

FIRST INGOLFIELLIDS FROM THE SOUTHWEST PACIFIC (CRUSTACEA: AMPHIPODA) WITH A DISCUSSION OF THEIR SYSTEMATICS

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Abstract. — Two new species of ingolfiellid amphipods, *Ingolfiella australiana* and *I. bassiana* are described from the continental shelf of Bass Strait, south-eastern Australia. *Ingolfiella australiana* is similar to some species of the subgenus *Trianguliella* Stock, 1976. *Ingolfiella bassiana* cannot be placed easily into any known subgenus, but shows some similarities to species described from the West Indies and the Canary Islands in the subgenus *Gevgeliella* Karaman, 1959. A re-analysis of sexually dimorphic characters casts doubt on current generic and subgeneric concepts. It is concluded that the ingolfiellidean "eye-lobe" is not homologous with the dorsal pedunculate eyestalk of other peracaridans because of its lateral position. This and other evidence from the Metaingolfiellidae place the ingolfiellidean families within the Gammaridea. The ingolfiellidean maxilliped, carpochele gnathopod 2, and the entire telson suggest similarities to the leucothooid gammarideans. Retention of shared plesiomorphic characters such as a maxilliped without an ischial endite and an entire telson indicates an early derivation from the amphipodan stem.

The ingolfiellidean amphipods comprise about 30 species in 2 families, Ingolfiellidae and Metaingolfiellidae. Ruffo (1970), Stock (1976, 1977, 1979), Ronde-Broekhuizen & Stock (1987), and Dojiri & Sieg (1987) have reviewed the systematics and zoogeography of the group. Although widely distributed from the deep sea to fresh water and hypogean habitats, ingolfiellideans have not previously been recorded from the Southwest Pacific.

Two new species of small ingolfiellids, described herein, were discovered in 2 of over 200 lots of amphipods sorted from benthic samples taken from the continental shelf and slope of Bass Strait, southeastern Australia. Material is lodged in the Museum of Victoria, Melbourne (NMV) and the Australian Museum, Sydney (AM).

The Ingolfiellidae is a conservative family of three genera (Stock 1976, Ruffo 1985). Few specific differences occur in overall body shape, antennae, mouthparts or peraeo-

pods. Nevertheless, Stock (1976) erected five subgenera within *Ingolfiella*, the largest genus. These are separated largely on the basis of sexually dimorphic differences in the second gnathopod and pleopods. We discuss some of the taxonomic problems associated with these subgenera. We also discuss the phylogenetic placement of the ingolfiellidean group.

Family Ingolfiellidae Hansen, 1903

Ingolfiella australiana, new species
Figs. 1-4

Type specimens. — Holotype, male, 2.3 mm, NMV J12851 with 2 slides, paratype, "female," 2.2 mm NMV J12850 with 2 slides, 34 km SW of King Island, 40°26.7'S 143°41.4'E, Bass Strait, Australia, 85 m, sandy shell, Smith-McIntyre grab, R. Wilson et al. on RV *Tangaroa*, 22 Nov 1981 (NMV station BSS 198).

