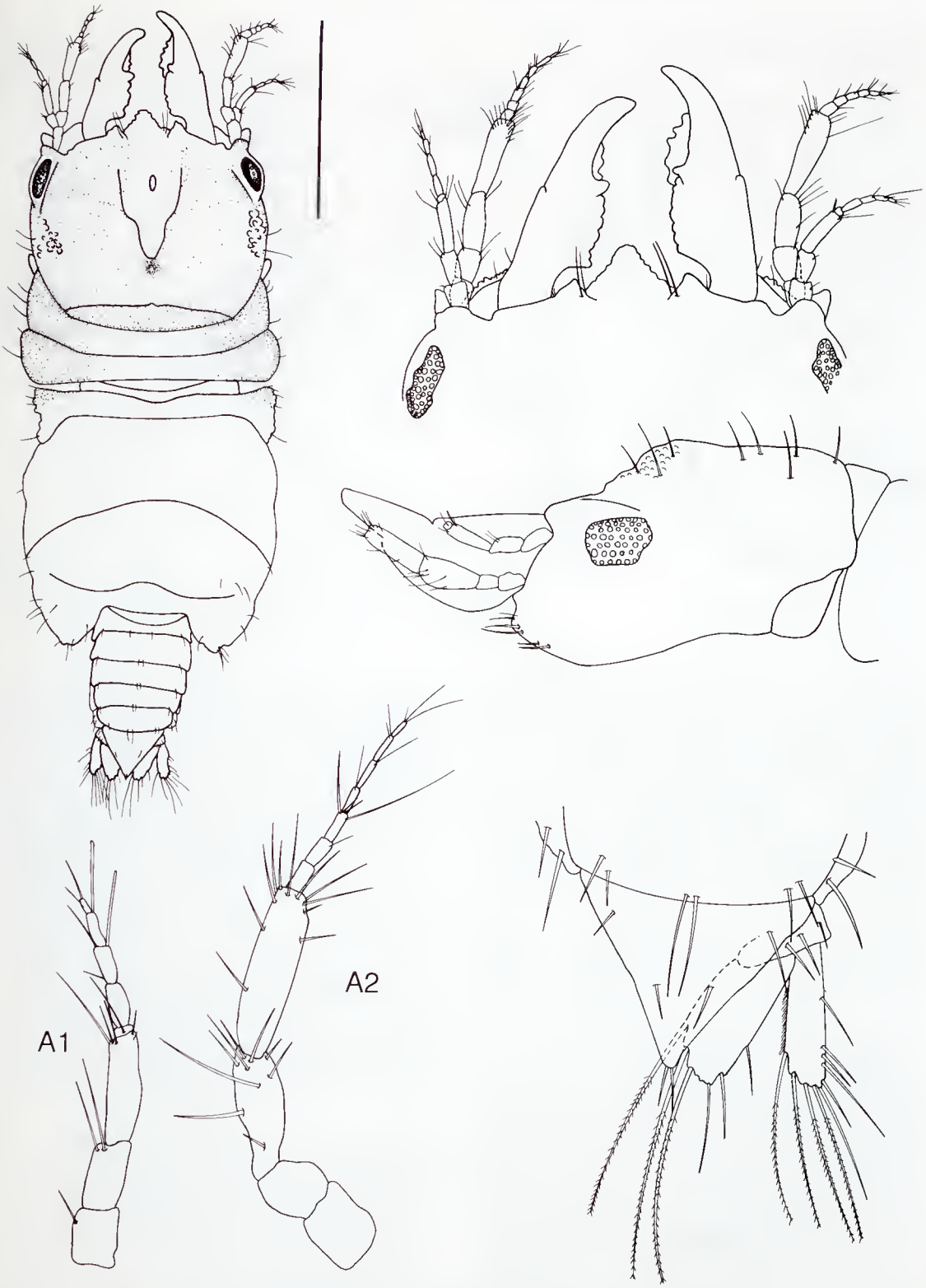

Figure 48. *Gnathia camponotus*. Holotype, NMV J27566.

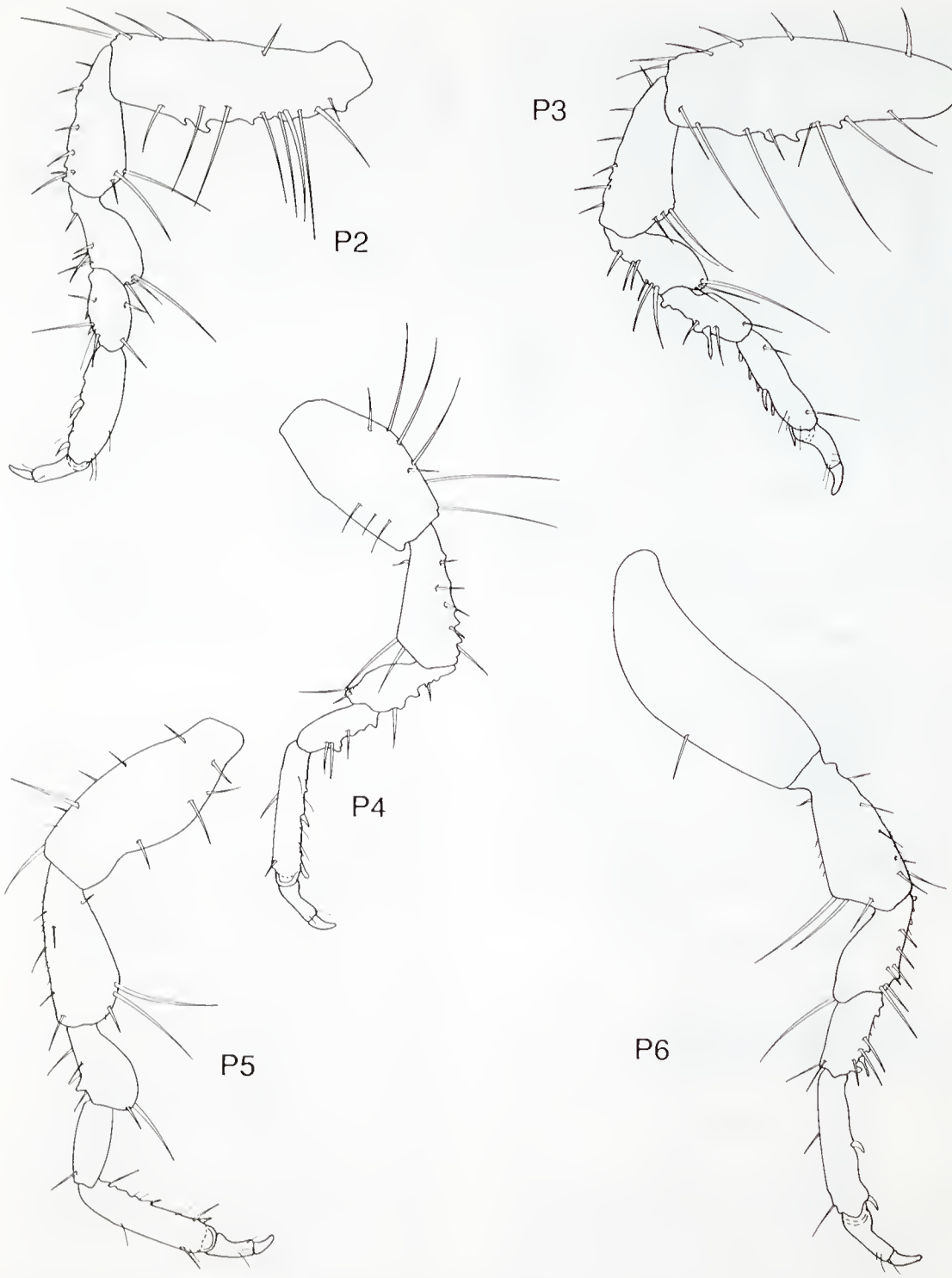

Figure 49. *Gnathia camponotus*. Holotype, NMV J27566.

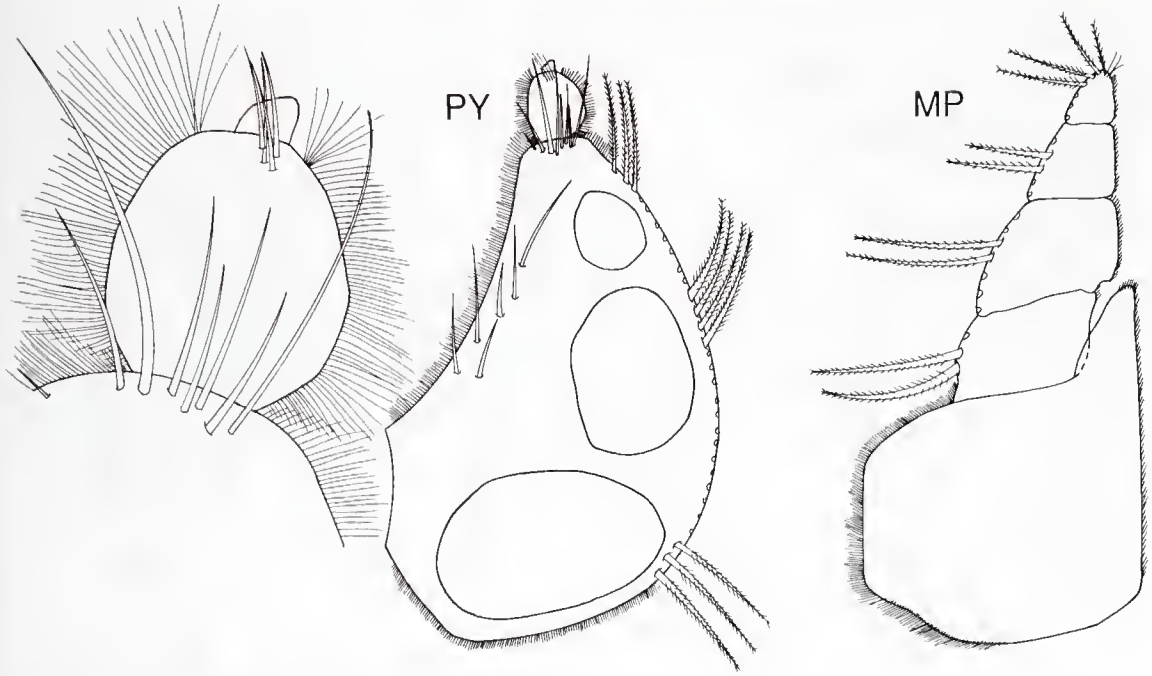

Figure 50. *Gnathia camponotus*. Holotype, NMV J27566.

not pronounced. Cephalosome with short, broad dorsal sulcus; crenulate paraocular ridge partially obscuring eyes. Antennae normal; antenna 2 twice as long as antenna 1; flagellum of antenna 1 of 5 articles, with 1 aesthetasc; flagellum of antenna 2 of 7 articles. Mandible raised distally, subequal to length of cephalosome; with long, acute apex, one-third length of mandible; unarmed carina and lacking incisor; seta at midpoint; with crenulate blade in middle third; proximally with internal lobe a crenulate lamina; basal neck obvious. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; maxilliped endite clearly reaching article 3, narrow. Pylopod 3-articled, internal margin of plumose setae; article 1 with 2 small areolae and 8 setae on ventral surface, 6 distally; article 2 with 8 setae on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome; covered with numerous simple setae. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 2 and 3 subequal; pereonite 4 with anterior constriction; pereonite 6 longest. Pereonite 7 very narrow, overlapping pleon. Pleonites subequal, pleonal epimera prominent. Pleotelson subtriangular, as wide as long, lateral margins sinuous; with 3 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 4 setae; rami subequal, reaching beyond apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods subequal, with moderate cover of simple setae; pereopod 2 with 1 posterior pectinate seta on carpus; posterior margin of merus of pereopods 5 and 6 with row of short, fine setae.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes prominent, present as 2 large papillae.

Distribution. Western Bass Strait, 81 m depth.

Remarks. Gnathia epopostruma is most similar to *G. falcipenis* Holdich and Harrison. Both species possess a trifid, produced frontal border; raised paraocular ornamentation and similarly proportioned cephalon and pereon. *G. epopostruma* differs in having a rounded, not sharply conical mediofrontal process; a more hirsute habitus; paraocular ornamentation which overhangs the eyes; and smaller, though still enlarged, anteriorly directed penes. The penes of *G. falcipensis* are posteriorly directed.

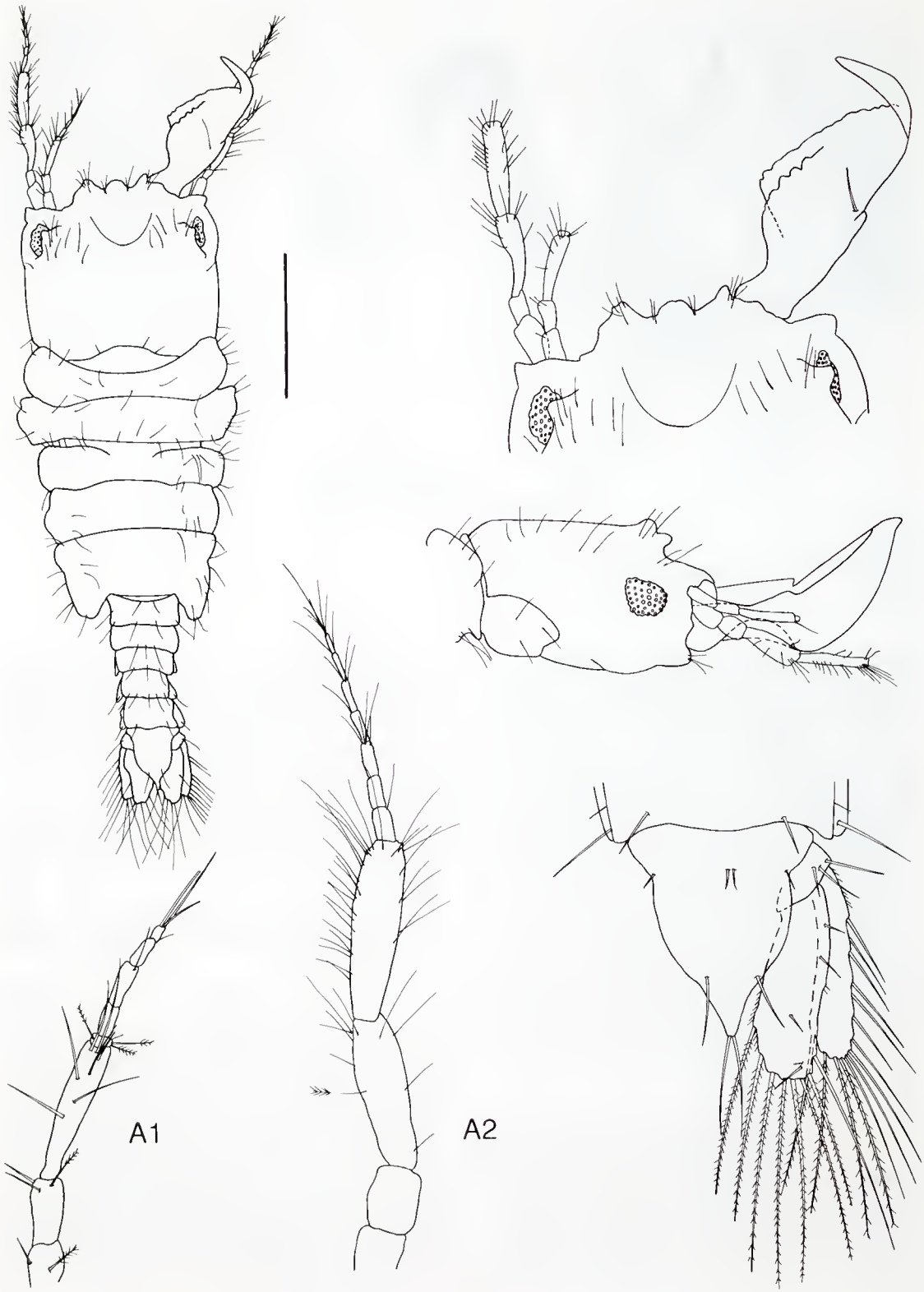

Figure 51. *Gnathia epopostruma.* Holotype, NMV J8373.

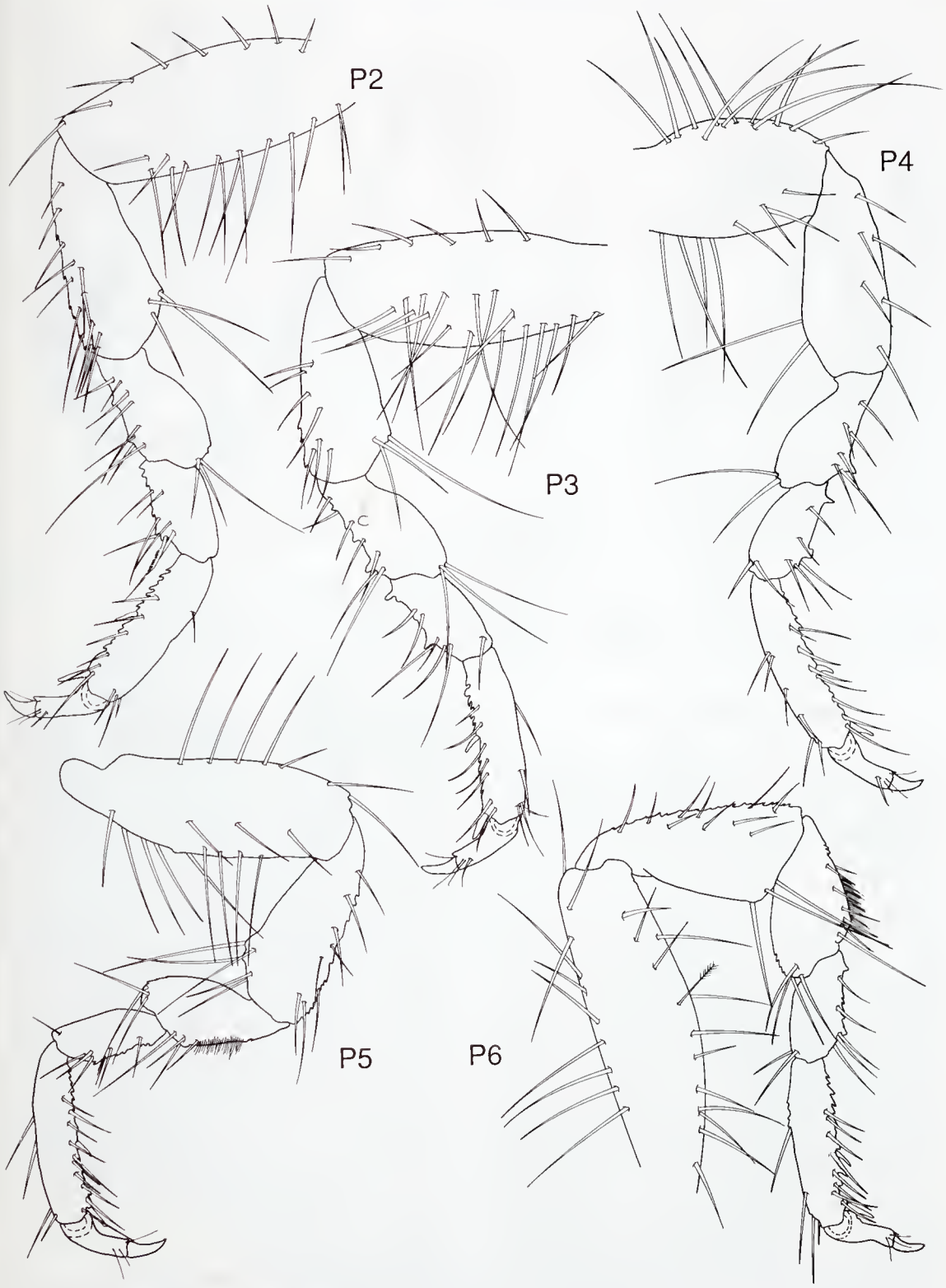

Figure 52. *Gnathia epopostruma*. Holotype, NMV J8373.

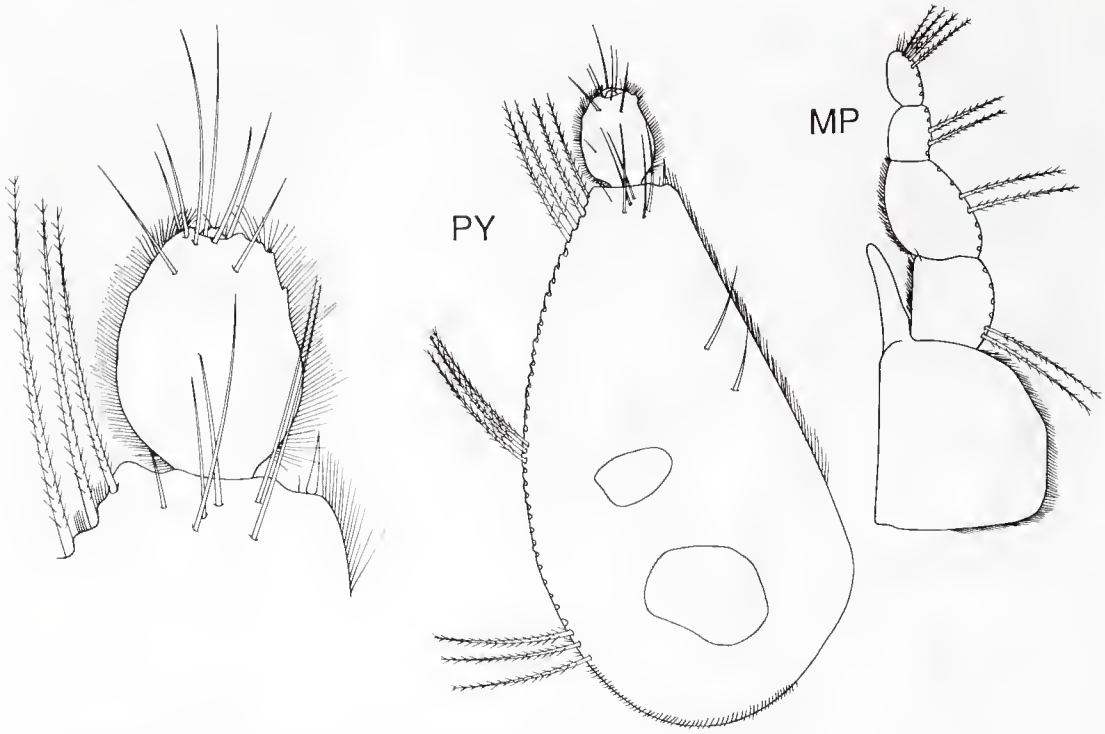

Figure 53. *Gnathia epopostruma*. Holotype, NMV J8373.