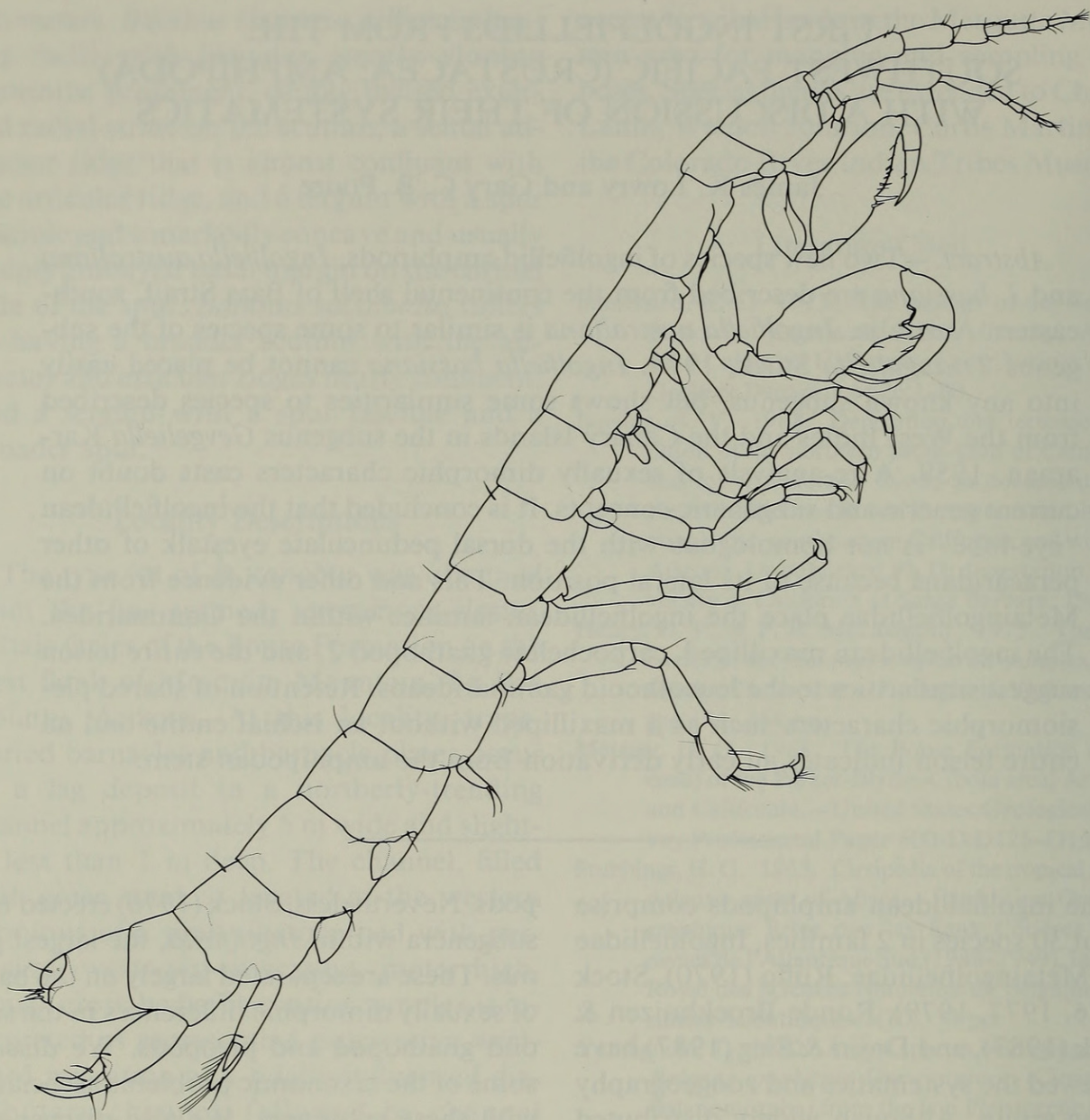


Fig. 1. *Ingolfiella australiana*, holotype male, NMV J12851; southwest of King Island, Bass Strait, Australia. Abbreviations are as follows: A1, A2 = Antennae 1–2; D = Penes; G1, G2 = Gnathopods 1–2; H = Head; LL = Lower lip; l = Left; MD = Mandible; MX1, MX2 = Maxillae 1–2; MP = Maxilliped; P3–P7 = Peraeopods 3–7; PL1–PL3 = Pleopods 1–3; r = Right; T = Telson; U1–U3 = Uropod 1–3; UR3 = Urosomite 3.

Description of holotype.—Body elongate, all segments laterally compressed. Head, anterodorsal margin angular, without rostrum; “eye-lobe” semicircular, small. Peraeonite 1 about half as long as head; posteroventral margin oblique; much deeper anteriorly than posteriorly such that peraeonites 1 and 2 are separated by a waist. Peraeonites 2 to 7 increasing in depth posteriorly. Pleonites 1 to 3 with posteriorly rounded epimera. Urosomites 1 and 2 not markedly differentiated from pleonites, of

similar length; urosomite 3 with lateral plates enclosing base of telson and uropod 3.

Antenna 1, peduncular article 1 as long as head; article ratio 1.0:0.4:0.3; flagellum slightly less than half length of peduncle, five articles, last minute; accessory flagellum just longer than article 1 of flagellum, three articles, last minute. Antenna 2, peduncle as long as peduncle of antenna 1; flagellum of five articles, about one-third length of peduncle.

Left mandible, incisor with four teeth; la-

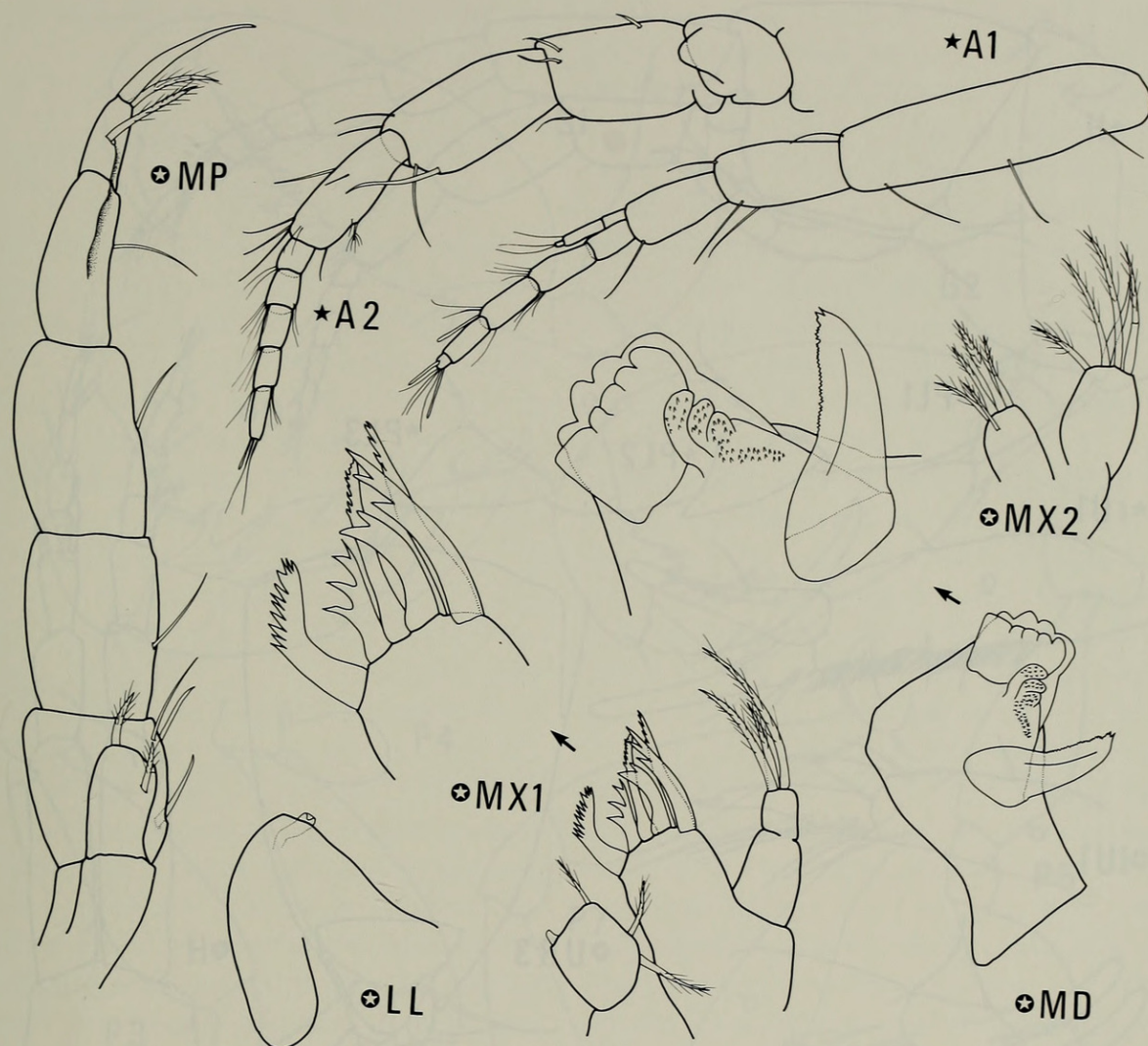


Fig. 2. *Ingolfiella australiana*, holotype male, NMV J12851 (circle star); paratype "female," NMV J12850 (star); southwest of King Island, Bass Strait, Australia. For Abbreviations see Fig. 1.

cinia mobilis as broad as incisor, with five teeth; spine row of three curved, denticulate spines; molar a long triangular blade with minutely denticulate margin. Maxilla 1, inner plate subquadrate, with four setae; outer plate with three strong cuspidate spines in anterior row, two denticulate spines in posterior row, and one well developed curved comb-spine medially; palp of two articles, with three apical plumose setae. Maxilla 2, inner plate with one subterminal seta and four terminal setae; outer plate with five setae. Maxilliped, basal endite with one subapical and one apical seta; palp articles 1 to 4 with three, one, one, and one mesial setae respectively, article 5 with long falcate unguis, seta at midlength and at base of unguis.

Gnathopod 1 carpocheate, palm strongly

oblique; coxa inserted at anteroventral corner of peraeonite; carpus 2.2 times as long as wide, palm with three proximal spines and eight setae, without teeth; dactylus with four serrations. Gnathopod 2 carpocheate, palm slightly oblique; carpus 1.6 times as long as wide; palm defined by strong curved spine, distally with triangular tooth and quadrate tooth separated by narrow notch, with one spine and four setae (one seta proximal to definitive palm spine); propodus with two triangular blades posteriorly, distal blade larger; dactylus with three teeth on posterior margin, dactylus longer than palm, extending over carpus.

Peraeopods 3 and 4, dactylus with two distal setae and cylindrical bifid unguis. Peraeopods 5 to 7, basis slightly broadened in