Gnathia iridomyrmex sp. nov.

Figures 54–56

Material examined. Holotype. Victoria, Saxon Reef, Portland (38°18.5′S, 141°38.5′E), 11 m, red coralline alga turf, SCUBA airlift, R.S. Wilson, 5 Mar 1992 (stn CRUST 178), NMV J27572 (1 male).

Description. Total length of holotype: 2.52 mm.

Preserved specimen dark brown. Cephalosome rectangular, 1.15 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border transverse. Mediofrontal process inferior, broad, trifid. Superior frontolateral process acute, directed anterolaterally, twice length of mediofrontal process with 4 setae evenly spaced on internal margin. External scissura rounded. Supraocular lobe not pronounced. Cephalosome with small dorsal sulcus; translucent elliptical region anteromedial above buccal cavity. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetases, distal peduncle article longer than 2 proximal articles; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; with unarmed carina; without incisura; seta at midpoint, irregularly crenulate blade on proximal two-thirds with short basal neck. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 areolae and 3 setae on ventral surface distally; article 2 with 4 setae on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome; covered with numerous plumose setae. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 2 and 3 subequal; pereonite 4 narrower than others, with anterior constriction; pereonite 5 and 6 longest. Pereonite 7 very narrow, overlapping pleon. Pleonite 5 shorter than others, pleonal epimera prominent. Pleotelson subtriangular, as wide as long; lateral margins sinuous; with 3 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 2 setae; rami subequal, reaching beyond apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods subequal, with moderate cover of simple setae and crenulate anterior margin of

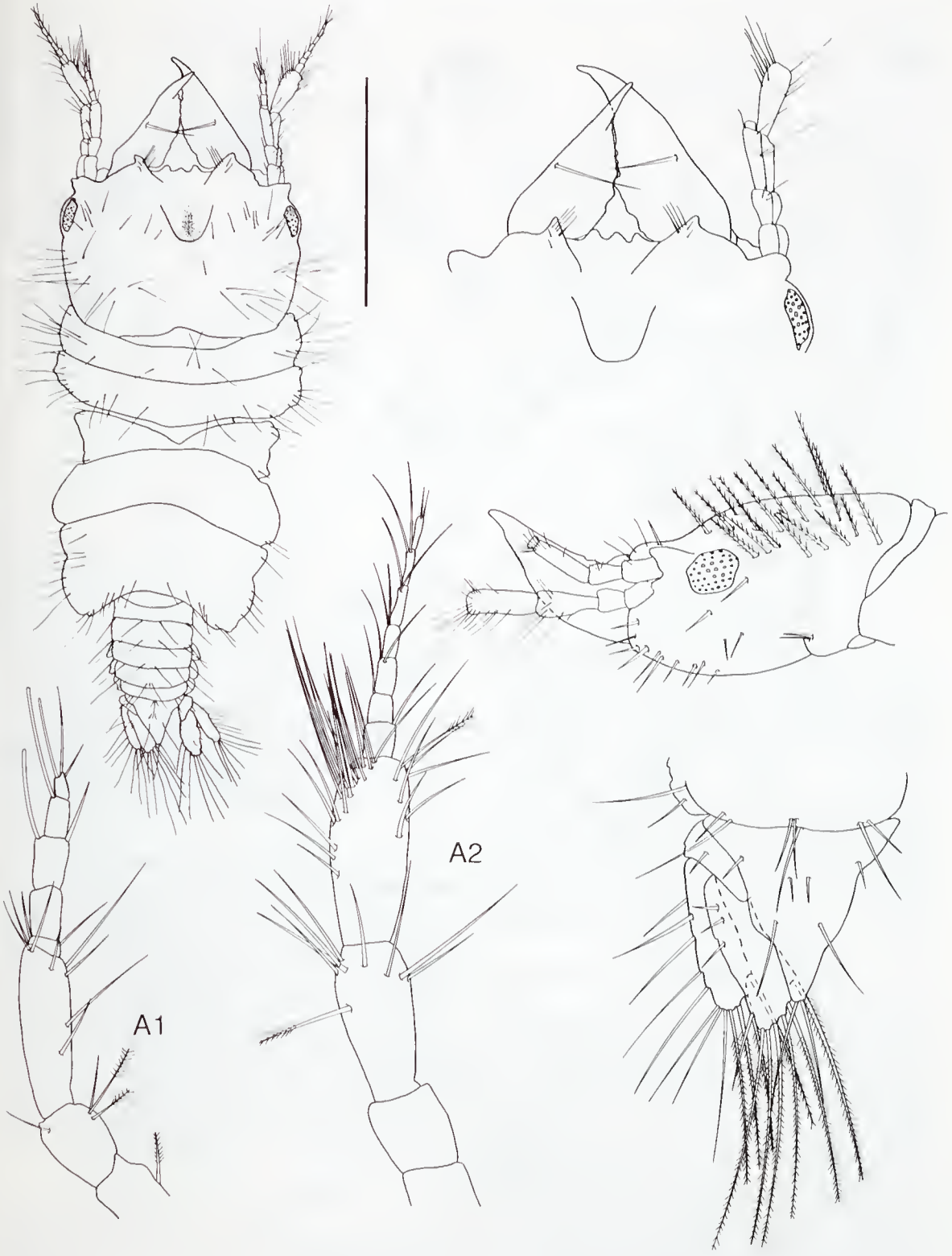

Figure 54. *Gnathia iridomyrmex*. Holotype, NMV J27572.

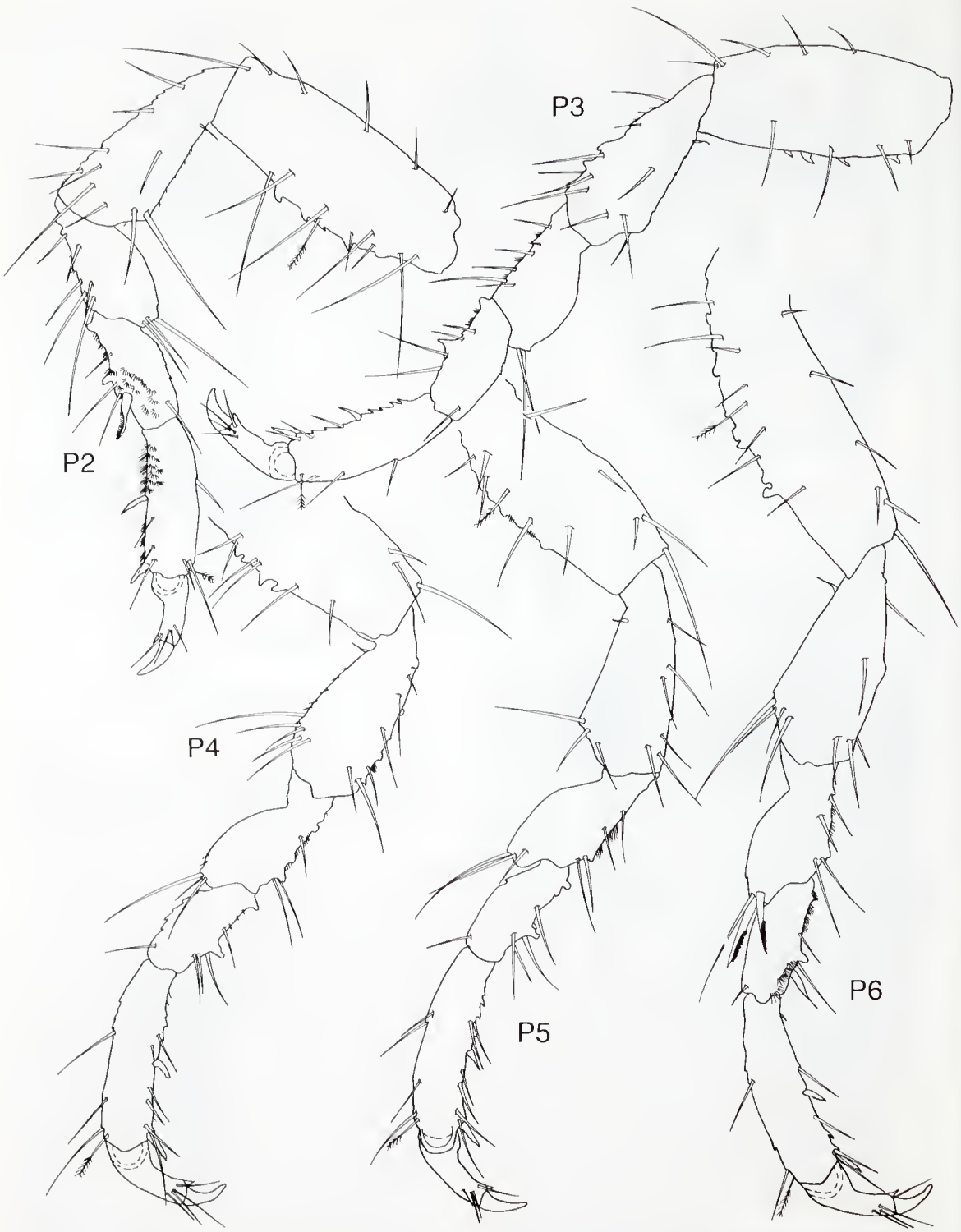

Figure 55. *Gnathia iridomyrmex*. Holotype, NMV J27572.

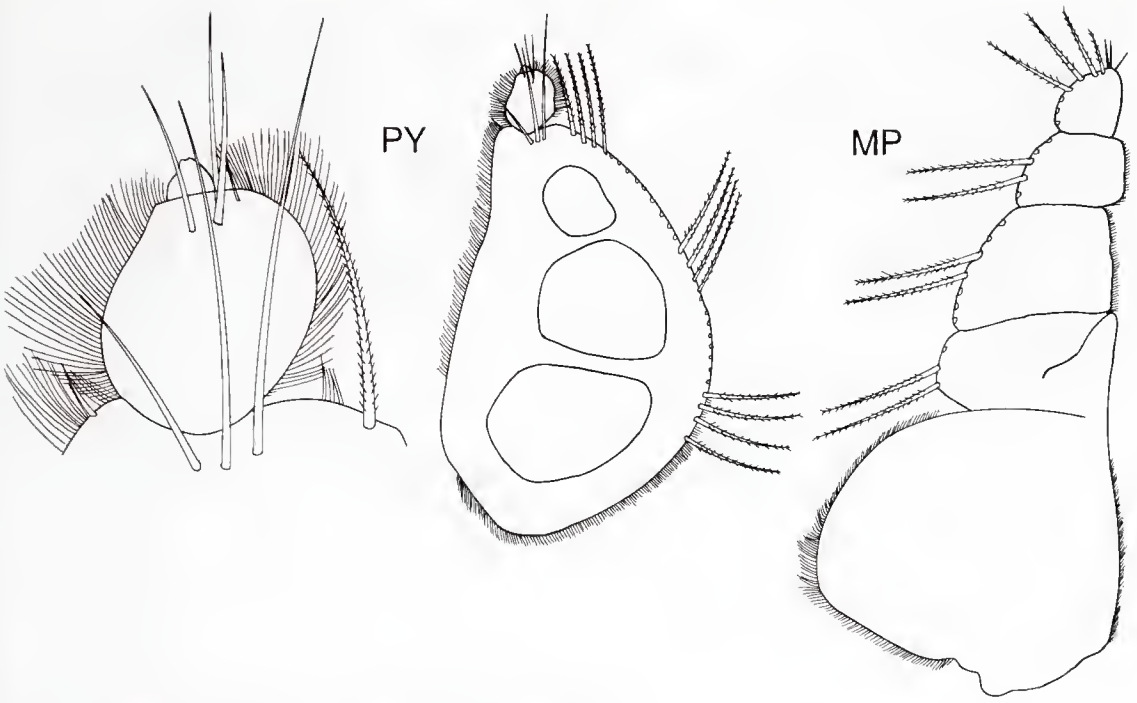

Figure 56. *Gnathia iridomyrmex*. Holotype, NMV J27572.

basis; pereopod 6 with 2 anterior pectinate setae on merus; pereopods 2 and 6 with 1 posterior seta on carpus.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

Distribution. Western Victoria, rocky substrate, 11 m depth.

Remarks. Gnathia iridomyrmex most closely resembles *G. calmani* Monod in the shape of the mediofrontal process, though in *G. iridomyrmex* the mediofrontal process is broader (half the width of the cephalon versus one-third the width). *G. iridomyrmex* also differs in being hirsute; lacking mandibular incisors, the posterior tubercle on the cephalon and anterolateral lobes on pereonite 4. *G. iridomyrmex* is also similar to *G. odontomachus* but differs in possessing a trifid mediofrontal process, more pronounced superior frontolateral processes and a simpler mandibular blade.

Gnathia mystrium sp. nov.

Figures 57–59

Material examined. Holotype. Tasmania, western Bass Strait, 36 km SSW of Stokes Point, King I. (40°26.7′S, 143°41.4′E), 85 m, medium sand, R.S. Wilson on RV *Tangaroa*, 22 Nov 1981 (stn BSS 198), NMV J27564 (1 male).

Paratypes. All collected by R.S. Wilson on RV *Tangaroa*, Nov 1981. Western Bass Strait, type locality, NMV J8352 (1). 20 km SSW of Stokes Point, King I. (40°19.5′S, 143°48.8′E), 71 m, sandy shell (stn BSS 199), NMV J8351 (1).

Eastern Bass Strait, 25 km NE of Deal I., Tasmania (39°14.8′S, 147°31.5′E), 57 m, medium sand (stn BSS 174), NMV J8353 (1). 100 km NE of North Point, Flinders I. (38°52.6′S, 148°25.2′E), 130 m, fine sand (stn BSS 170), NMV J8354 (1). 37 km NNE of Eddystone Point (40°40.7′S, 148°36.9′E), 67 m, muddy sand (stn BSS 164), NMV J8350 (1).

Description. Total length of holotype: 3.07 mm.

Cephalosome quadrate, large, one-third length of animal, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border slightly produced; mediofrontal process inferior, broad with bifid projection; superior frontolateral process conical, with 3 setae on internal margin. Inferior frontolateral process conical, ventral to superior frontolateral process. External scissura very shallow. Supraocular lobe very low, acute. Cephalosome with broad dorsal sulcus; paraocular tubercles and setae; translucent elliptical region anteromedially, above buccal cavity. Antenna 2 longer than

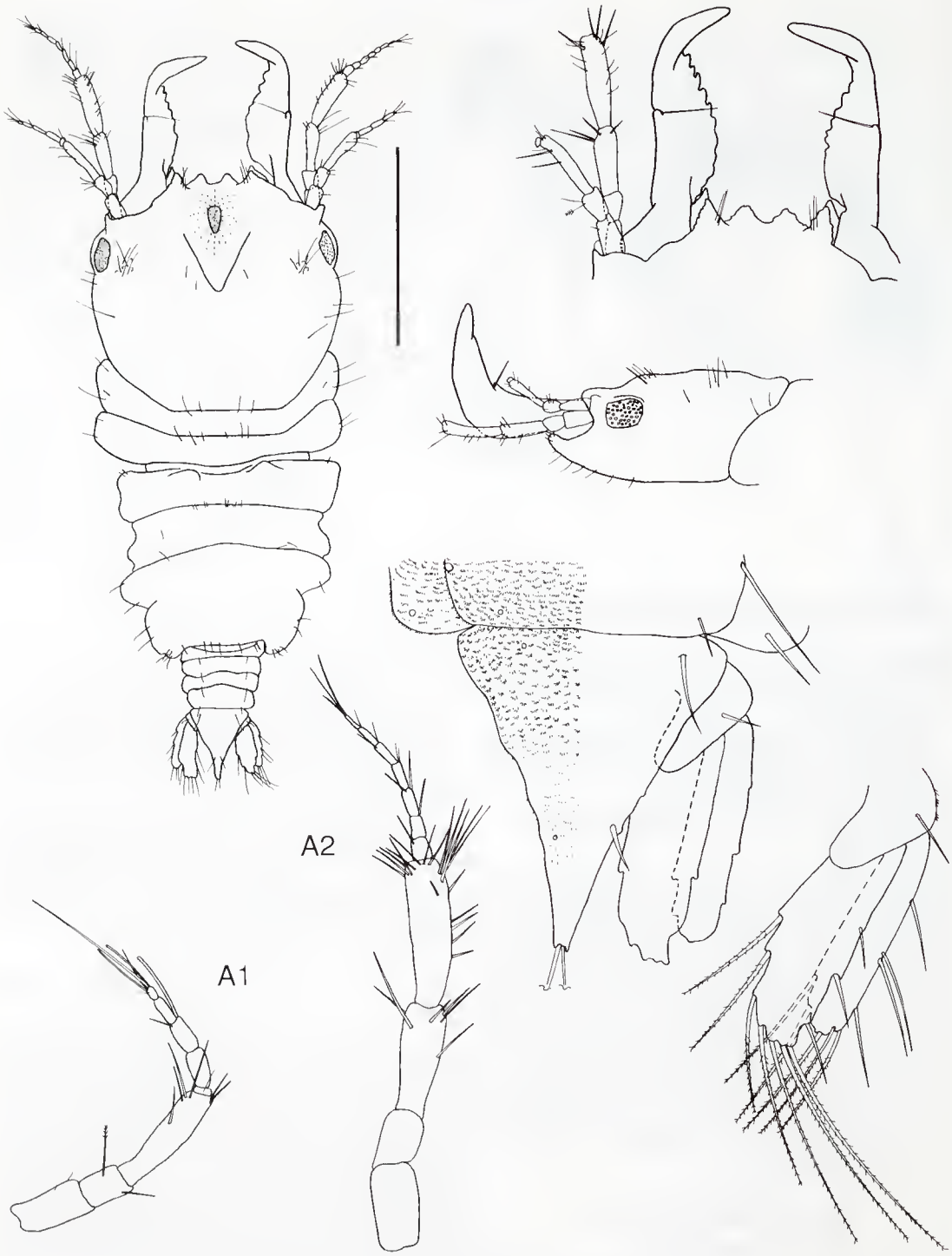

Figure 57. *Gnathia mystrium*. Holotype, NMV J27564.

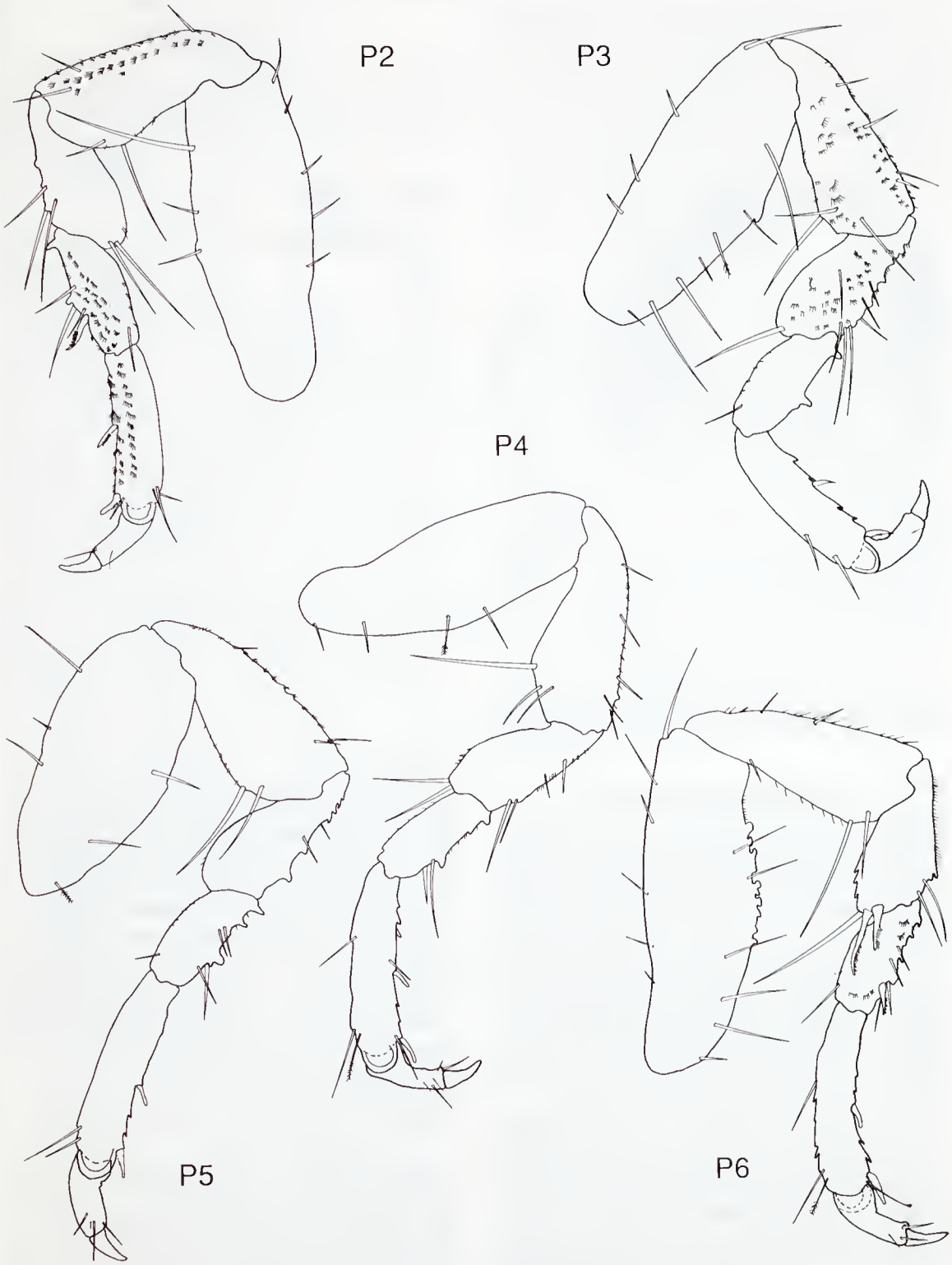

Figure 58. *Gnathia mystrium*. Holotype, NMV J27564.

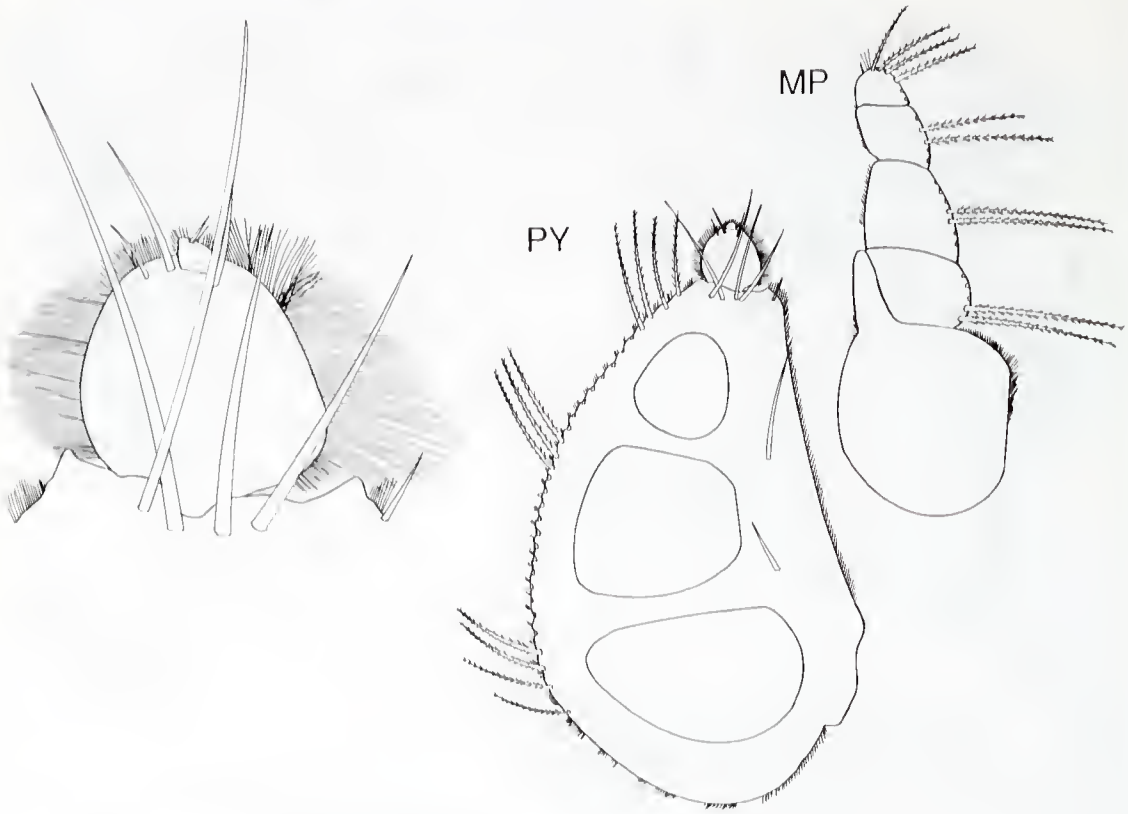

Figure 59. *Gnathia mystrium*. Holotype, NMV J27564.

antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetases; flagellum of antenna 2 of 7 articles. Mandible long, two-thirds length of cephalosome; apex inflexed, distally raised in lateral view at 90°; with unarmed carina; slight mandibular incisor half way along; crenulate blade distally as far as cylindrical apex; seta at midpoint; crisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3, narrow. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 areolae and 6 setae on ventral surface, 4 distally; article 2 with 3 setae on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome, margins with numerous setae. Pereonite 1 dorsally fused with cephalosome, not visible. Pereonites 2 and 3 subequal. Pereonite 4 with anterior constriction and 2 anterior lobes. Pereonite 6 long, at least twice as long as other pleonites. Pereonite 7 very narrow, overlapping pleon. Pleon with only 4 segments visible dorsally, other pleonite obscured by pereon; epimera not visible dorsally. Pleotelson subtriangular, longer than wide; lateral margins straight; with 2 pairs of simple setae laterally and pair of setae on distal apex. Uropodal peduncle with 1 seta; rami subequal, reaching apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods with few simple setae; pereopod 6 with 2 anterior spines on merus and crenulate anterior margin of basis; pereopod 2 and pereopod 6 with posterior spiniform seta on carpus.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

Distribution. Bass Strait, 57–130 m depth.

Remarks. *Gnathia mystrium* is characterised by a bifid mediofrontal process and the presence of both superior and inferior lateral processes. The cephalosome is very large, one-third the length of the whole animal. The mandibles are long and dorsally inflected and pereonite 1 is indistinguishable.

Gnathia notostigma sp. nov.

Figures 60–62

Material examined. Holotype. Victoria, S of Point Hicks (38°14.80′S, 149°9.30′E), 200 m, coarse sand, gravel, WHOI epibenthic sled, M.F. Gomon et al. on ORV *Franklin*, 24 Jul 1986 (stn SLOPE 41), NMV J27574 (1 male).

Paratype. Type locality, NMV J19121 (1 male).

Description. Total length of holotype: 4.75 mm.

Cephalosome rectangular, 1.25 times as wide as long, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border produced; mediofrontal process broad with bifid projection, with 3–4 setae laterally in indentation between processes; superior frontolateral process conical, with 4 setae spread evenly along external margin. Mediofrontal process paler than rest of frontal border in some specimens, appearing to be located ventral to superior frontolateral process but no sutures were found between processes. External scissura rounded. Supraocular lobe very low, acute. Cephalosome with short dorsal sulcus; very pronounced paraocular tubercles forming slight mesolateral ridge, ornamentation particularly noticeable in lateral view. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, without aesthetases; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; with unarmed carina; slight mandibular incisor half-way along; ventral dentate blade on distal half, with smooth pseudoblade dorsally; internal lobe on proximal half a long crenulate lamina; seta at midpoint; crisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite short, narrow. Pylopod 3-articled, internal margin of simple setae; article 1 with 3 areolae along internal margin, with 12 setae distally on ventral surface and along internal margin, article 2 with 6 setae on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal. Pereonite 4 with anterior constriction. Pereonites 5 and 6 together longer than rest combined. Pereonite 7 very narrow, overlapping pleon. Pleonites 1-4 subequal, 5 narrower; pleonal epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins sinuous, slightly notched distally; with 2 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 1 seta; rami subequal, reaching apex of pleotelson, bearing numerous plumose setae distally.

Pereopods with a moderate cover of simple setae; pereopod 6 with 2 anterior spiniform setae on merus; pereopod 2 with 1 posterior spiniform seta on carpus; pereopods 2, 5 and 6 with crenulate anterior margin of basis.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

Distribution. Eastern Bass Strait, 200 m depth.

Remarks. Gnathia notostigma is differentiated from other Australian species by the very pronounced paraocular ornamentation and ridge most clearly seen in lateral view. *G. lignophila* Müller from Malaysia also has similar paraocular ornamentation and both species possess a narrow maxilliped endite. *G. notostigma* differs from *G. lignophila* in possessing shorter and more robust mandibles with a pseudoblade; a conical mediofrontal process with notched lateral margins and only a slight median depression while the mediofrontal process of *G. lignophila* is bifid (large median depression) with smooth lateral margins; and *G. lignophila* unlike *G. notostigma*, is densely covered in granules anteriorly. *G. notostigma* is also similar to *G. camponotus* but differs in possessing a more pronounced and anterior paraocular ornamentation and a mediofrontal process with a slight median notch.

Gnathia odontomachus sp. nov.

Figures 63–65

Material examined. Holotype. Victoria, Western Port, off Crib Point (38°20.94′S, 145°13.33′E), 8 m, fine sand mud, Smith-McIntyre grab, A.J. Gilmour, Marine Studies Group on FV *Melita*, 29 Mar 1965 (stn CPBS-N 21), NMV J4374 (1 male).

Paratypes. Western Port, off Crib Point (38°20.81′S, 145°13.85′E), 13 m, gravel sand, Smith-McIntyre grab, A.J. Gilmour, Marine Studies Group on FV *Melita*, 30 Mar 1965 (stn CPBS-N 41), NMV J4370 (1 male); 10 m, 10 Mar 1965 (stn CPBS-N 23), NMV J4372 (1 male).

Description. Total length of holotype: 2.95 mm.

Cephalosome rectangular, 1.33 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border transverse; mediofrontal process inferior, small, conical; superior frontolateral process rounded, with 3 large setae clumped on internal margin and 3 smaller setae evenly spaced on

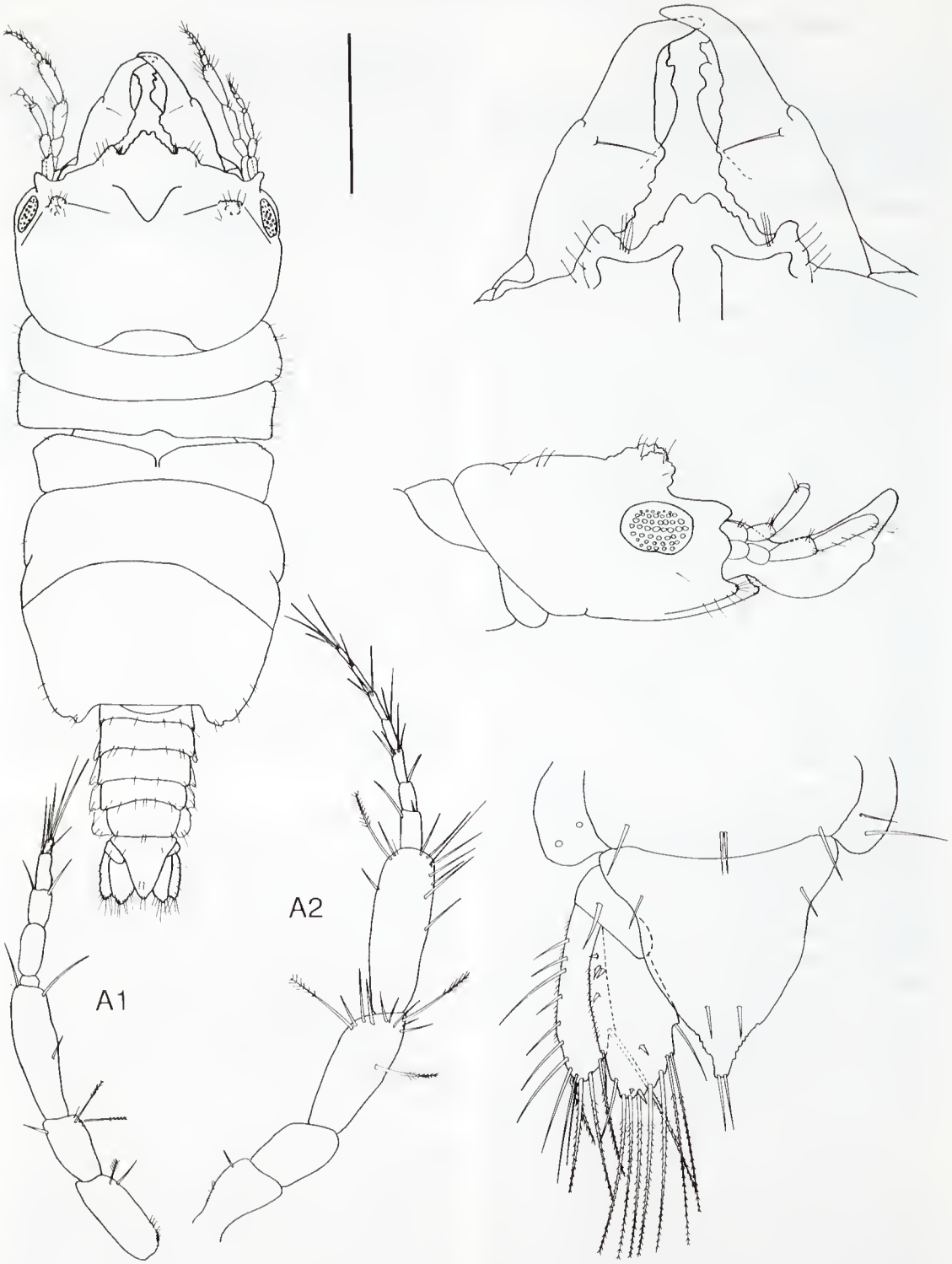

Figure 60. *Gnathia notostigma*. Holotype, NMV J27574.

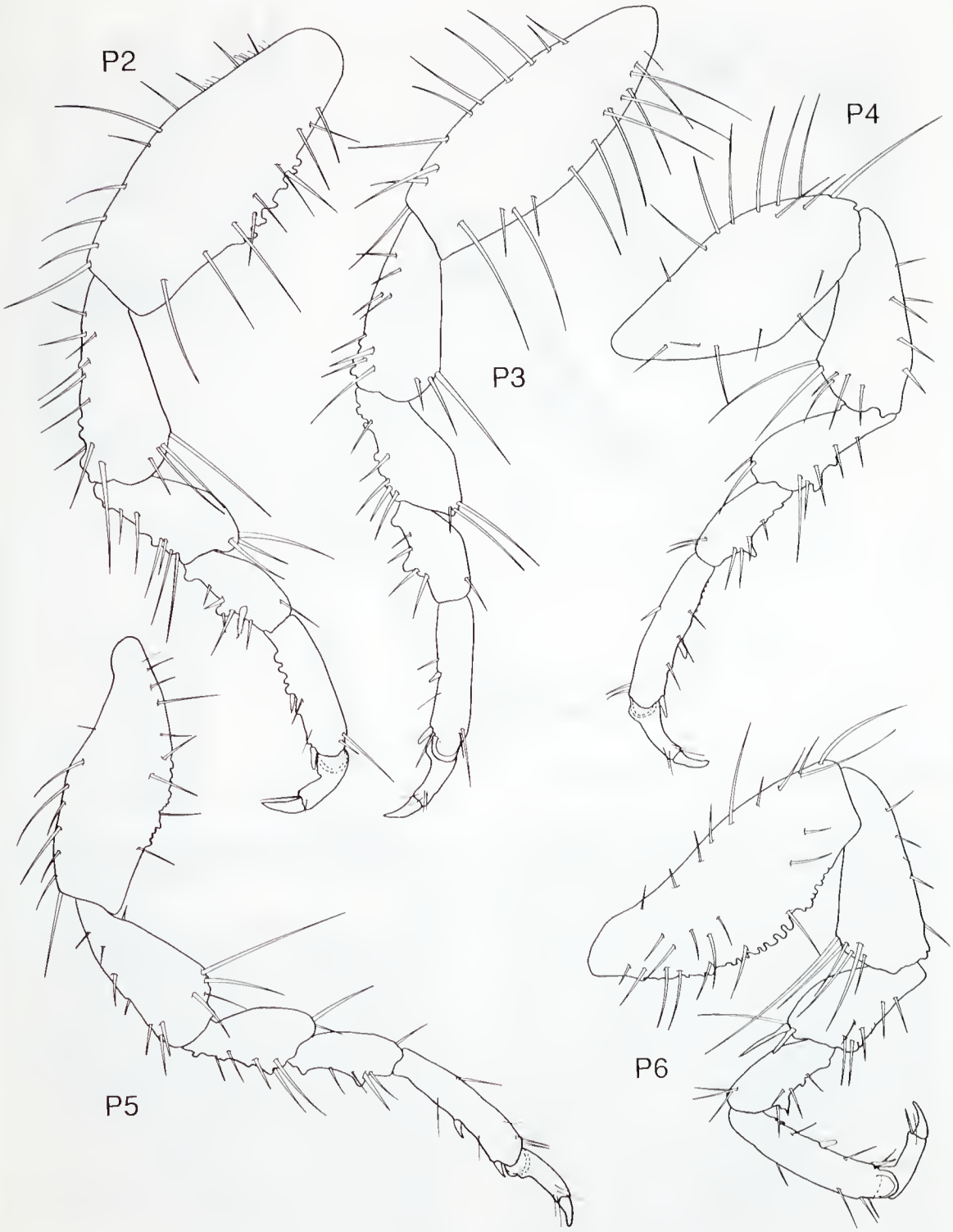

Figure 61. *Gnathia notostigma*. Holotype, NMV J27574.

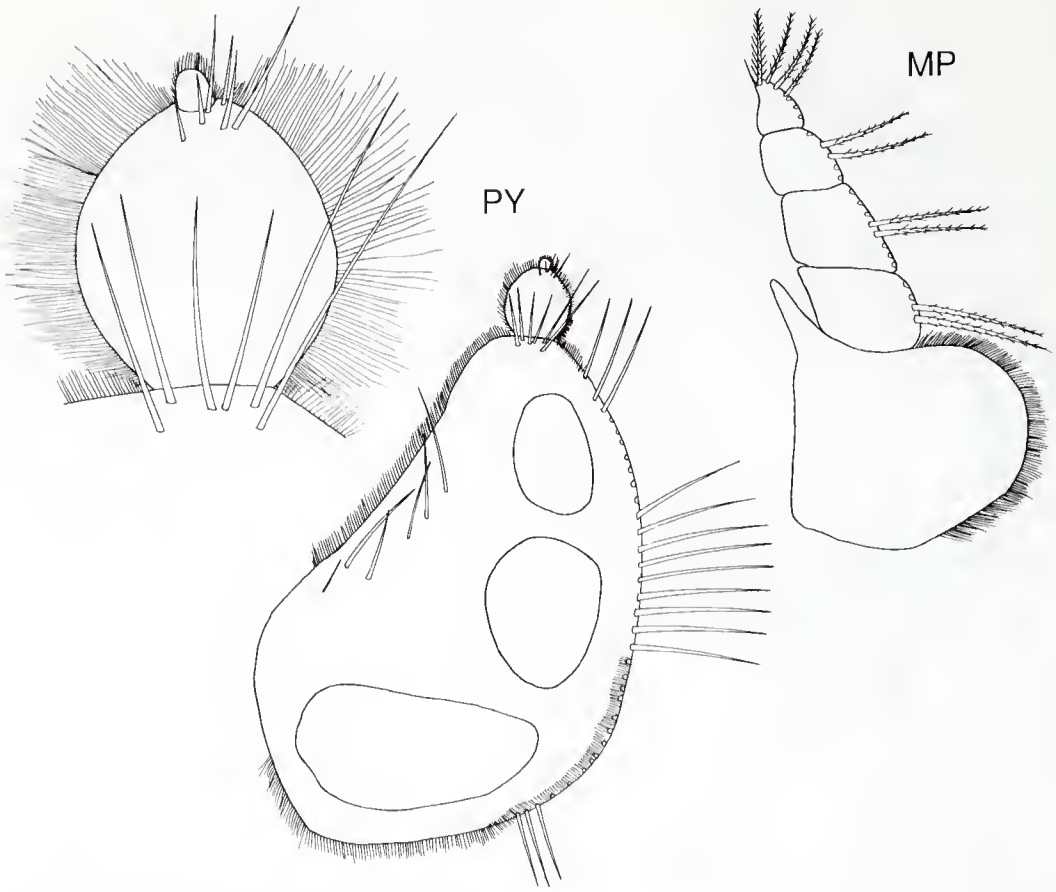

Figure 62. *Gnathia notostigma*. Holotype, NMV J27574.

external margin. External scissura very shallow. Supraocular lobe not pronounced. Cephalosome with small dorsal sulcus and translucent, elliptical region anteromedially, within sulcus and above buccal cavity. Antenna 2 twice as long as antenna 1; flagellum of antenna 1 of 5 articles, with 2 aesthetases, peduncle length subequal to flagellum; flagellum of antenna 2 of 7 articles. Mandible straight, two-thirds length of cephalosome; proximal third a pronounced basal neck; middle third progressively narrower, ventral dentate blade; distal third a long, cylindrical apex; with unarmed carina; mandibular incisor half-way along; seta at midpoint near incisor; crisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose endite barely reaching article 3, narrow. Pylopod 3-articled, internal margin of plumose setae; article 1 with ring of short, stouter setae posteriorly, with 3 areolae distally and 12 setae distally on ventral surface and along median margin; article 2 with 7 setae on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome, covered with numerous simple setae. Pereonite 1 dorsally reaching lateral margins, partially obscured laterally by pereonite 2; pereonite 4 with a slight anterior constriction and wide median groove; pereonite 5 with areae laterales. Pereonite 7 very narrow, overlapping pleon. Pleonites progressively narrower, pleonal epimera prominent. Pleotelson subtriangular, as wide as long, with few tubercules; lateral margins slightly sinuous; with 3 pairs of simple setae and pair of setae on distal apex. Uropodal peduncle with 1 seta; endopod longer than exopod, reaching apex of pleotelson; rami bearing numerous plumose setae distally.