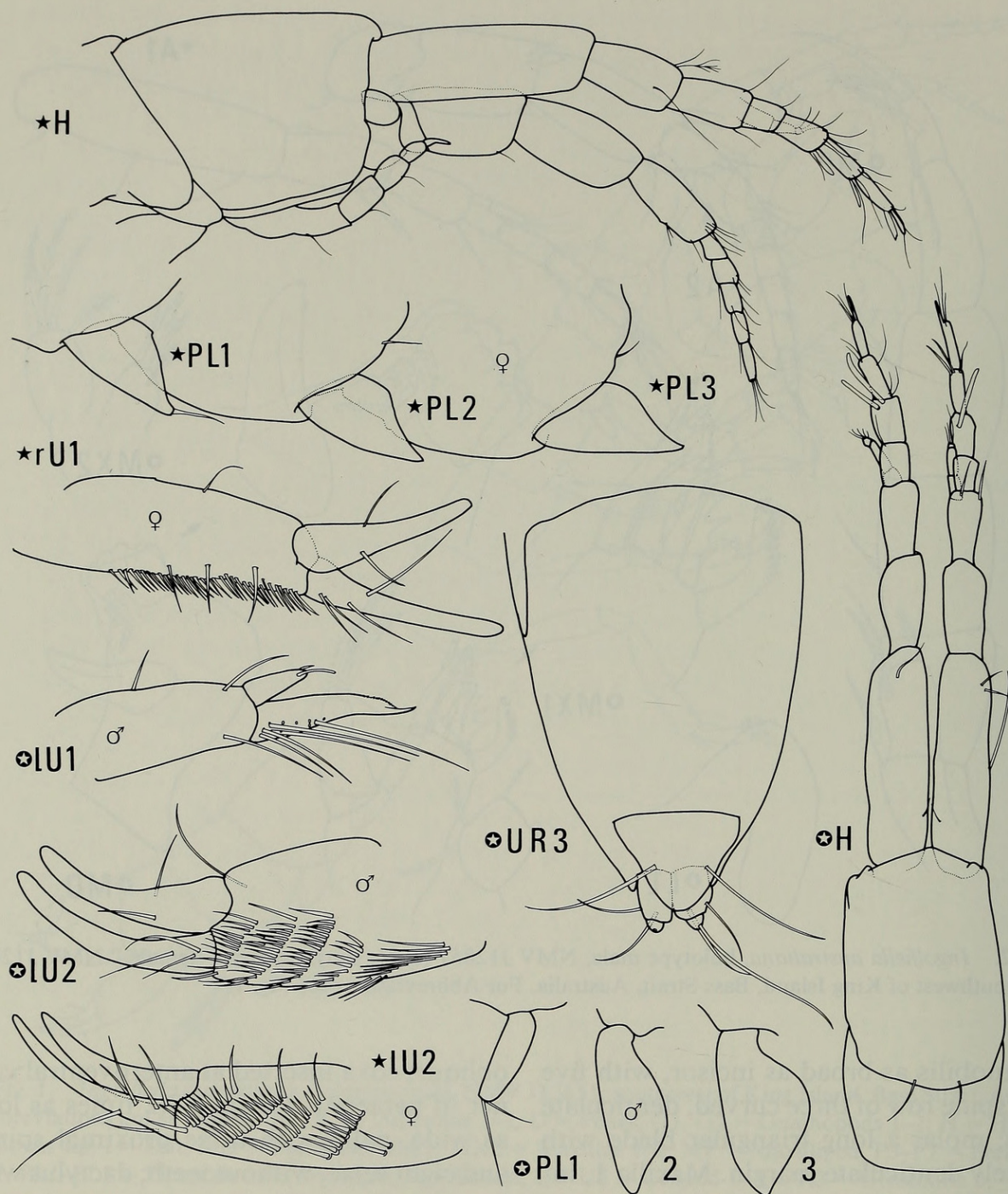


Fig. 3. *Ingolfiella australiana*, holotype male, NMV J12851 (circle star); paratype "female," NMV J12850 (star); southwest of King Island, Bass Strait, Australia. For Abbreviations see Fig. 1.

peraeopod 5, becoming progressively narrower in peraeopods 6 and 7; dactylus stout, curved, unguis not defined.

Pleopod 1 cylindrical with two setae; pleopods 2 and 3 subtriangular.

Uropod 1, peduncle 1.3 times as long as inner ramus; inner ramus with lateral row of 10 long setae, 4 apical spines in dished

tip, edges of apex finely denticulate; outer ramus 2.2 times as long as inner ramus, with 2 distal setae. Uropod 2, peduncle with 5 oblique rows of (proximal to distal) 11, 9, 17, 15, 12 spines mesially (2 spines between rows 4 and 5); inner ramus $\frac{3}{4}$ length of peduncle, with 3 proximal setae; outer ramus shorter than inner with 2 setae near mid-