Pereopods subequal, with moderate cover of simple setae; pereopod 2 with 1 posterior peeti-

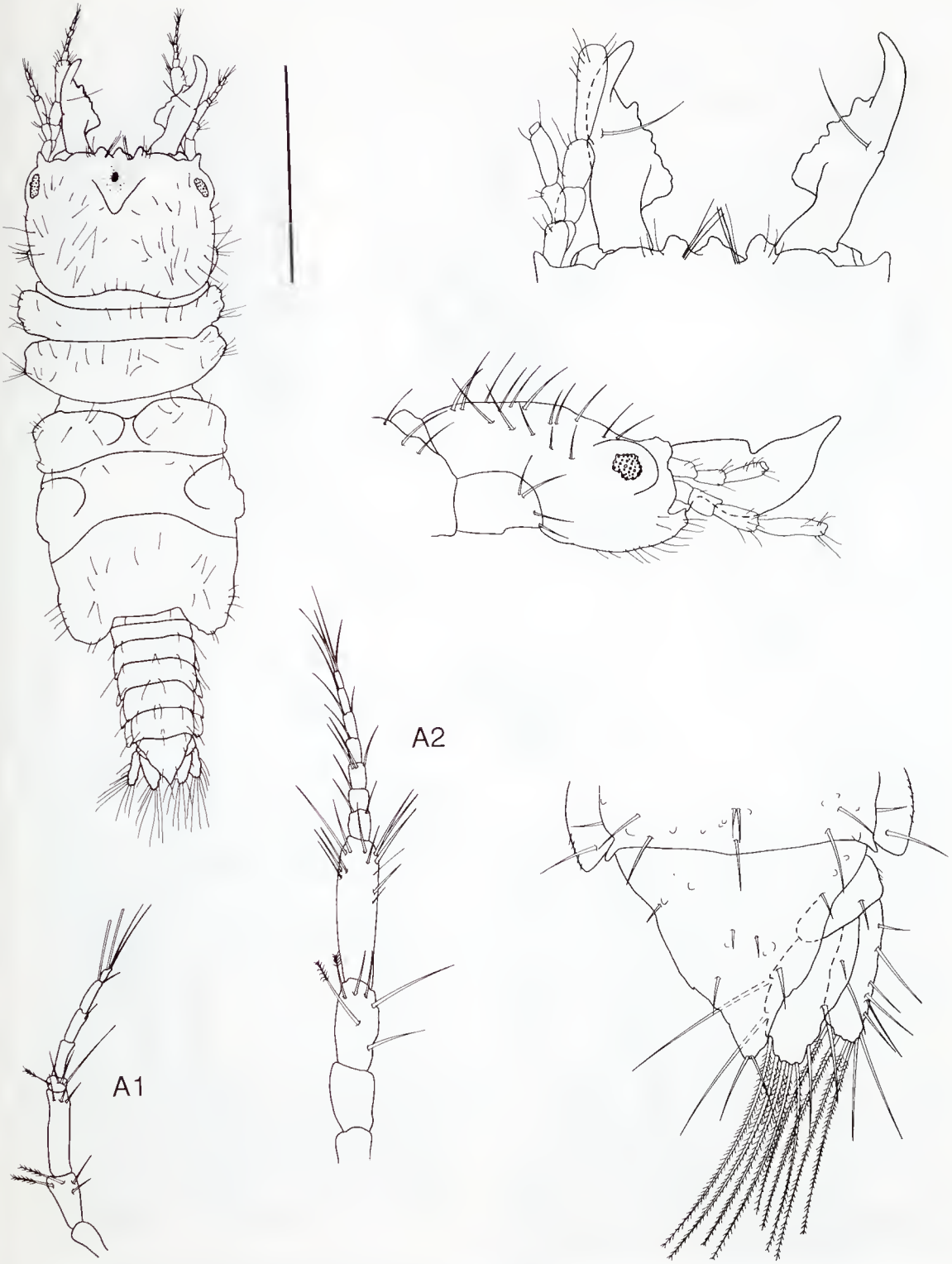

Figure 63. *Gnathia odontomachus*. Holotype, NMV J4374.

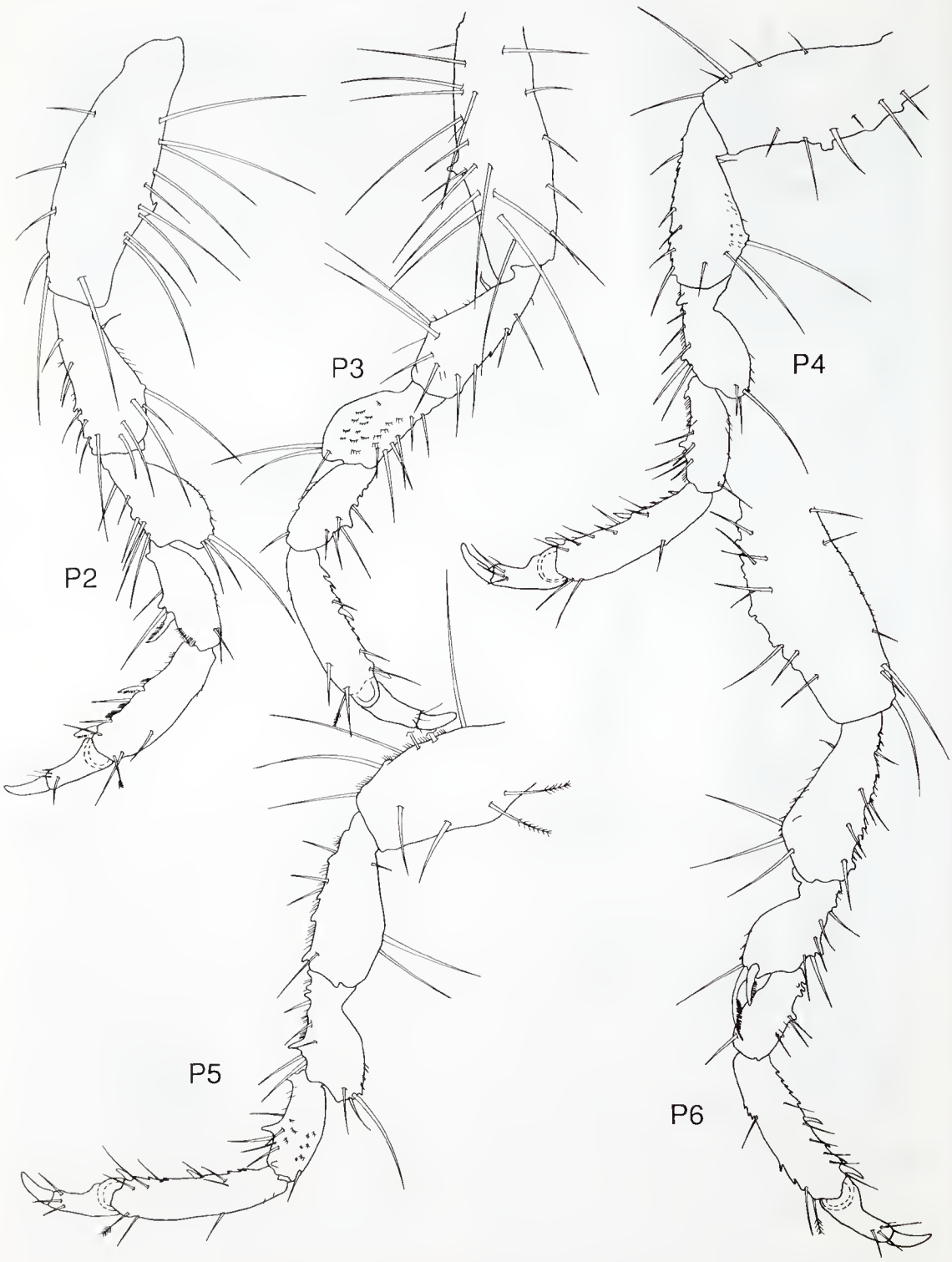

Figure 64. *Gnathia odontonachus*. Holotype, NMV J4374.

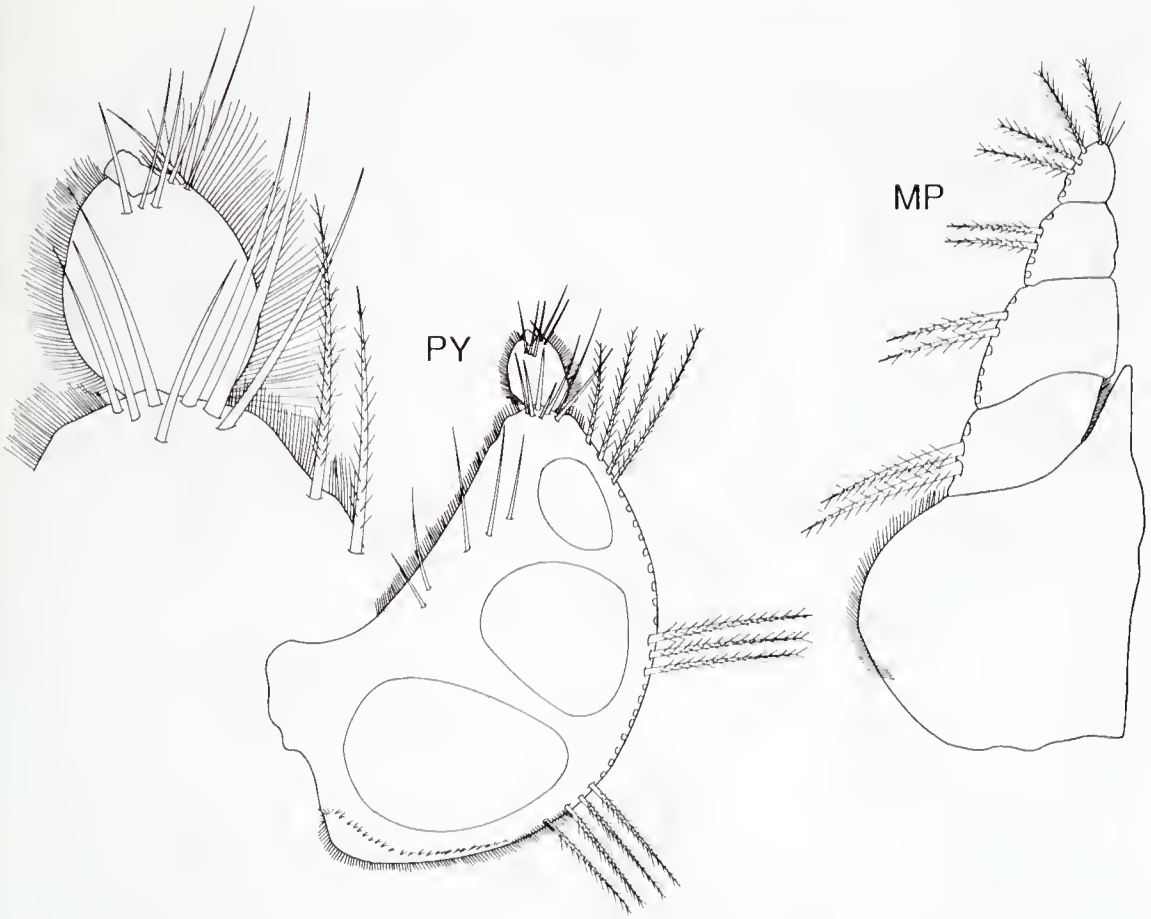

Figure 65. *Gnathia odontomachus*. Holotype, NMV J4374.

nate seta on carpus; pereopod 6 with 2 anterior pectinate setae on merus and crenulate anterior margin of basis.

Pleopods setose. Pleopod 2 endopod with appendix masculina half length of rami. Penes 2 small contiguous papillae.

Distribution Off Crib Point, Western Port, Victoria, 8–13 m depth.

Remarks. G. odontomachus is one of many species from around the world which possess a inferior, conical medifrontal process and conical superior processes. Of the Australian fauna it most closely resembles *G. latidens* (Beddard) though is easily disinguished by its hirsute nature; more rounded mediofrontal process; and the lack of a pseudoblade.

Gnathia prolasius sp. nov.

Figures 66–68

Material examined. Holotype. Victoia, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on ORV *Franklin*, 23 Jul 1986 (stn SLOPE 32), NMV J27577 (1 male).

Paratypes. All collected with WHOI epibenthic sled by G.C.B. Poore et al. on ORV *Franklin*, Jul 1986. Tasmania, off Freycinet Peninsula (42°0.20′S, 148°37.70′E), 720 m, coarse shelly sand (stn SLOPE 46), NMV J19111 (1 male). 42°2.20′S, 148°38.70′E, 800 m, coarse shelly sand, (stn SLOPE 45), NMV J19113 (1 male).

Victoria, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m (stn SLOPE 32), NMV J27573 (20 males). 38°16.40′S, 149°27.60′E, 800 m, coarse shell (stn SLOPE 34), NMV J19112 (2 males).

Other material. New South Wales, off Eden (37°0.60′S, 150°20.70′E), 363 m, coarse shell (stn SLOPE 22), NMV J19114 (34).

Victoria, S of Point Hicks (38°21.90′S, 149°20.00′E), 1000 m (stn SLOPE 32), NMV J19115 (500).

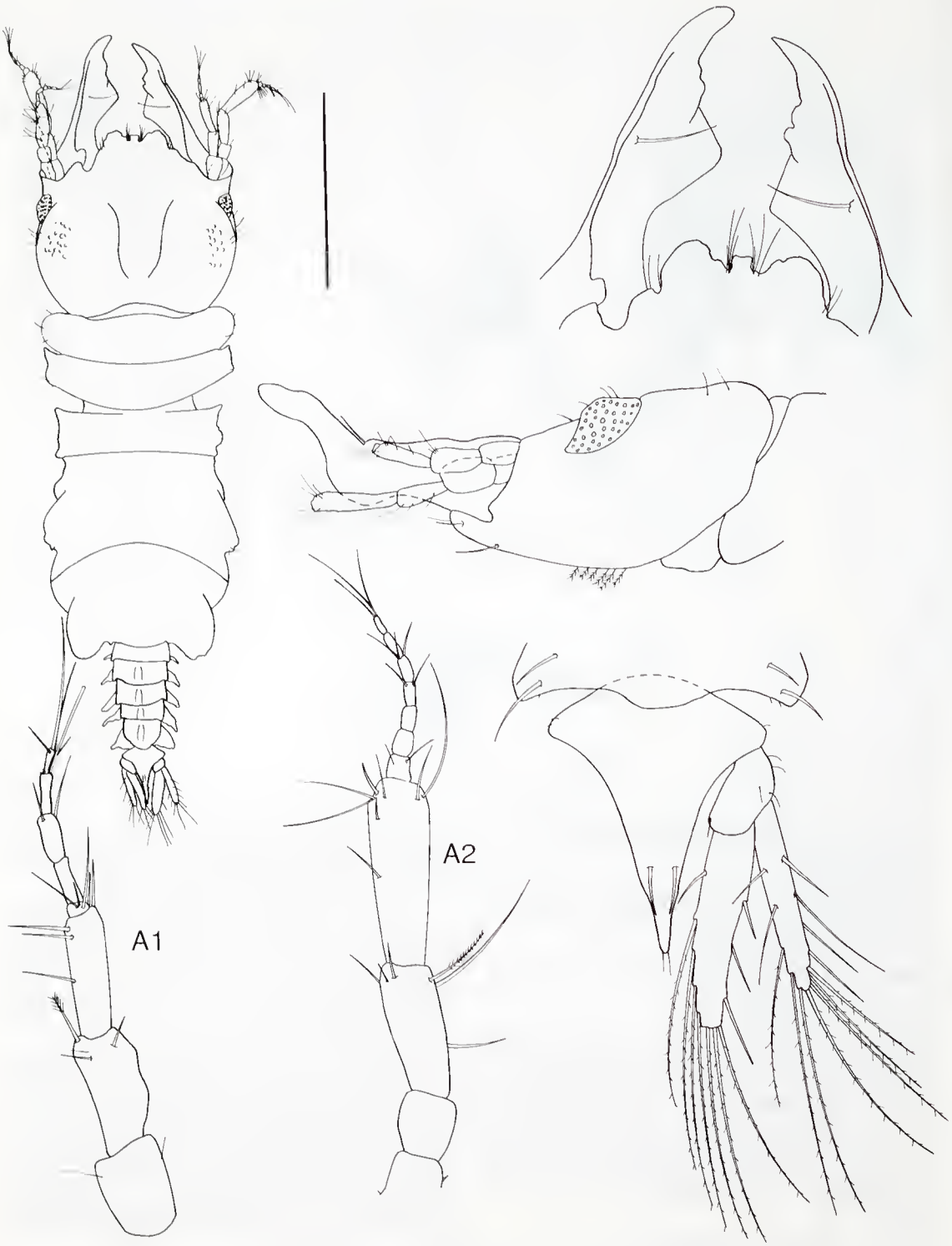

Figure 66. *Gnathia prolasius*. Holotype, NMV J27577.

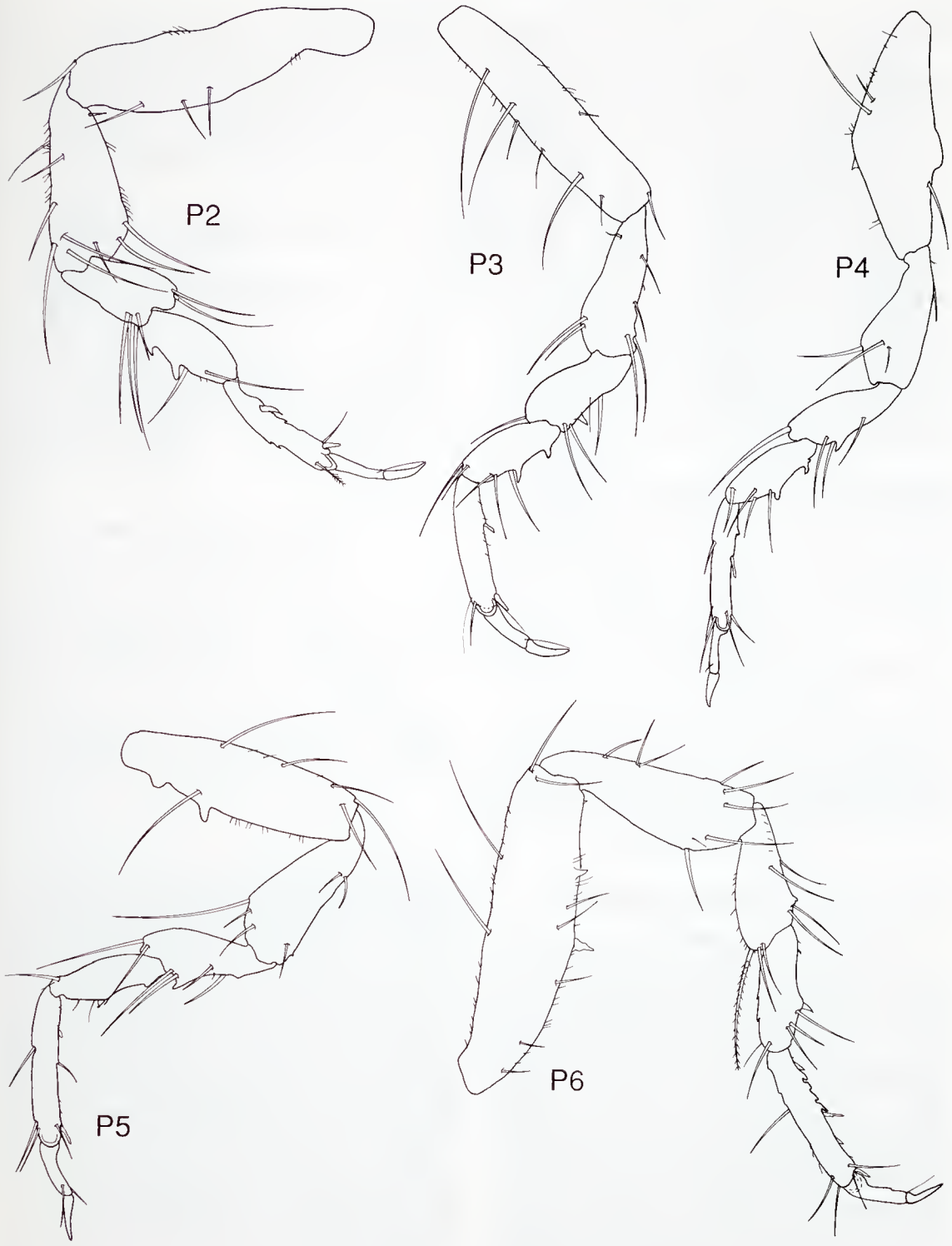

Figure 67. *Gnathia prolasius*. Holotype, NMV J27577.

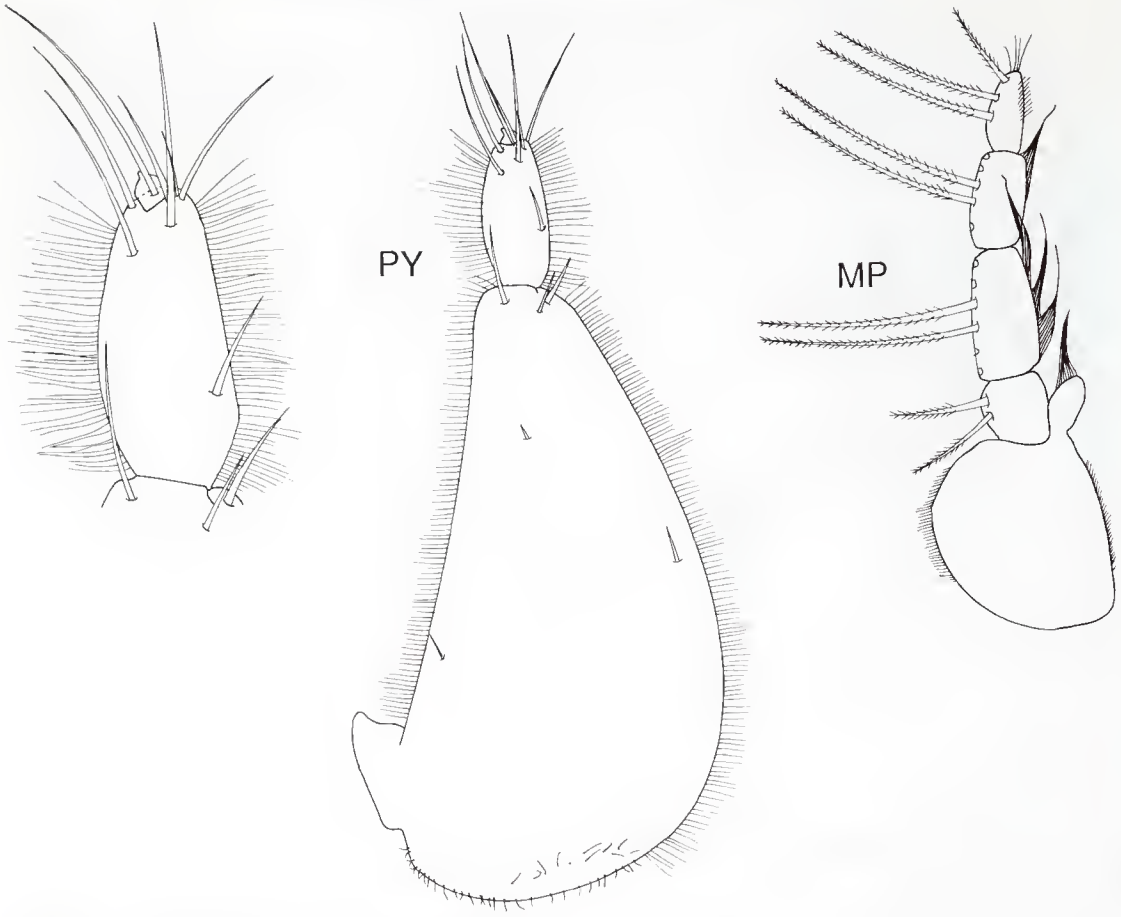

Figure 68. *Gnathia prolasius*. Holotype, NMV J27577.

Description. Total length of holotype: 3.49 mm.

Cephalosome rectangular, 1.2 times as wide as long, lateral margins convex. Eyes well developed, lateral and sessile. Frontal border produced; mediofrontal process quadrate, with 4 setae laterally; superior frontolateral process large, rounded, with anteromedial notch, twice length of mediofrontal process, with 2 small setae laterally. External scissura smoothly rounded. Supraocular lobe very low, acute. Cephalosome with broad dorsal sulcus; paraocular granules posterior to eye. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 1 aesthetase; flagellum of antenna 2 of 7 articles. Mandible straight, raised distally; two-thirds length of cephalosome; with unarmed carina; blade complex, crenulate distally while smooth and linear proximally; seta at midpoint; basal neck smoothly arced; erisma pronounced, external lateral margin flattened. Maxilliped 5-articled, palp thin and elongate; external margins of articles 2–4 bearing plumose setae; internal margin with long setae joined together into 5 strands; endite short, narrow. Pylopod 3-articled, elongate and narrow, internal margin of fine short setae; with ring of short, stouter setae posteriorly; article 1 with 6 setae on ventral surface; article 2 elongate, with 7 setae distally on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal; pereonite 4 rectangular, longer than 2 and 3, with anterior constriction. Pereonite 5 and 6 rounded, as long as others together. Pleonites progressively narrower, pleonal epimera prominent. Pleotelson

subtriangular, longer than wide; lateral margins slightly concave; with pair of simple setae and pair of setae on distal apex. Uropodal peduncle with 5 small setae; endopod longer than exopod, reaching beyond apex of pleotelson.

Pereopods narrow, with few simple setae; ischium to carpus with small lateral projections.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Eastern Bass Strait and south-eastern slope, 363–1000 m depth.

Remarks. Gnathia prolasius is similar to *G. stigmacros* in overall body proportions, particularly the pereopods and mouthparts. *G. prolasius* is easily recognised by the large, semicircular frontolateral processes.

Gnathia rhytidoponera sp. nov.

Figures 69–71

Material examined. Holotype. Western Coral Sea, NE of Townsville, Queensland (17°57′S, 147°02′E), 287–300 m, epibenthic sledge, M. Pichon et al. on RV *Cidaris*, 16 Jun 1986 (stn 146.2), QM W19962 (1 male).

Paratype. Western Coral Sea, NE of Townsville, Queensland (17°22′S, 146°48′E), 303–296 m, epibenthic sledge, M. Pichon et al. on RV *Cidaris*, 15 Jun 1986 (stn 143.2), QM W19963 (1 male)

Description. Total length of holotype: 3.86 mm.

Cephalosome subquadrate with a pronounced ventral rostrum, lateral margins convex. Rostrum narrow, conical with small lateral indentations. External scissura smoothly rounded. Cephalosome with a narrow dorsal sulcus extending medianly, all the way to frontal border. Antenna 2 two times longer than antenna 1; flagellum of antenna 1 of 5 articles with 3 aesthetascs; flagellum of antenna 2 of 7 articles, peduncle articles 3 and 4 with numerous small setae. Mandible straight, two-thirds length of cephalosome; with unarmed carina; seta at midpoint; smooth ventral blade on proximal two-thirds, visible in lateral view, with a dentate pseudoblade dorsally; a quadrate internal lobe on proximal dorsal surface of mandible, clearly visible in lateral view. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite barely reaching article 3. Pylopod 3-articled, internal margin of plumose setae; article 1 with 3 large areolae and 7 setae on ventral surface, 4 distally; article 2 with 4 setae distally on ventral surface; article 3 minute.

Pereon widest anteriorly, as wide as cephalosome. Pereonite 1 weakly fused with cephalosome, barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal; pereonite 4 narrower than others, with anterior constriction; pereonites 5 and 6 together longer than others together. Pereonite 6 with small lobuli. Pereonite 7 very narrow, overlapping pleon. Pleon widest in middle; pleonites 3–5 with prominent epimera. Pleotelson subtriangular, longer than wide; lateral margins sinuous; with 1 pair of simple setae medianly and pair of setae on distal apex. Uropodal peduncle with 2 setae; rami subequal, reaching apex of pleotelson; internal margins of rami bearing numerous plumose setae.

Pereopods subequal, with few long simple setae. Pereopod 6 with 2 anterior pectinate setae on merus; pereopods 2 and 6 with posterior spiniform seta on carpus.

Pleopods setose. Pleopod 2 endopod with appendix masculina subequal length to rami. Penes 2 small contiguous papillae.

Distribution. Western Coral Sea, NE of Townsville, Queensland, 287–303 m depth.

Remarks. Gnathia rhytidoponera is very similar to *G. halei* Cals from southern Queensland. *G. rhytidoponera* differs in possessing a dorsally directed quadrate lobe on the posterior mandibles and lacking a row of setae each side of the base of the mediofrontal process.

Gnathia stigmacros sp. nov.

Figures 72–74

Material examined. Holotype. Victoria, S of Point Hicks (38°14.80′S, 149°9.30′E), 200 m, coarse sand, gravel, WHOI epibenthic sled, M.F. Gomon et al. on ORV *Franklin*, 24 Jul 1986 (stn SLOPE 41), NMV J27576 (1 male).

Paratypes. Type locality, NMV J19122 (22 males).

Other material. Tasmania, eastern Bass Strait, 82 km ENE of North Point, Flinders I. (39°27.7′S, 148°41.4′E), 293 m, coarse sand, naturalists' dredge, G.C.B. Poore on HMAS *Kimbla*, 28 Mar 1979 (stn BSS 36), NMV J7793 (8); 70 km ENE of North Point, Flinders I. (39°28.4′S, 148°41.8′E), 110 m, coarse sand (stn BSS 35), NMV J7794 (2); 50 km NE of Babel I. (39°40.3′S, 148°46.5′E), 293 m, rock, coarse sand (stn BSS 33), NMV J7795 (11).

Victoria, eastern Bass Strait, near Pt Ricardo (37°53′S, 148°30′E), 27–45 m, medium sand, Smith-

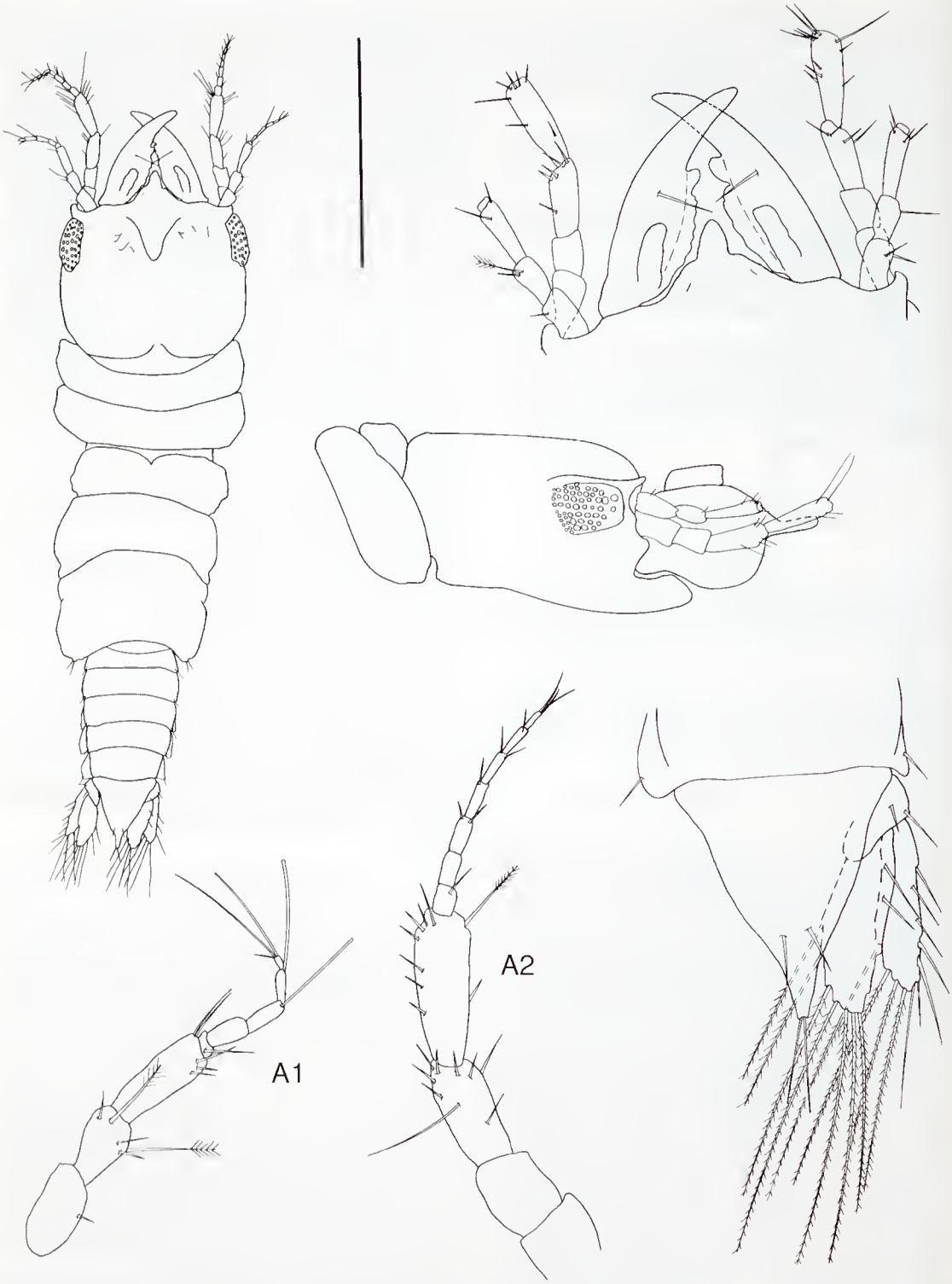

Figure 69. *Gnathia rhytidoponera*. Holotype, QM W19962

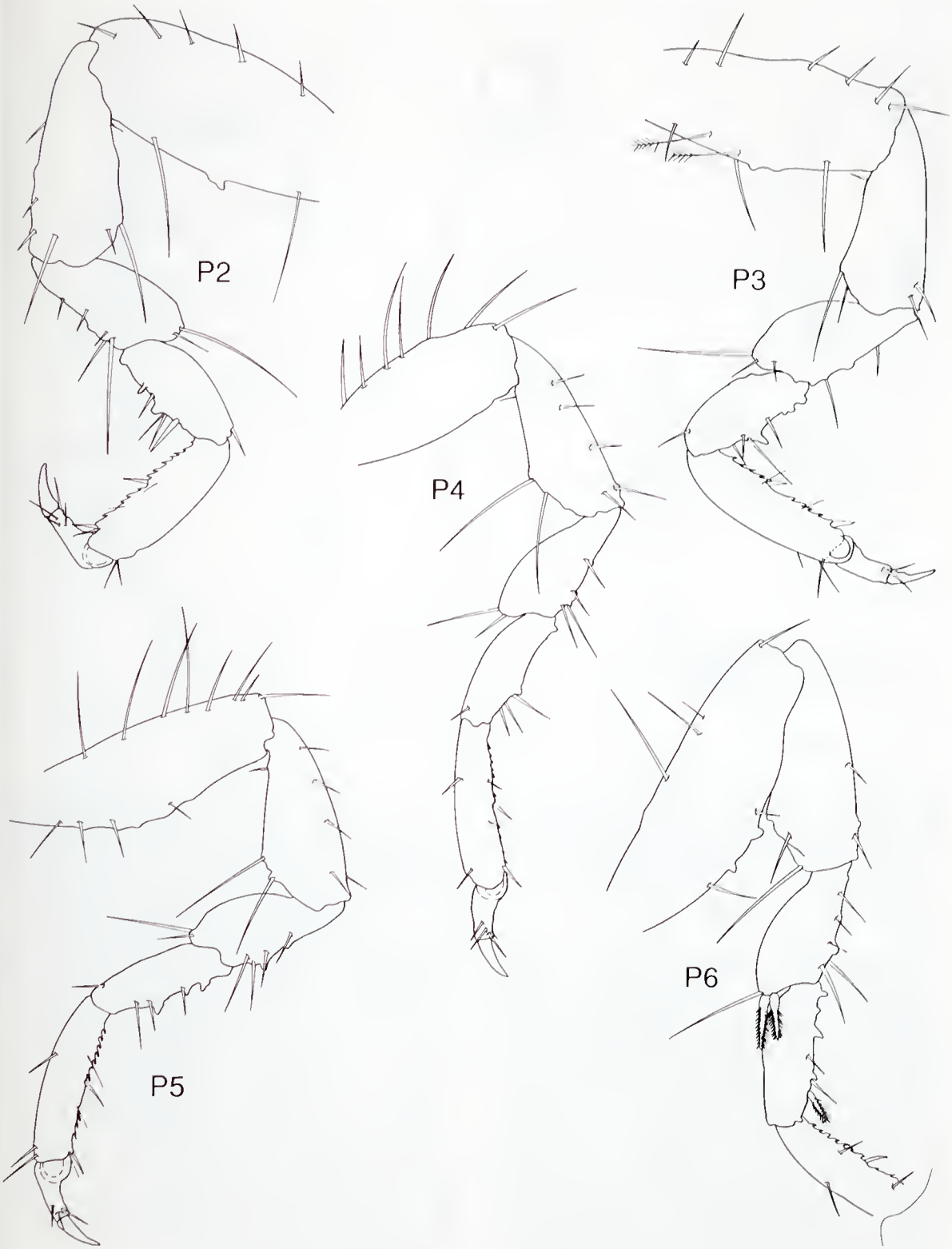

Figure 70. *Gnathia rhytidoponera*. Holotype, QM W19962

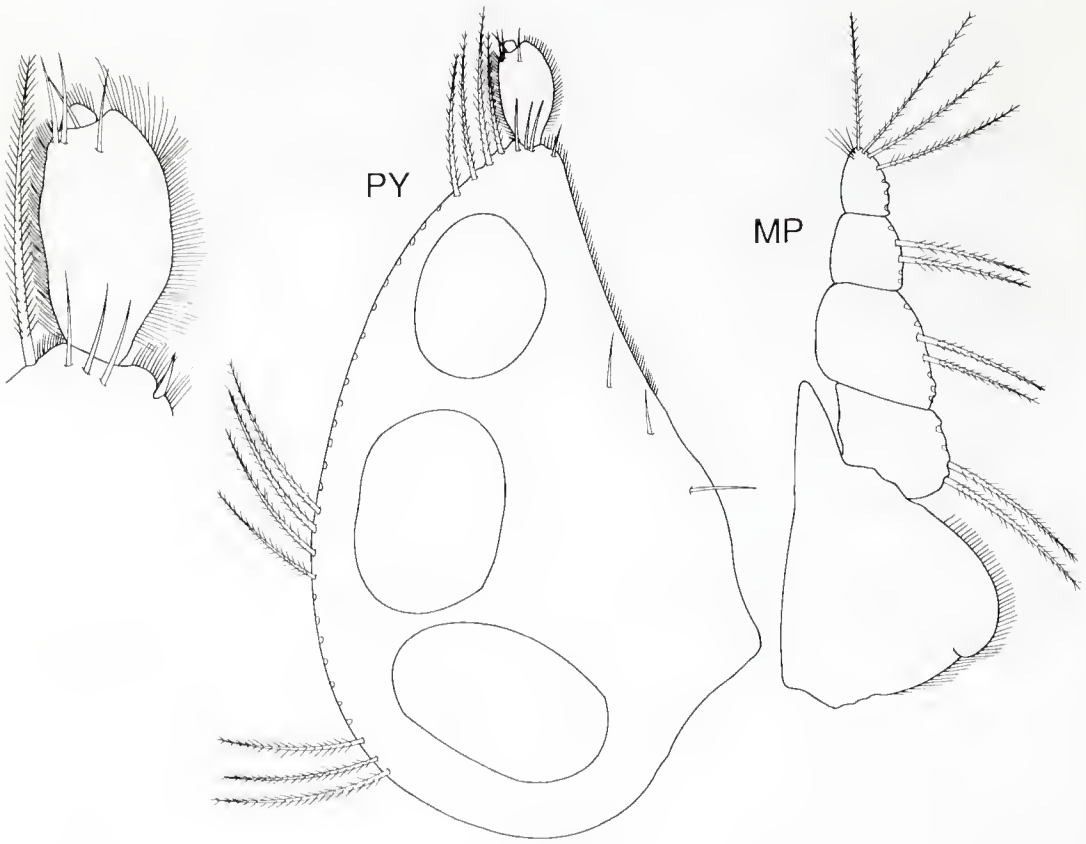

Figure 71. *Gnathia rhytidoponera*. Holotype, QM W19962

McIntyre grab, N. Coleman on FV *Sarda*, Feb 1991 (stn MSL-EG 107), NMV J24631 (2); (stn MSL-EG 106), NMV J24630 (1); (stn MSL-EG 103), NMV J24628 (2); (stn MSL-EG 104), NMV J24629 (1).

Description. Total length of holotype: 3.10 mm.

Cephalosome rectangular, 1.1 times as wide as long, lateral margins slightly convex. Eyes well developed, lateral and sessile. Frontal border produced, transverse between mandible; mediofrontal process translucent, with median notch and 3–4 long setae laterally; superior frontolateral process conical, with 5–6 short setae on lateral margin and 4 larger setae near mandible base. External scissura rounded. Supraocular lobe very low, acute. Cephalosome with broad dorsal sulcus; pronounced paraocular tubercles and setae. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, without aesthetascs; flagellum of antenna 2 of 7 articles. Mandible elongate, curved; two-thirds length of cephalosome; with unarmed carina; smooth arc-shaped blade on distal two-thirds, produced proximally; seta at midpoint; long, smooth straight basal neck; erisma pronounced. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; palp thin and elongate; endite barely reaching article 3, narrow, with 1 coupling hook. Pylopod 3-articled, elongate and narrow, internal margin of fine short setae; with ring of short, stouter setae posteriorly; article 1 with 9 setae on ventral surface, predominantly along median axis; article 2 elongate, with 12 setae on ventral surface; article 3 minute.

Pereon evenly sided, as wide as cephalosome; margins with numerous setae. Pereonite 1 barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonites 2 and 3 subequal, pereonite 4 rectangular, longer than 2 and 3; with anterior constriction. Pereonites 5 and 6 rounded, together as long as others combined. Pereonite 7 not visible. Pleonites 2–4 subequal; posterior border of pleonite 5 produced; pleonal epimera prominent. Pleotelson

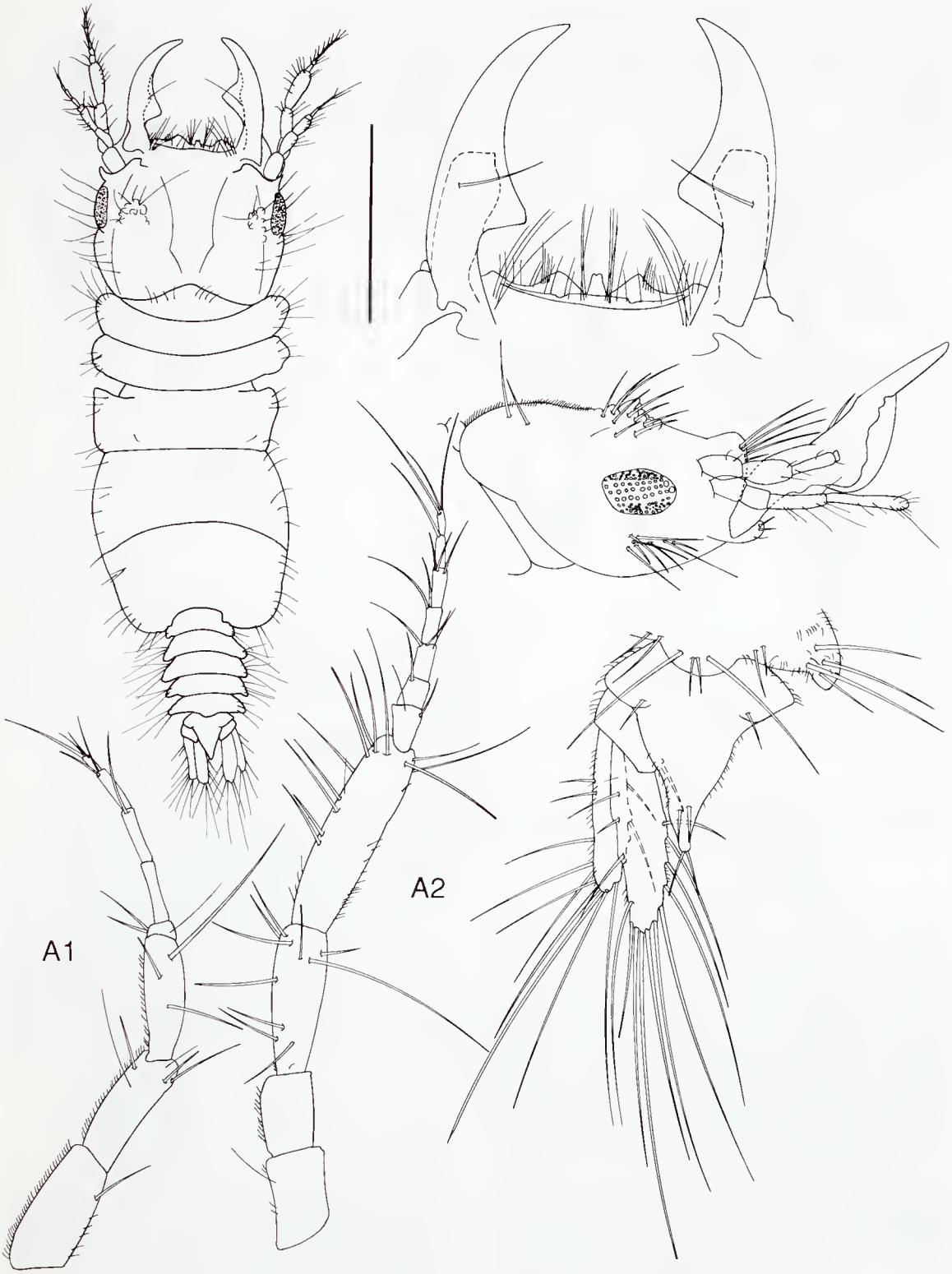

Figure 72. *Gnathia stigmacros*. Holotype, NMV J27576.