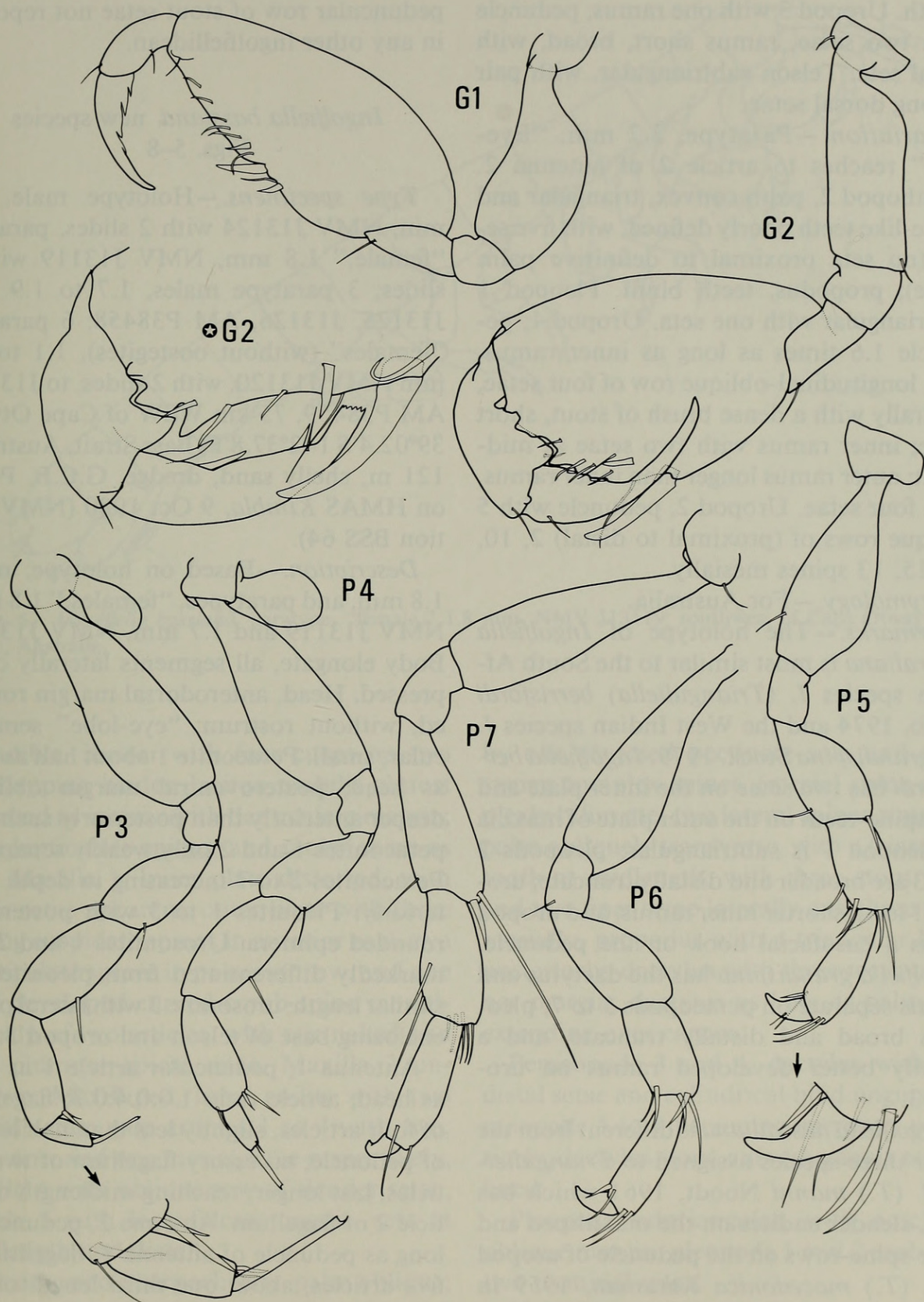


Fig. 4. *Ingolfiella australiana*, holotype male, NMV J12851 (circle star); paratype "female," NMV J12850; southwest of King Island, Bass Strait, Australia. For Abbreviations see Fig. 1.

length. Uropod 3 with one ramus; peduncle with two setae, ramus short, broad, with distal seta. Telson subtriangular, with pair of long dorsal setae.

Variation.—Paratype, 2.2 mm. “Eye-lobe” reaches to article 2 of antenna 2. Gnathopod 2, palm convex, triangular and blade-like teeth poorly defined, with five setae (no seta proximal to definitive palm spine); propodus, teeth blunt. Pleopod 1 subtriangular with one seta. Uropod 1, peduncle 1.6 times as long as inner ramus, with longitudinal-oblique row of four setae, ventrally with a dense brush of stout, short setae; inner ramus with two setae at midpoint; outer ramus longer than inner ramus, with four setae. Uropod 2, peduncle with 5 oblique rows of (proximal to distal) 2, 10, 13, 15, 13 spines mesially.

Etymology.—For Australia.

Remarks.—The holotype of *Ingolfiella australiana* is most similar to the South African species *I. (Trianguliella) berrisfordi* Ruffo, 1974 and the West Indian species *I. (T.) grandispina* Stock, 1979. *Ingolfiella berrisfordi* has two setae on the inner plate and five spine-teeth on the outer plate of maxilla 1; pleopod 1 is subtriangular; pleopods 2 and 3 are broader and distally truncate; uropod 1 has a shorter inner ramus; and uropod 2 has a basofacial hook on the peduncle. *Ingolfiella grandispina* has the dactylus and unguis separate on peraeopods 5 to 7; pleopods broad and distally truncate, and a slightly better developed ramus on uropod 3.

Ingolfiella australiana is different from the other three species assigned to *Trianguliella*: *I. (T.) manni* Noodt, 1961 which has long, slender endites on the maxilliped and three spine-rows on the peduncle of uropod 2; *I. (T.) macedonica* Karaman, 1959 in which the palmar spine and the dactylus of gnathopod 2 are not enlarged; and *I. (T.) thibaudi* Coineau, 1968 in which males have only pleopod 1 and females have no pleopods.

Uropod 1 of the paratype of this species is unusual in the possession of a ventral

peduncular row of stout setae not reported in any other ingolfiellidean.

Ingolfiella bassiana, new species
Figs. 5–8

Type specimens.—Holotype male, 1.8 mm, NMV J13124 with 2 slides, paratype “female,” 1.8 mm, NMV J13119 with 2 slides; 3 paratype males, 1.7 to 1.9 mm J13125, J13126, AM P38458; 6 paratype “females” (without oostegites), 1.1 to 1.8 mm NMV J13120, with 2 slides, to J13123, AM P38459, 75 km WSW of Cape Otway, 39°02.4'S 142°37.8'E, Bass Strait, Australia, 121 m, shelly sand, dredge, G.C.B. Poore on HMAS *Kimbla*, 9 Oct 1980 (NMV station BSS 64).

Description.—Based on holotype, male, 1.8 mm, and paratypes, “females,” 1.8 mm, NMV J13119 and 1.7 mm, NMV J13120. Body elongate, all segments laterally compressed. Head, anterodorsal margin rounded, without rostrum; “eye-lobe” semicircular, small. Peraeonite 1 about half as long as head; posteroventral margin oblique; deeper anteriorly than posteriorly such that peraeonites 1 and 2 only weakly separated. Peraeonites 2 to 7 increasing in depth posteriorly. Pleonites 1 to 3 with posteriorly rounded epimera. Urosomites 1 and 2 not markedly differentiated from pleonites, of similar length; urosomite 3 with lateral plates enclosing base of telson and uropod 3.

Antenna 1, peduncular article 1 as long as head; article ratio 1.0:0.4:0.3; flagellum of four articles, slightly less than half length of peduncle; accessory flagellum of two articles, last longer, reaching midlength of article 2 of flagellum. Antenna 2, peduncle as long as peduncle of antenna 1; flagellum of five articles, about one-third length of peduncle.

Mouthparts of juvenile (NMV J13120) (Fig. 6). Left mandible, incisor with three cusps; lacinia mobilis as broad as incisor, with five cusps; spine row of three curved, denticulate spines; molar a long triangular blade with minutely serrate margin. Right

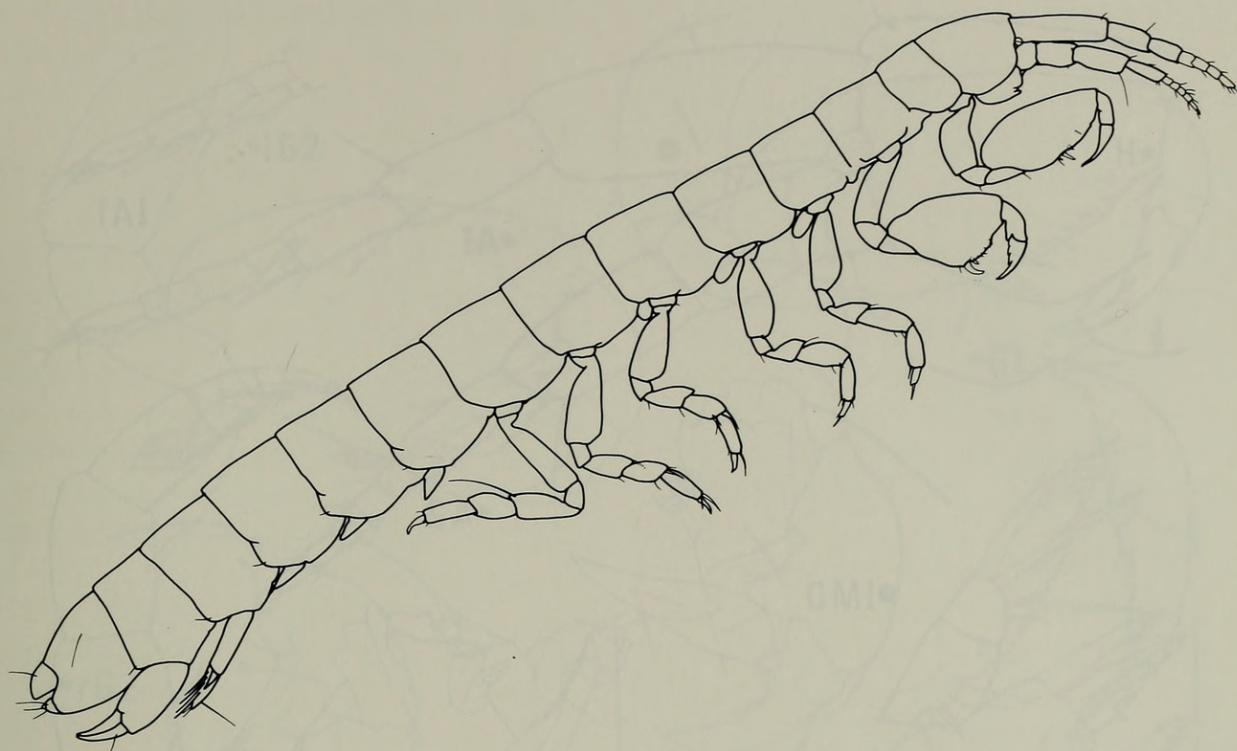


Fig. 5. *Ingolfiella bassiana*, paratype, "female," 1.8 mm, NMV J13119; southwest of Cape Otway, Bass Strait, Australia.

mandible, incisor with four cusps on two overlapping blades; lacinia mobilis almost as broad as incisor with denticulate margin; two denticulate spines, and molar same as left. Maxilla 1, inner plate distorted, with three setae apparent; outer plate with three strong cuspidate spines in anterior row, two denticulate spines in posterior row, and one well developed curved comb-spine mesially; palp of two articles, with one naked and two plumose apical setae. Maxilla 2 unknown. Maxilliped, basal endite with two apical setae; palp articles 1 to 4 with two, one, one, and one mesial setae respectively, article 4 with oblique row of slender setae, article 5 with long falcate unguis, seta at midlength and distally.