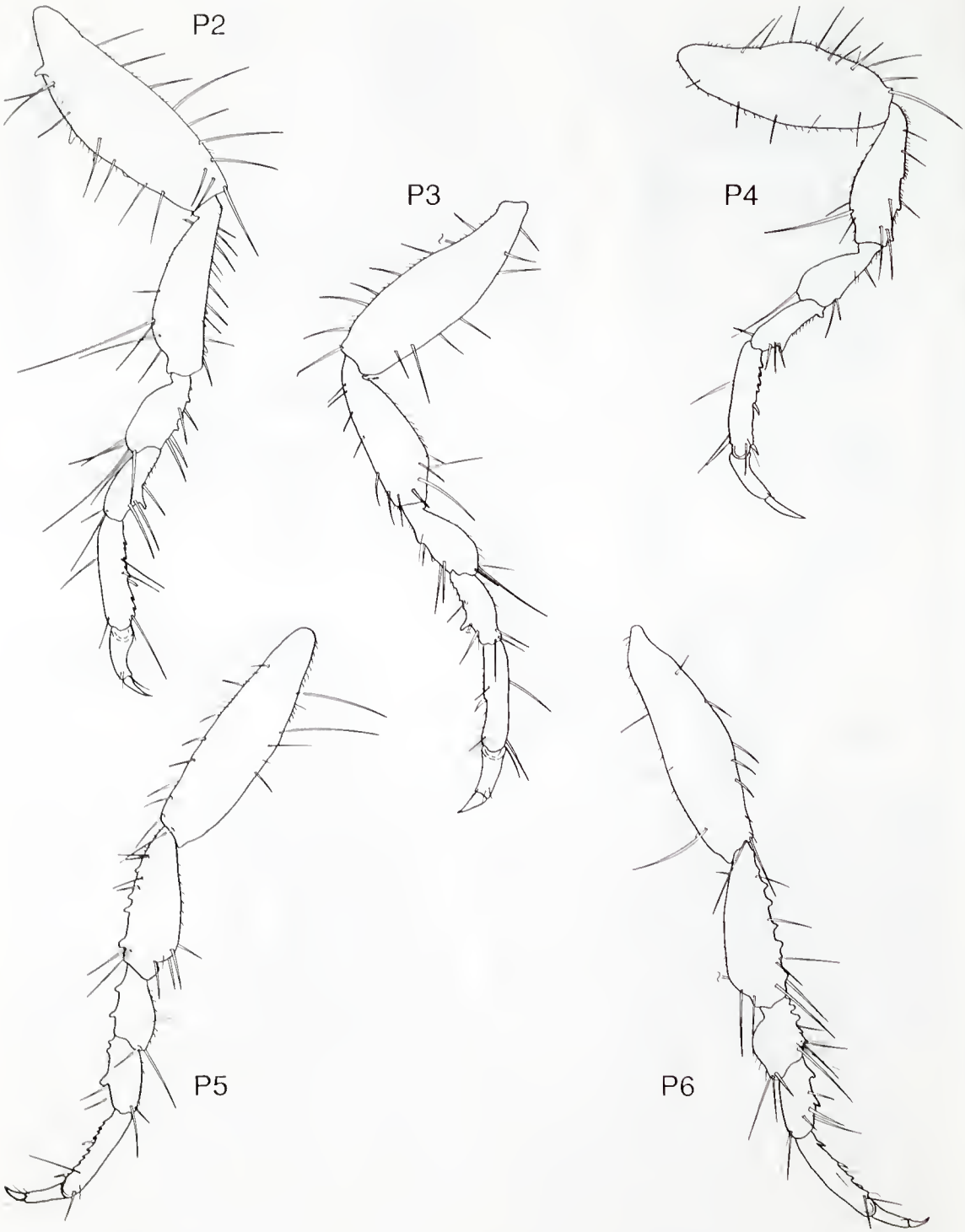

Figure 73. *Gnathia stigmacros*. Holotype, NMV J27576.

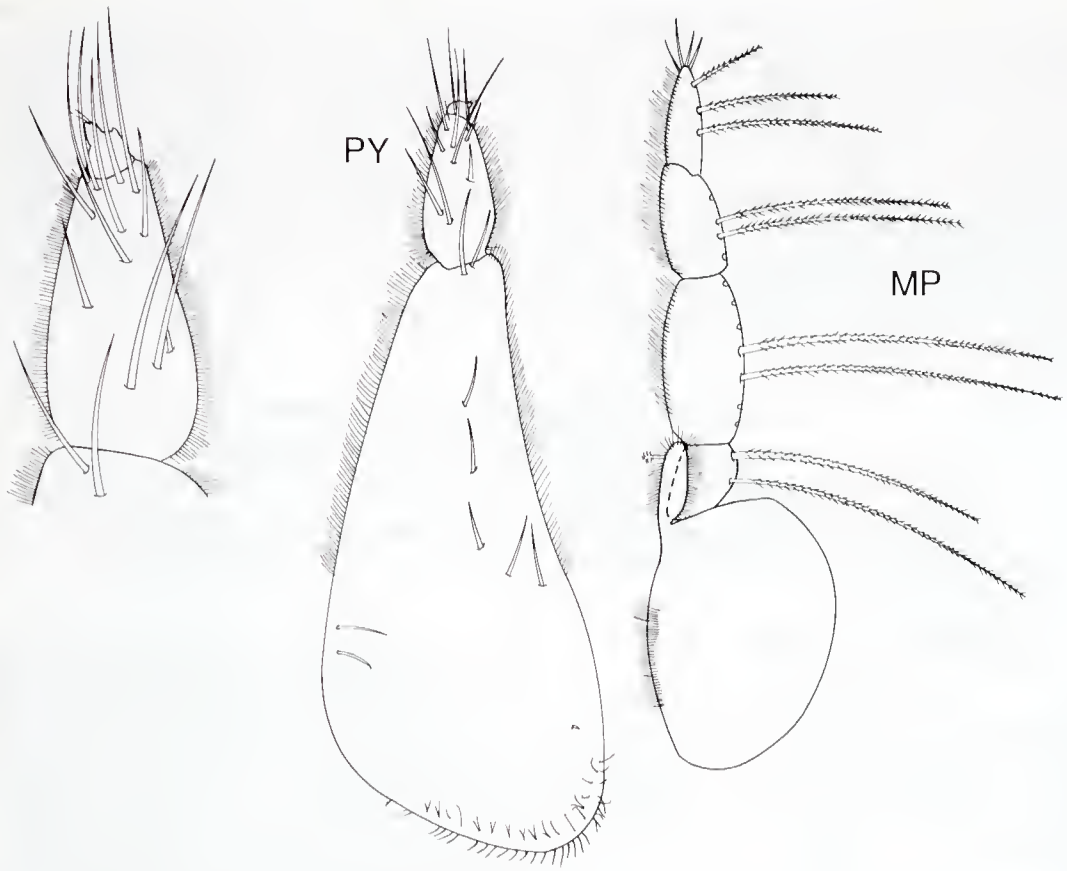

Figure 74. *Gnathia stigmacros*. Holotype, NMV J27576.

subtriangular, longer than wide; lateral margins slightly sinuous; with 2 pairs of simple setae and pair of setae on distal apex. Uropod peduncle without setae; endopod longer than exopod, reaching beyond apex of pleotelson; rami margins with numerous long simple setae.

Pereopods narrow, with few simple setae; ischium to carpus with small lateral projections, particularly on pereopods 5 and 6.

Pleopods setose. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Victoria, eastern Bass Strait, 27–293 m depth.

Remarks. *Gnathia stigmacros* differs from *G. prolasius* in possessing a completely smooth blade, many setae on the frontal border and more pronounced paraocular tubercles. *G. stigmacros* resembles *G. malaysiensis* Müller in the shape of the mediofrontal process and the mandible but is easily distinguished by its much shorter superior frontolateral processes and relatively straight frontal border.

Monodgnathia gen. nov.

Type species. *Monodgnathia ponera* sp. nov.

Diagnosis. Eyes absent. Frontal border produced as distinct delineated region (chalky white in Australian species); without processes. Mandible with occluding, smooth mandibular blade. Pereonite 1 immersed in cephalon. Pylopod 5-articled; operculate, article 2 enlarged; article 3 with spines; lacking plumose setae on external margin. Pereopod 4 basis with anterior quadrate lobe and ischium distally expanded into circular cusp.

Etymology. For Théodore Monod whose monumental 1926 work on Gnathiidae has become a classic study of a family of Isopoda.

Remarks. *Monodgnathia* and *Bathygnathia* are closely related genera (see cladogram) with

almost identical pylopods. Both genera possess a 5-articled, operculate pylopod with greatly enlarged second article and a minute fifth article. *Monodgnathia* is characterised by the presence of a curved mandible with a smooth mandibular blade, a distinct frontal border which is not produced into a rostrum and the absence of a protruding buccal cavity wall. Four species are recognised, two newly described and two transferred from *Akidognathia*. Remaining species of *Akidognathia* are now members of *Bathygnathia* of which *Akidognathia* is now a junior synonym. *Akidognathia poteriophora* Monod, 1926 is tenatively placed in the new genus on the basis of the mandible and rostrum although the pylopod is not operculate and the basis of percopod 4 lacks the anterior quadrate lobe. The pylopod, maxilliped and fusion of pereonites 5 and 6 suggest that *A. poteriophora* is a subadult specimen with some features not fully developed but it must be stressed that this conclusion has been reached based on the literature.

Key to males of *Monodgnathia* from Australia

1. Frontal border produced medianly, lacking setae; cephalon lacking projections covering base of mandibles ..... *M. ponera*

— Entire frontal border produced, with setae; cephalon with quadrate projections covering base of mandibles ..... *M. colobostruma*

Monodgnathia colobostruma sp. nov.

Figures 75–77

Material examined. Holotype. Victoria, S of Point Hicks (38°21.9'S, 149°20.0'E), 1000 m, WHOI epibenthic sled, G.C.B. Poore et al. on ORV *Franklin*, 23 Jul 1986 (stn SLOPE 32), NMV J19115 (1 male).

Description. Total length of holotype: 6.97 mm.

Cephalosome rectangular, 1.25 times as long as wide, lateral margins convex. Eyes absent. Entire frontal border produced, truncated, with 6 large setae medianly and 4–5 smaller setae spreading submarginally; distinct chalky white region between mandibles at end of short dorsal sulcus. Cephalosome with low posterior median tubercle and distinct quadrate cover over base of mandible. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetases; flagellum of antenna 2 of 7 articles. Mandible half length of cephalosome; apex curved inwards; with unarmed carina; smooth occluding blade proximally and flat dorsal lobe, proximally. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae; endite clearly reaching article 3, with 6 coupling hooks. Pylopod 5-articled, with many simple setae medianly, mainly on articles 3 and 4; articles 2 and 3 with large areolae; article 3 with 2 pectinate spiniform setae on external anterolateral margin; article 5 minute.

Pereon evenly sided, slightly wider than cephalosome; pereonites progressively longer. Pereonite 1 dorsally small, not reaching lateral margins of pereon and partially obscured laterally by pereonite 2. Pereonite 4 with slight anterior constriction and median groove. Pereonite 5 with dorsal sulcus and areae laterales. Pereonite 6 with lobi laterales and small lobuii. Pereonite 7 small, a thin band; overlapping pleon. Pleonites similar, pleonite 5 slightly longer than others; pleonal epimera prominent. Pleotelson subtriangular, as wide as long; lateral margins slightly sinuous with 5–6 pairs of simple setae laterally and 1 medianly. Uropodal peduncle with 2 setae; rami of subequal length, reaching apex of pleotelson; internal margins of rami bearing few plumose setae.

Pereopods 2 and 3 less robust than others, with dense cover of simple setae; others with moderate cover of simple setae; pereopod 4 basis with pronounced anterior quadrate lobe, ischium distally expanded as flat, circular projection with 4 large tubercles; carpus to unguis extending at right angle to basal pereopod, forming a surface with circular cusp of ischium.

Pleopods with short marginal setae. Pleopod 2 endopod with appendix masculina subequal to length of rami. Penes 2 contiguous papillae.

Distribution. Eastern Bass Strait slope, 1000 m depth.

Remarks. Monodgnathia colobostruma and *M. ponera* are the first records of this genus from Australian waters. *M. colobstruma* and the other members of this genus differ from the only known specimen of *M. poteriophora* (which we believe to be a subadult specimen – see *Monodg-*

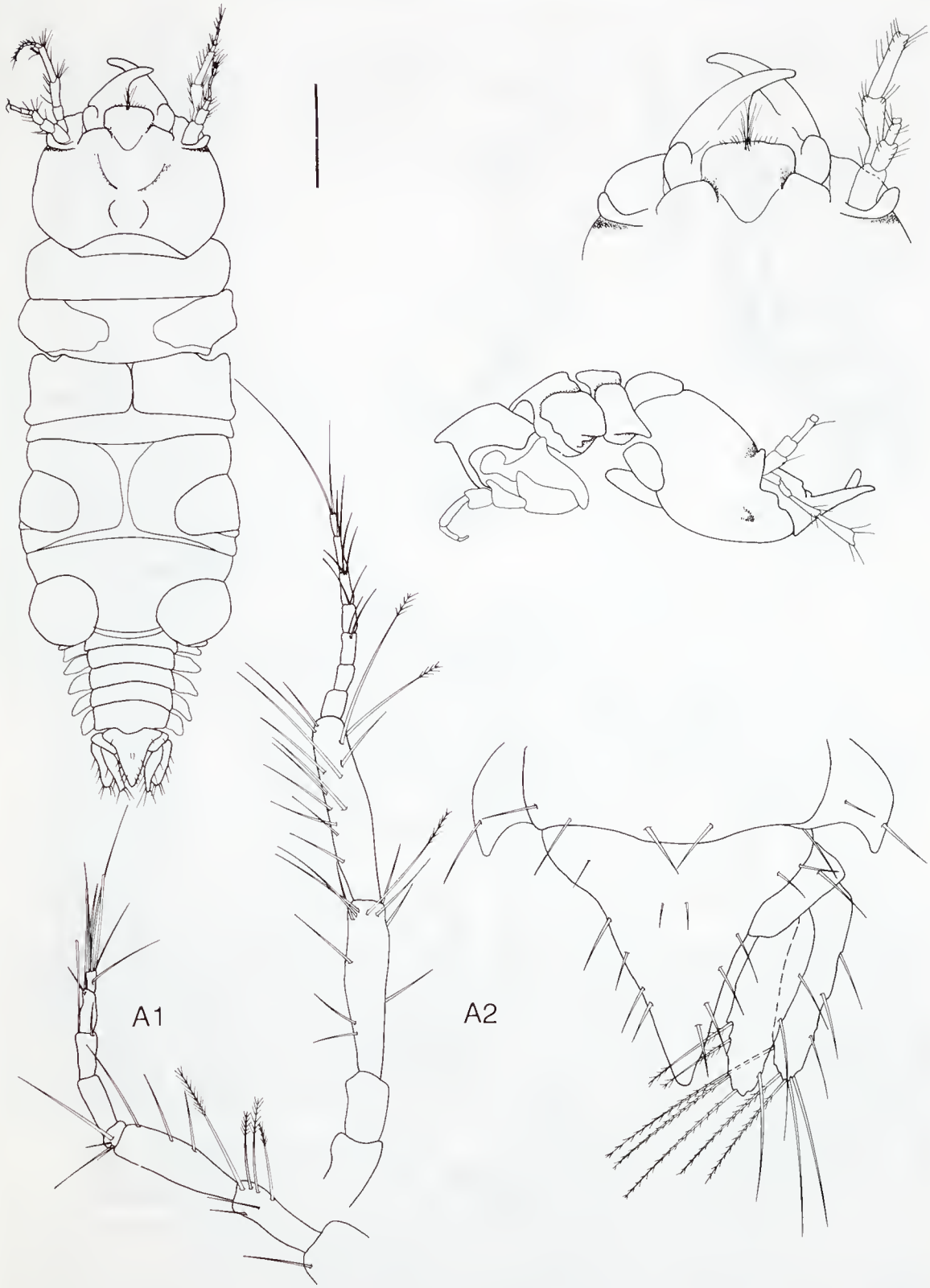

Figure 75. *Monodgnathia colobostruma*. Holotype, NMV J19115.

Figure 76. *Monodgnathia colobostruma*. Holotype, NMV J19115.

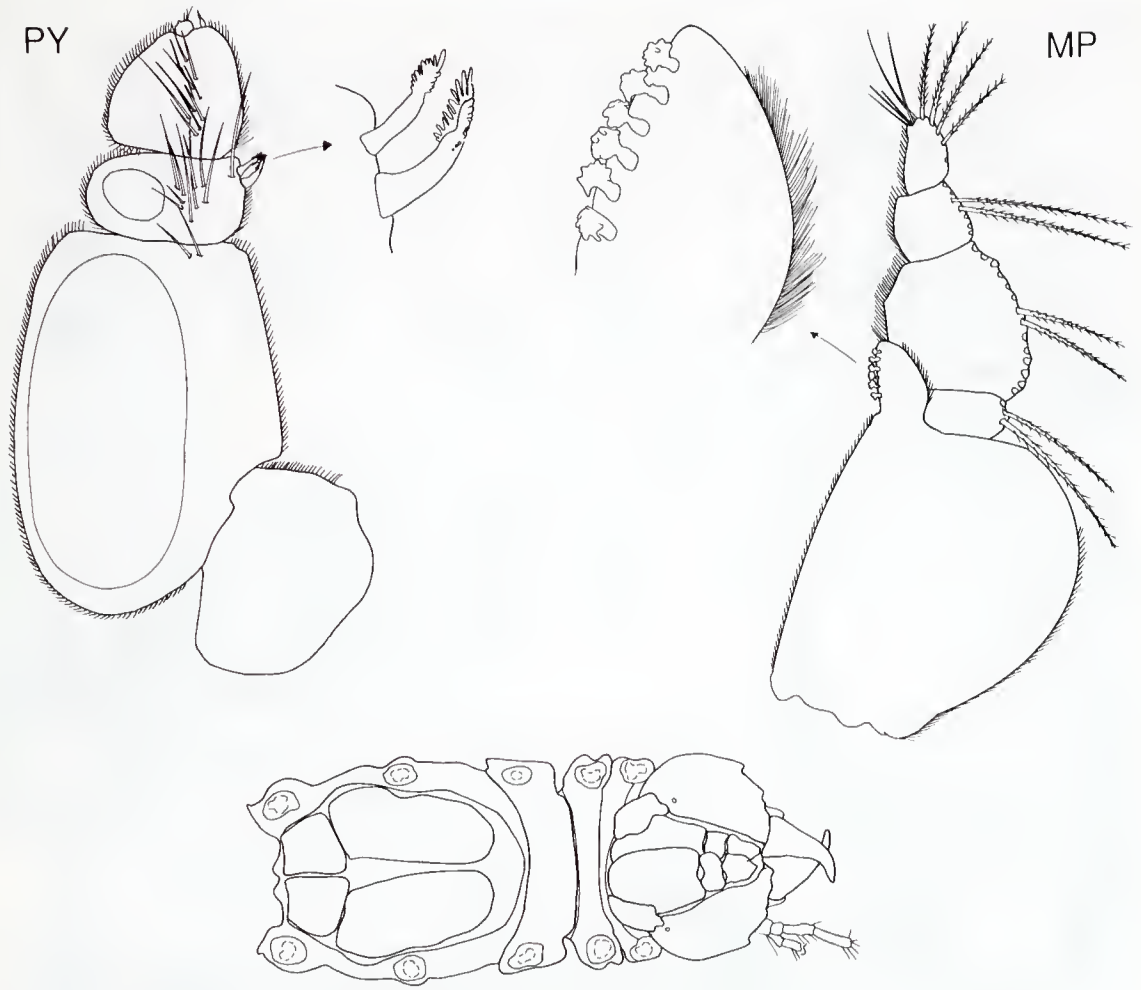

Figure 77. *Monodgnathia colobostruma*. Holotype, NMV J19115.

nathia remarks) in possessing a operculate pylopod and lacking fused pereonites 5 and 6.

M. colobostruma possesses a more robust habitus than other species of *Monodgnathia* and is characterised by a square frontal border produced across its entire length, not only between the base of the mandibles; raised protrusions on the cephalon at the base of the mandibles and slight dorsal lobes on the mandibles.

Monodgnathia ponera sp. nov.

Figures 78–80

Material examined. Holotype. Lord Howe Rise, southwestern Pacific Ocean (29°13.3′S, 160°35.4′E), 1550 m, epibenthic sled, Australian Musuem party on ORV *Franklin*, 4 May 1989 (stn 05/89 site 20), AM P41294 (1 male).

Description. Total length of holotype: 11.98 mm.

Cephalosome rectangular, 1.4 times as wide as long, lateral margins convex. Eyes absent. Frontal border produced, smoothly rounded as a distinct chalky white region, devoid of setae. External scissura rounded. Supraocular lobe smoothly convex. Cephalon with 2 small depressions medianly; anterior one larger at base of short sulcus; smaller posterior one near anterior border of peronite 1. Antenna 2 longer than antenna 1; flagellum of antenna 1 of 5 articles, with 3 aesthetascs; flagellum of antenna 2 of 8 articles. Mandible subequal to length of cephalosome; apex curved inwards; with unarmed carina; slight mandibular incisor one-third way along; small basal neck obscured dorsally by rostrum; blades smooth proximally,

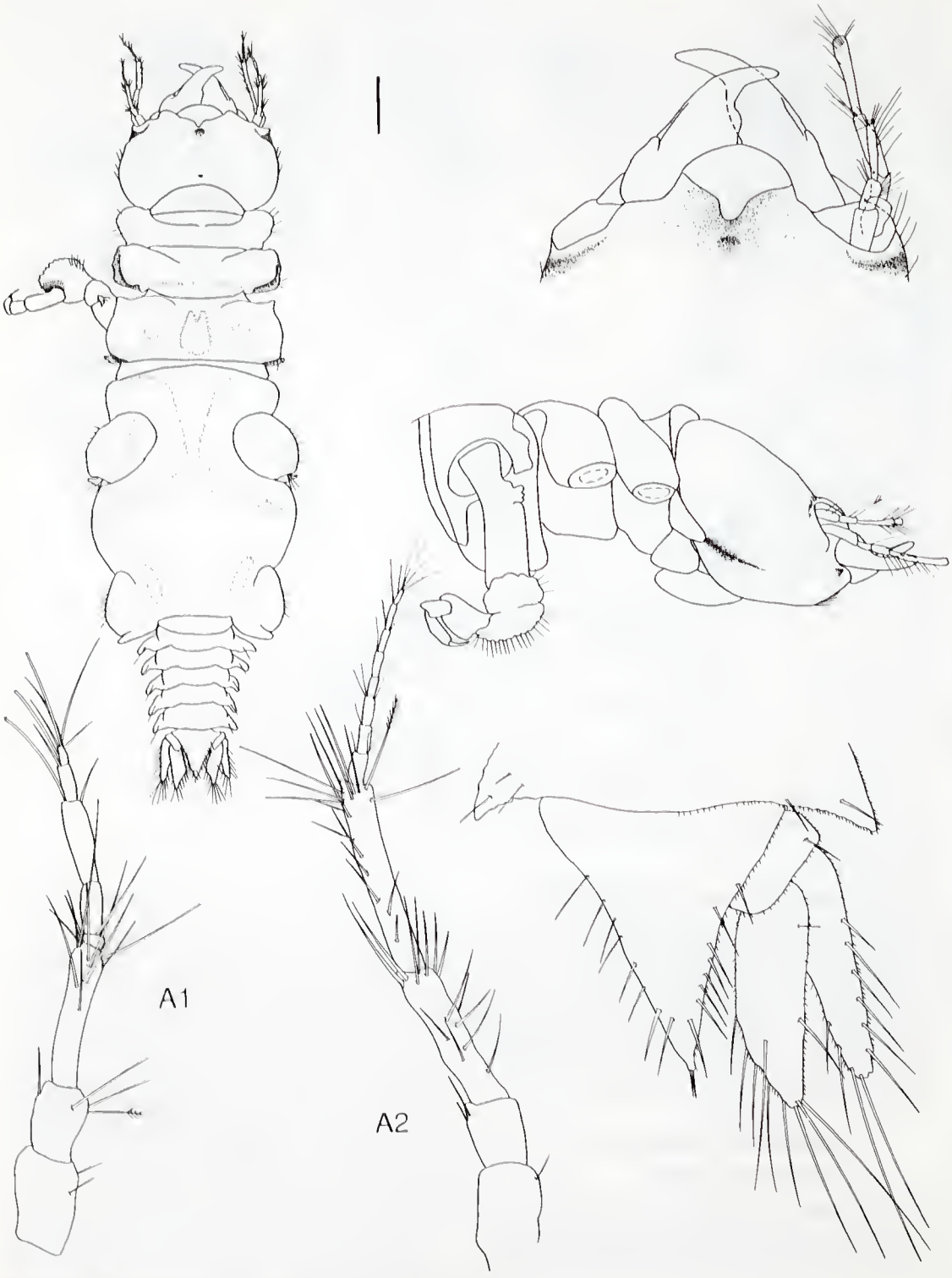

Figure 78. *Monodgnathia ponera*. Holotype, AM P41294.

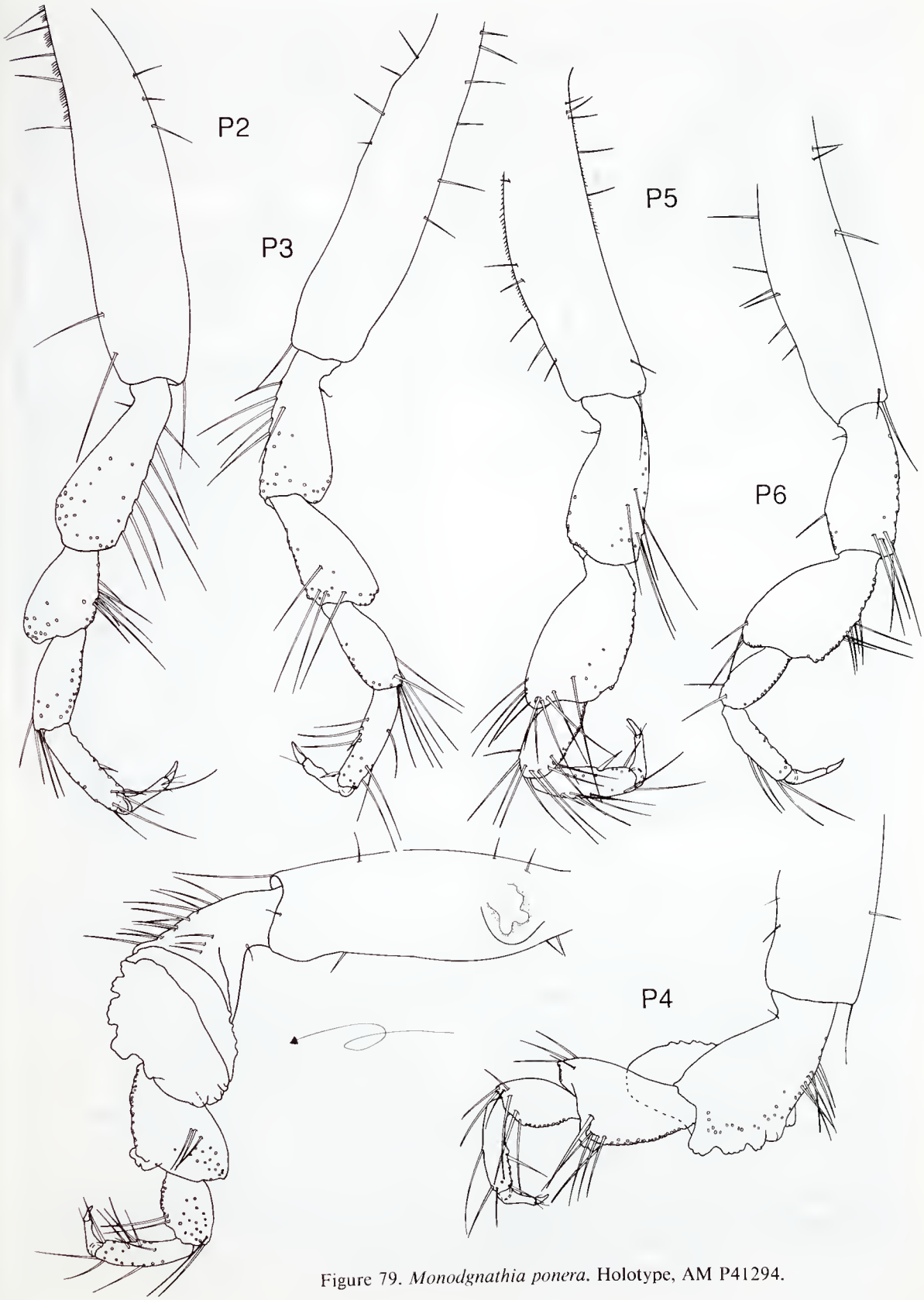

Figure 79. *Monodgnathia ponera*. Holotype, AM P41294.

Figure 80. *Monodgnathia ponera*. Holotype, AM P41294.

occluding. Maxilliped 5-articled; external margins of articles 2–4 bearing plumose setae, article 2 short; endite clearly reaching article 3, narrow, with 6 coupling hooks. Pylopod 5-articled, with many simple setae medianly, from distally on article 2 to base of article 5; article 3 with at least 1 pectinate spiniform seta on internal anterolateral margin (second seta damaged distally); article 5 minute.

Pereon widest posteriorly at peronites 5 and 6, 1.25 times as wide as cephalosome; pereonites length and width increasing progressively. Pereonite 1 produced slightly, barely reaching lateral margins dorsally and partially obscured laterally by pereonite 2. Pereonite 4 with anterior constriction, median groove as bilobed sulcus. Pereonite 5 with dorsal sulcus and areae laterales. Pereonite 6 with small lobi laterales and pronounced lobuii; pereonites 5 and 6 longer than other pereonites combined. Pereonite 7 very narrow, overlapping pleon. Pleon progressively narrower, epimera prominent. Pleotelson subtriangular, longer than wide; lateral margins slightly sinuous; with 8 pairs of simple setae laterally and pair of small setae on distal apex. Uropodal peduncle with 1 seta; rami subequal, reaching beyond apex of pleotelson, bearing long simple setae.

Pereopods with dense cover of simple setae particularly on ischium to dactylus; pereopod 4 basis with anterior quadrate lobe, ischium distally expanded as flat, large circular cusp-shaped projection with 4–5 large tubercles; carpus to unguis extending at right angle to basis, forming surface with circular cusp of ischium.

Pleopods without setae. Pleopod 2 endopod with appendix masculina three-quarters length of rami. Penes 2 contiguous papillae.

Distribution. South-western Pacific Ocean, 1550 m depth.

Remarks. *M. ponera* most resembles *M. cristatipes* (Stebbing). Both species possess a smoothly rounded frontal border that protrudes between the mandibles; relatively simple mandibles; and pronounced lobuii. *M. ponera* differs from *M. cristatipes* principally in the proportions of the cephalon. *M. cristatipes* possesses a rounded cephalon while the cephalon of *M. ponera* is more rectangular.

Paragnathia Omer-Cooper and Omer-Cooper

Paragnathia Omer-Cooper and Omer-Cooper, 1916: 26. — Omer-Cooper 1916: 124. — Monod, 1926: 308.

Metagnathia Monod, 1922: 645 (type species: *Anceus formica* Hesse, 1864).

Type species. *Anceus halidaii* Bate and Westwood, 1868 (original designation), junior subjective synonym of *Anceus formica* Hesse, 1864.

Diagnosis. Eyes present. Frontal margin of cephalon produced, without processes. Mandibles with simple crenulate blade. Pereonite 1 immersed in cephalon. Pereonite 4 with anterior constriction. Pylopod 6-articled; operculate (articles 1, 3 and 4 enlarged, article 2 reduced); without margin of plumose setae. Pleonites without setae.

Remarks. *Paragnathia* is a monotypic Afro-European genus, the only species being *P. formica* (Hesse, 1864). The species has a complex synonymy (Monod, 1926). It is the only species of Gnathiidae with an operculate, 6-articled pylopod with a reduced second article and mandibles with a crenulate blade.

Thaumastognathia Monod

Thaumastognathia Monod, 1926: 304.

Type species. *Thaumastognathia diceros* Monod, 1926 (monotypy).

Diagnosis. Eyes present. Frontal border variable. Mandibles strongly curved with a crenulate blade. Antenna 1 with stout peduncle, antenna 1 longer than antenna 2. Pereonite 1 immersed in cephalon. Mouthparts small, no articles enlarged. Pylopod 4- or 5-articled, pediform, not operculate. Maxilliped highly reduced or absent. Pereon smooth, cephalosome quasipentagonal, pereonite 7 not visible dorsally. Pleon often folded under peron.

Remarks. *Thaumastognathia* is characterised by the very small size of the pylopod which can be clearly seen only under a compound microscope, and the reduction or absence of the maxilliped; pereon smooth, cephalosome quasipentagonal, antennae curved under the mandibles, antennae 1 longer than antenna 2, absence of pereonite 7, and the pleon folded under the pereon.

These are the first records of *Thaumastognathia* since Monod (1926) described the type species, *T. diceros*, from New Zealand. The three new species bring the total number of species to four, all found in Australasia. A specimen belonging to another species of *Thaumastognathia* was collected from north Queensland but was not described because of its poor condition. All species of *Thaumastognathia* are small, less than 2.5 mm long.

Key to males of species of *Thaumastognathia*

1. Mandibles with pronounced mandibular incisura; pleotelson tapering, margins deeply concave ..... *T. wasmannia*
— Mandibles without mandibular incisura; pleotelson subtriangular, margins straight or slightly sinuous 2
2. Frontal border slightly excavated, maxillipeds absent ..... *T. metaphone*
— Frontal border produced, maxillipeds present 3
3. Ventral margin of cephalon with pair of strong projections lateral to mandibles; carpi of percopods with row of even spines ..... *T. diceros*
— Ventral margin of cephalon without strong projections; carpi of percopods with uneven spination ..... *T. orectognathus*

Thaumastognathia metaphone sp. nov.

Figures 81, 82

Material examined. Holotype. South Australia, Pearson I., E side in bay (33°57.30′S, 134°15.70′E), 20 m, bryozoans, sponges etc. on shaded surface, SCUBA, G.C.B. Poore, 17 Apr 1985 (stn SA 55), NMV J27570 (1 male).

Paratype. Type locality, NMV J27560 (1 male).

Description. Total length of holotype: 2.51 mm.

Cephalosome quasipentagonal, 2.3 times as wide as long, lateral margins slightly concave. Eyes well developed, lateral and sessile. Frontal border roughly transverse, excavated medianly; mediofrontal process small, rounded, located at base of excavation; superior frontolateral process smoothly rounded, forming lateral border for median excavation, with 5–6 setae submarginally spreading laterally, along slight excavation at base of mandible. Inferior frontolateral process conical, mostly transparent, directly ventral to superior frontolateral process. Supraocular lobe not pronounced. Antennae stout, curved under mandible, antenna 1 longer than 2; flagellum of antenna 1 of 3 articles, with 2 aesthetases; flagellum of antenna 2 of 3 articles, shorter than last article of peduncle. Mandible strongly curved, depressed in lateral view, half length of cephalosome; with unarmed carina; slight incisura; dentate blade slightly produced on proximal half; seta at midpoint. Maxilliped absent. Pylopod thin, elongate, 5-articled, first and third with seta, fifth minute.

Pereon oval, wider than cephalosome. Perconite 1 dorsally small, not reaching lateral margins and partially obscured laterally by perconite 2. Peronites 2, 3 and 4 progressively longer. Perconites 5 and 6 fused, longer than others together. Percone 7 not visible dorsally. Pleon folded under pereon, pleonite 5 almost as wide but longer than other pleonites, all without setae. Pleotelson subtriangular, wider than long with pair of simple setae laterally and pair of setae on distal apex. Uropodal peduncle without setae, endopod twice as long as exopod, not reaching apex of pleotelson, with 4 setae distally and 1 seta laterally; exopod with 3 distal setae.

Percopods with posterior and lateral faces of ischium-carpus with irregular acute projections, elsewhere few simple setae.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. South Australia, rocky substrate, 20 m depth.

Remarks. Thaumastognathia is characterised by an oval pereon, cephalosome with concave posterolateral margins and a pleon curving under the pereon. *T. diceros* Monod from New Zealand is easily distinguishable from *T. metaphone* and the other newly described species by the frontal, horn-like protrusions. *T. metaphone* is characterised by the slight median indentation of the frontal border.

Thaumastognathia orectognathus sp. nov.

Figures 83, 84

Material examined. Holotype. Victoria, central Bass Strait, 66 km S of Rodondo I., (39°48.6′S, 146°18.8′E), 82 m, sand-silt-mud, WHOI epibenthic sled, R.S. Wilson on RV *Tangaroa*, 13 Nov 1981 (stn BSS 158), NMV J27567 (1 male).

Paratypes. Most collected using WHOI epibenthic sled by R.S. Wilson on RV *Tangaroa*, Nov 1981. Tasmania, Central Bass Strait, 9 km SSW of Cape Adansan, Three Hummock I. (40°30.9′S, 144°56′E), 27 m,

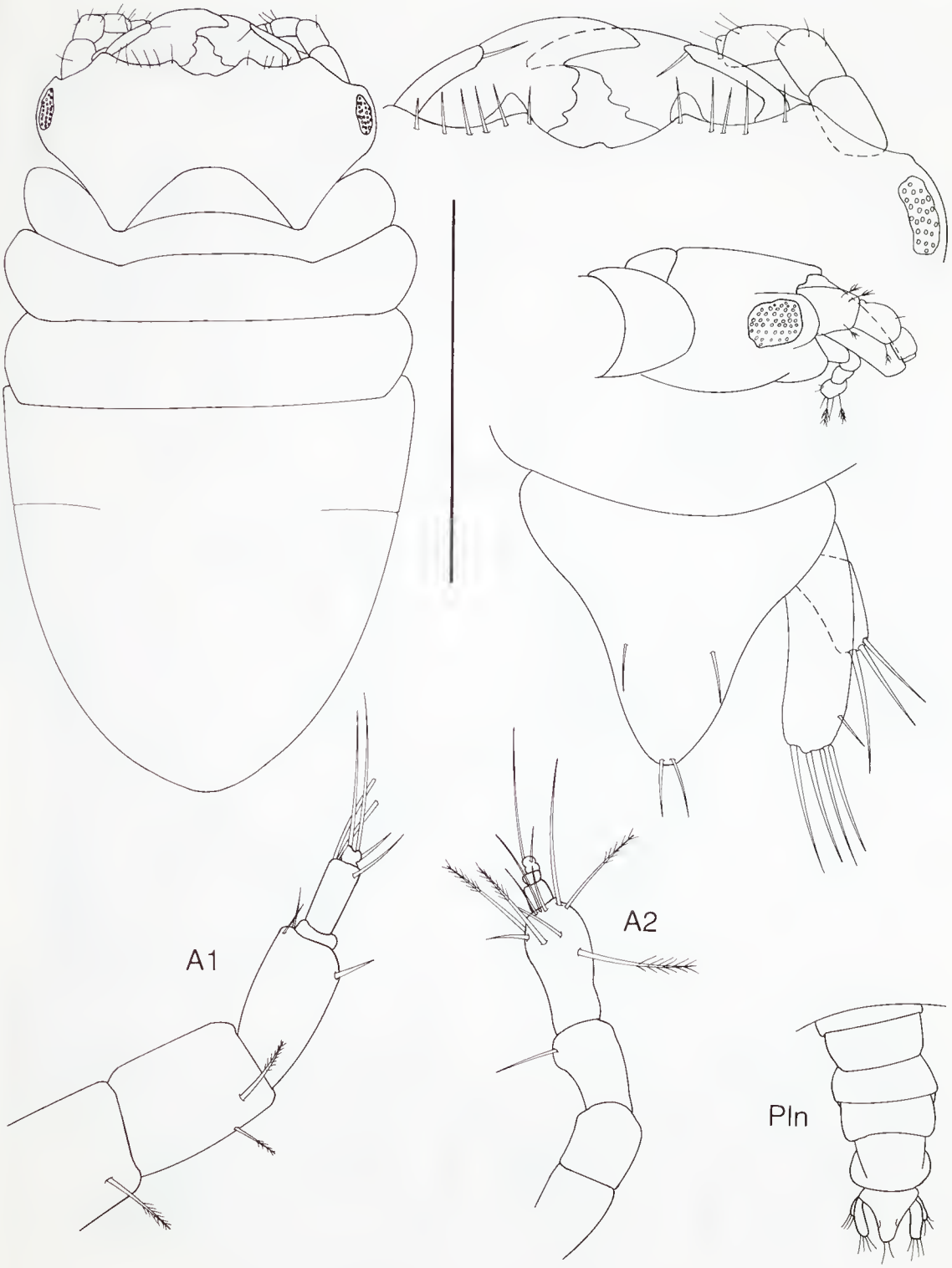

Figure 81. *Thaumastognathia metaphone*. Holotype, NMV J27570.

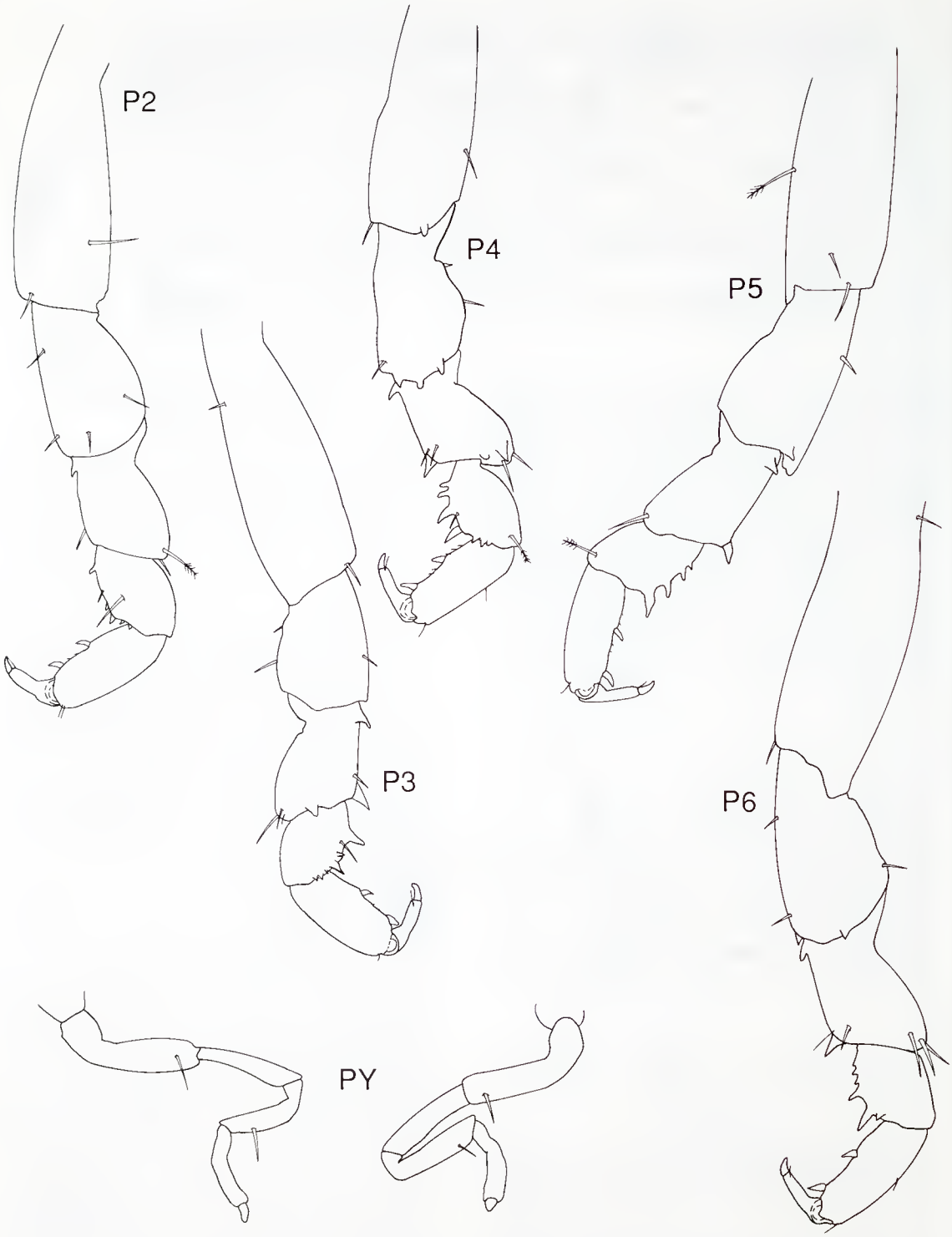

Figure 82. *Thaumastognathia metaphone*. Holotype, NMV J27570.