Gnathopod 1 carpocheate, palm oblique; coxa at anterior of peraeonite; carpus 2.2 times as long as wide, palm with three proximal spines, three weaker spines and three setae, without teeth; dactylus with three spines along posterior margin. Gnathopod 2 carpocheate, palm nearly transverse; carpus 1.6 times as long as wide; palm defined

by one reversed pectinate seta and three strong complex spines, (mesial spine complexly bifurcate, two lateral spines simpler), palm obliquely transverse, with a triangular tooth at midlength, with three stout setae and two finer setae laterally and three setae mesially, propodus with a triangular blade posteriorly; dactylus with three teeth on inner margin; dactylus as long as palm, not extending over carpus.

Peraeopods 3 and 4, dactylus with two distal setae and cylindrical bifid unguis. Peraeopods 5 to 7 becoming narrower posteriorly; dactylus stout, curved, unguis not defined.

Pleopods subtriangular, with notch on oblique margin; pleopods 1 and 2 each with two terminal setae.

Uropod 1, peduncle 1.4 times as long as inner ramus with lateral, plumose setae; inner ramus with a mesial row of four long setae and four distal spines; outer ramus 0.6 times as long as inner ramus, with one seta. Uropod 2, peduncle with proximoventral hook and 4 obliquely transverse rows of

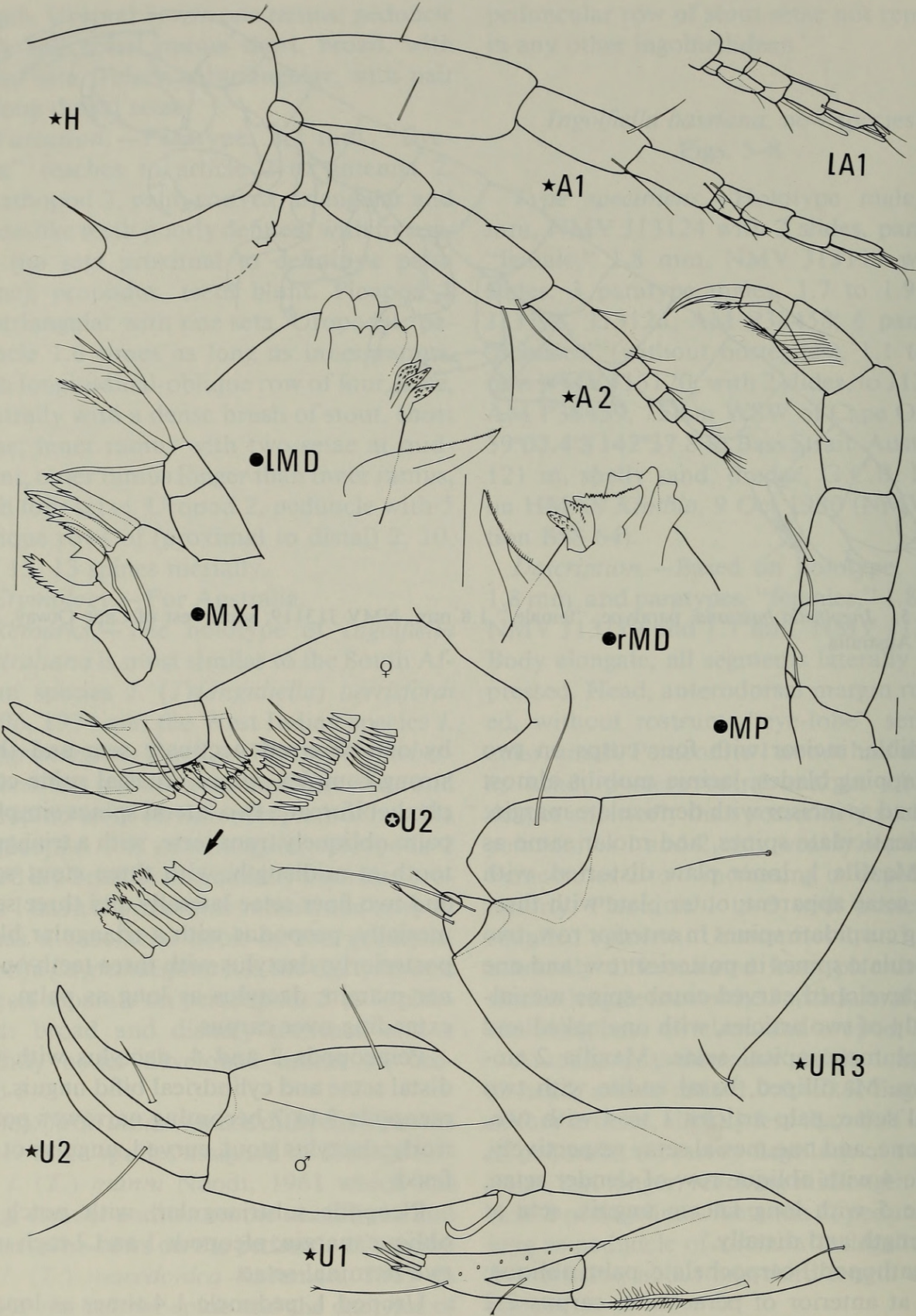


Fig. 6. *Ingolfiella bassiana*, holotype, male, 1.8 mm, NMV J13124 (closed star); paratype, "female," 1.7 mm, NMV J13120 (closed circle); paratype, "female," 1.8 mm, NMV J13119 (circle star); southwest of Cape Otway, Bass Strait, Australia. For Abbreviations see Fig. 1.