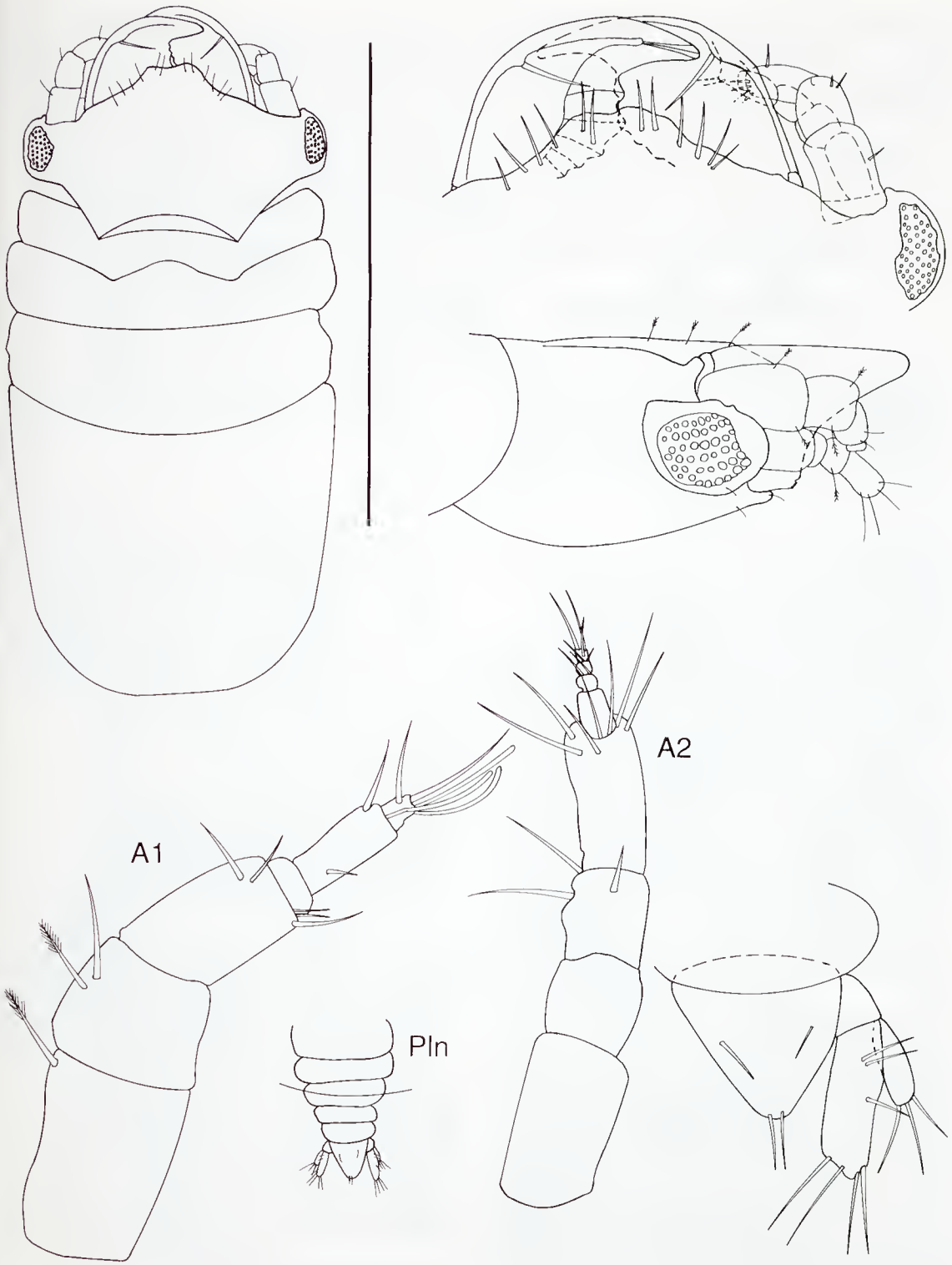

Figure 83. *Thaumastognathia orectognathus*. Holotype, NMV J27567.

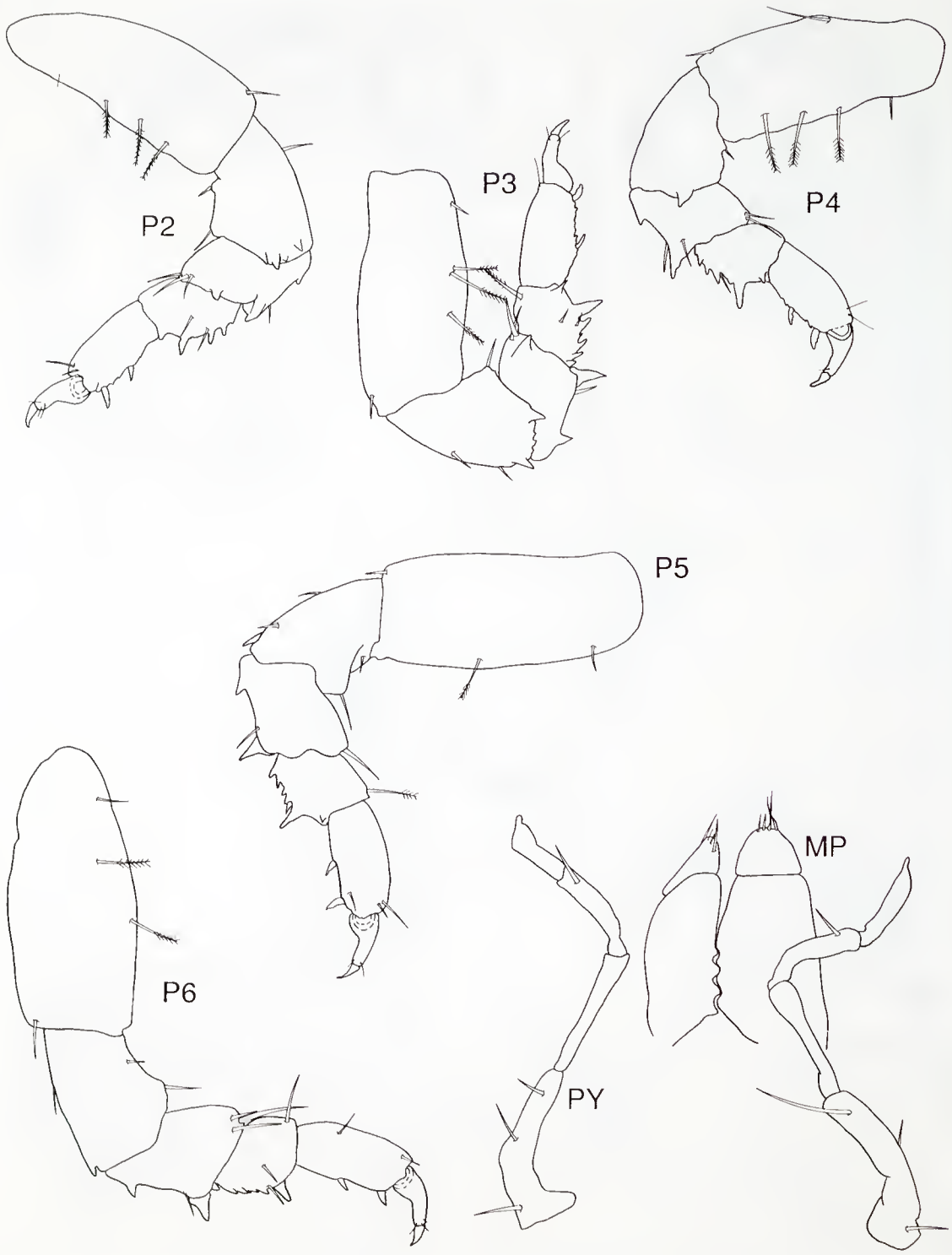

Figure 84. *Thaumastognathia orectognathus*. Holotype, NMV J27567.

very coarse sand. 2 Nov 1980 (stn BSS 109), NMV J8356 (1). Eastern Bass Strait, 100 km NE of North Point, Flinders I., (38°52.6′S, 148°25.2′E), 130 m, fine sand, (stn BSS 170), NMV J8361 (1). 85 km NE of North Point, Flinders I. (39°02.4′S, 148°30.6′E), 120 m, muddy sand (stn BSS 169), NMV J8355 (1).

Victoria. Central Bass Strait, 66 km S of Rodondo I. (39°48.6′S, 146°18.8′E), 82 m, sand-silt-mud (stn BSS 158), NMV J8360 (3). Eastern Bass Strait, 43 km SE of Port Albert (38°53.7′S, 147°06.5′E), 58 m, coarse shell (stn BSS 177), NMV J8358 (1), NMV J8357 (2). 14.3 km WSW of Pt Ricardo (37°50.74′S, 148°28.40′E), 32 m, rock-sand-mud, Smith-McIntyre grab, Marine Science Laboratories on RV *Sarda*, 26 Sep 1990 (stn MSL-EG 46), NMV J24632 (4).

Other material. Bass Strait, 15 km S of Cape Wellington, (39°03.2′S, 146°39.5′E), 55 m, muddy fine sand (stn BSS 179), NMV J8359 (2); S of Point Hicks (38°14.80′S, 149°9.30′E), 200 m, coarse sand (stn SLOPE 41), NMV J19124 (2).

Description. Total length of holotype: 1.50 mm.

Cephalosome quasipentagonal, 1.8 times as wide as long, lateral margins slightly concave. Eyes well developed, lateral and sessile. Frontal border produced dorsally with slightly excavate truncate midanterior margin, with 6 setae submarginally each side. Supraocular lobe not pronounced. Antennae stout, subequal, curved under mandible; flagellum of antenna 1 of 3 articles, with 4 aesthetases; flagellum of antenna 2 of 4 articles, shorter than last article of pedunele. Mandible strongly curved, half length of cephalosome; with unarmed carina; without incisura; crenulate blade produced on proximal half; seta at midpoint. Maxilliped very reduced, of 2 articles; first with crenulate mesial margin, second much shorter, with 4 apical setae. Pylopod thin, elongate, of 4 articles, first with 3 setae, third with 1 seta.

Pereon oval-rectangular, as wide as cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and not visible laterally. Pereonites 2, 3 and 4 progressively longer. Pereonites 5 and 6 fused, longer than others together. Pereonite 7 not visible dorsally. Pleon folded under pereon, pleonites similar, progressively narrower, all without setae. Pleotelson subtriangular, wider than long, with pair of simple setae laterally and pair of setae on apex. Uropodal pedunele without setae, endopod twice as long as exopod, reaching beyond apex of pleotelson, dorsolaterally with 3 setae, distally with 4 setae, exopod with 3 distal setae.

Pereopods 2–6 bases with plumose setae on anterior margins, elsewhere few simple setae, posterior and lateral faces of ischium-carpus with irregular acute projections, propodus palms with 2 short spiniform setae.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Central and eastern Bass Strait, 27–200 m depth.

Remarks. Thaumastognathia orectognathus is most easily recognised by its produced frontal border.

Thaumastognathia wasmannia sp. nov.

Figures 85, 86

Material examined. Holotype. Tasman Sea, 20 km E of Falmouth, Tasmania (41°32.9′S, 148°35.0′E), 122 m, WHOI epibenthic sled, R.S. Wilson on RV *Soela*, 10 Oct 1984 (stn S05/84 5), NMV J27579 (1 male).

Paratype. Type locality, NMV J27559 (1 male).

Description. Total length of holotype: 1.73 mm.

Preserved specimen opaque. Cephalosome quasipentagonal, 2.5 times as wide as long, lateral margins slightly concave. Eyes well developed, lateral and sessile. Frontal border transverse, produced very slightly at base of mandible with shallow excavate midanterior margin, 5 setae submarginally each side forming slight arc. External scissura very shallow. Supraocular lobe not pronounced. Antennae stout, subequal, curved under mandible; flagellum of antenna 1 of 2 articles, with 2 aesthetases; flagellum of antenna 2 of 4 articles, shorter than last article of pedunele. Mandible strongly curved, two-thirds length of cephalosome; with unarmed carina; pronounced mandibular incisor about 0.2 length of mandible, thin and very translucent; crenulate blade weakly produced on proximal two-thirds; setae one-third way along. Maxilliped absent. Pylopod thin, elongate, of 4 articles, first with 2 or 3 setae.

Pereon oval, wider than cephalosome. Pereonite 1 dorsally small, not reaching lateral margins and partially obscured laterally by pereonite 2. Pereonite 4 longer than 2 and 3. Peronites 5 and 6 weakly fused, longer than others together. Pereonite 7 not visible dorsally. Pleon folded under pereon, pleonites 4 and 5 as wide and longer than anterior ones, all without setae. Pleotelson elongate, sharply tapering, as wide as long, lateral margins deeply concave with 2 pairs of simple setae medianly and pair of setae on distal apex. Uropodal pedunele with 1 seta, rami subequal, reaching just beyond apex of pleotelson; endopod dorsolaterally with 3 setae, distally

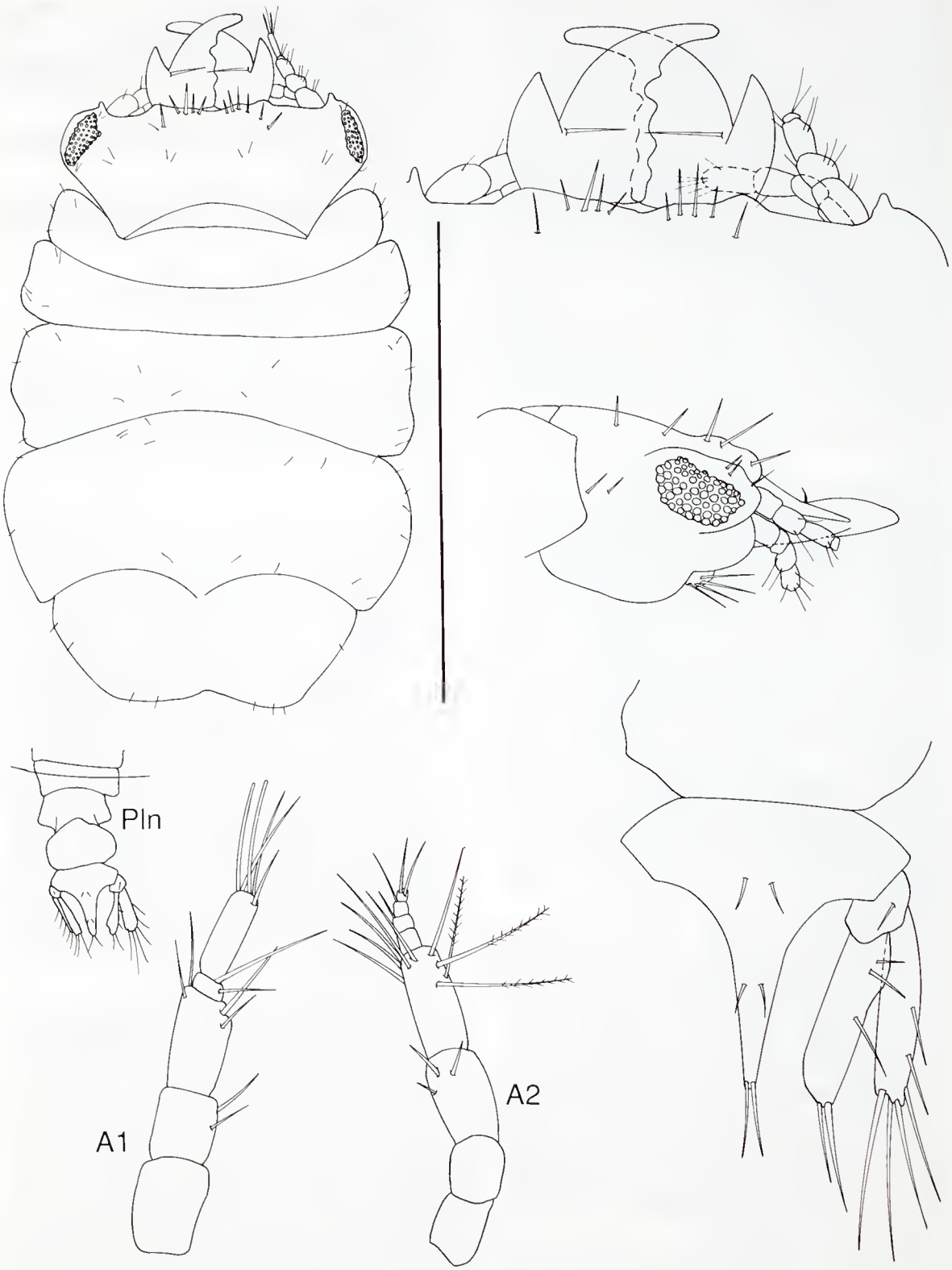

Figure 85. *Thaumastognathia wasmannia*. Holotype, NMV J27579.

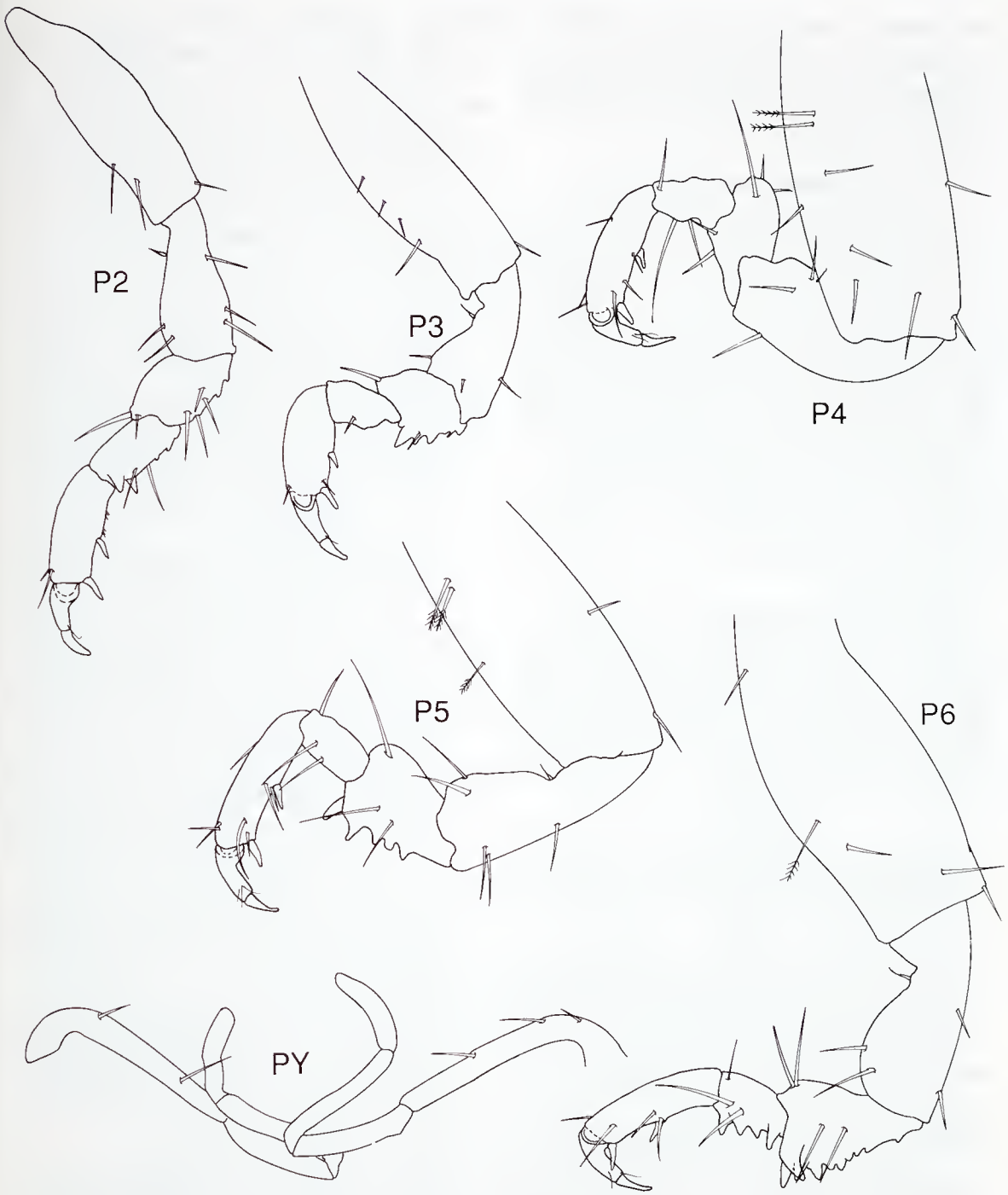

Figure 86. *Thaumastognathia wasmannia*. Holotype, NMV J27579.

with 2 setae; exopod with 3 lateral and 3 distal setae.

Pereopods 4–6 larger than 2 and 3; their bases with few plumose setae on anterior margins, elsewhere few simple setae; posterior and lateral faces of merus-carpus with irregular acute projections, most pronounced on pereopod 6.

Pleopods without setae. Pleopod 2 endopod lacking appendix masculina. Penes 2 small contiguous papillae.

Distribution. Eastern Tasmania, 122 m depth.

Remarks. T. wasmannia is characterised by pronounced mandibular incisors, relatively straight frontal border and deeply concave lateral margins on the pleotelson.

Acknowledgments

This project is part of a wide-ranging exploration of the continental shelf and slope of south-eastern Australia and has been supported by grants from the Australian Research Grants scheme and by the Victorian Institute of Marine Sciences. We are grateful to the ORV *Franklin* Steering Committee and to CSIRO Marine Laboratories, Hobart, for the provision of ship-time and to the master and crew of the vessel for help aboard during the collection of the deep-water material. We are especially grateful to Jean Just for sorting the material. Much of the shallow-water material in the collections of the Museum of Victoria was obtained with assistance from the Australian Biological Resources Study which we thank.

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