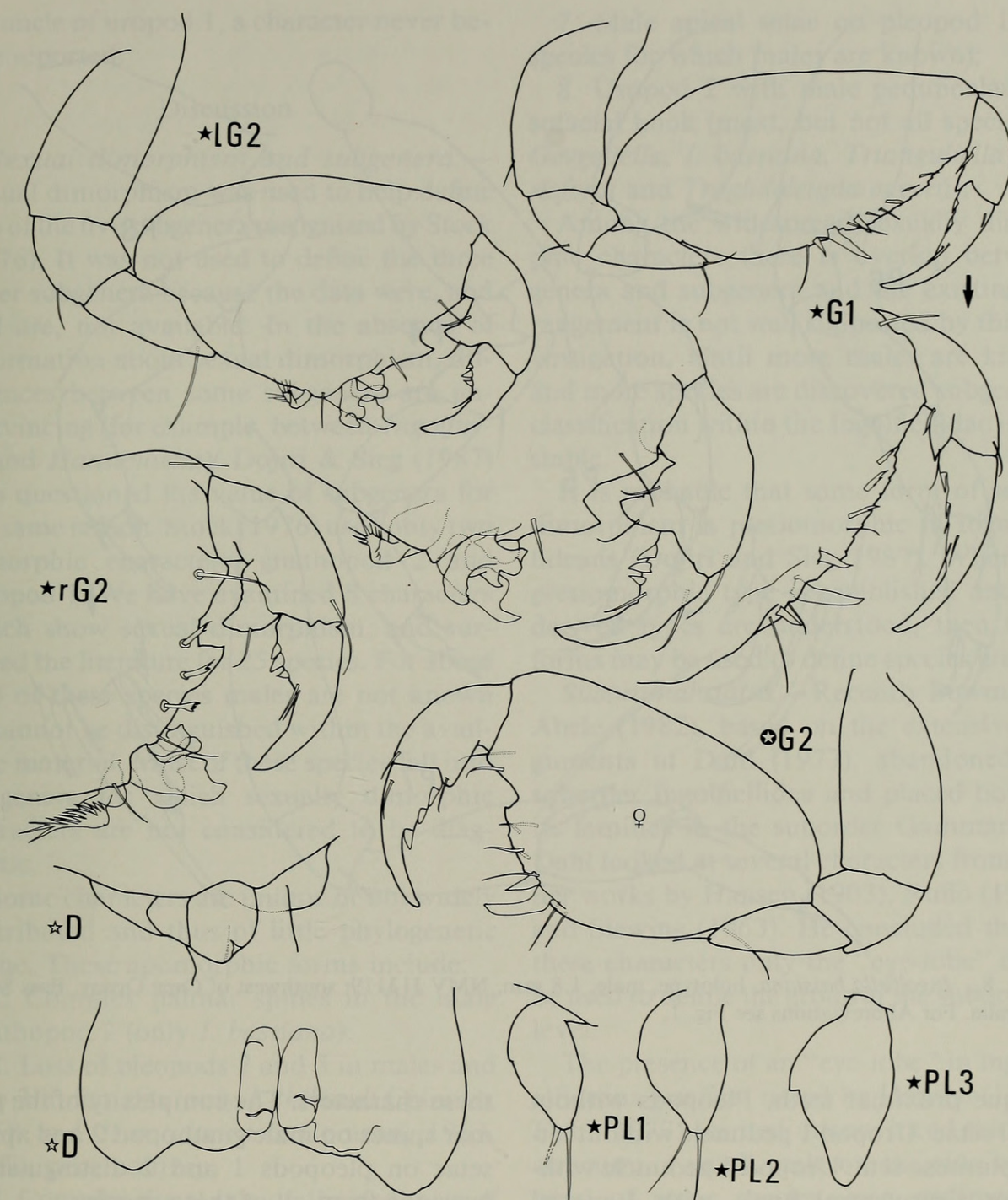


Fig. 7. *Ingolfiella bassiana*, holotype, male, 1.8 mm, NMV J13124 (closed star); paratype "female," 1.8 mm NMV J13119 (circle star); paratype, male, 1.8 mm, NMV J13125 (open star); southwest of Cape Otway, Bass Strait, Australia. For Abbreviations see Fig. 1.

(proximal to distal) 12, 16, 13, 8 spines (those ventrally in third and fourth rows apically complex); rami 1-articulate, equal, 0.6 times length of peduncle, inner ramus with 4 setae; outer ramus with transverse row of 3 spines plus 3 setae. Uropod 3 with one ramus; peduncle with two lateral setae,

ramus short, broad, with long distal seta. Telson subtriangular, with pair of long dorsal setae.

"Females."—As in male but: gnathopod 2 carpus palm defined by two spines, palm oblique and with distal notch; propodus with straight posterior margin; dactylus with three

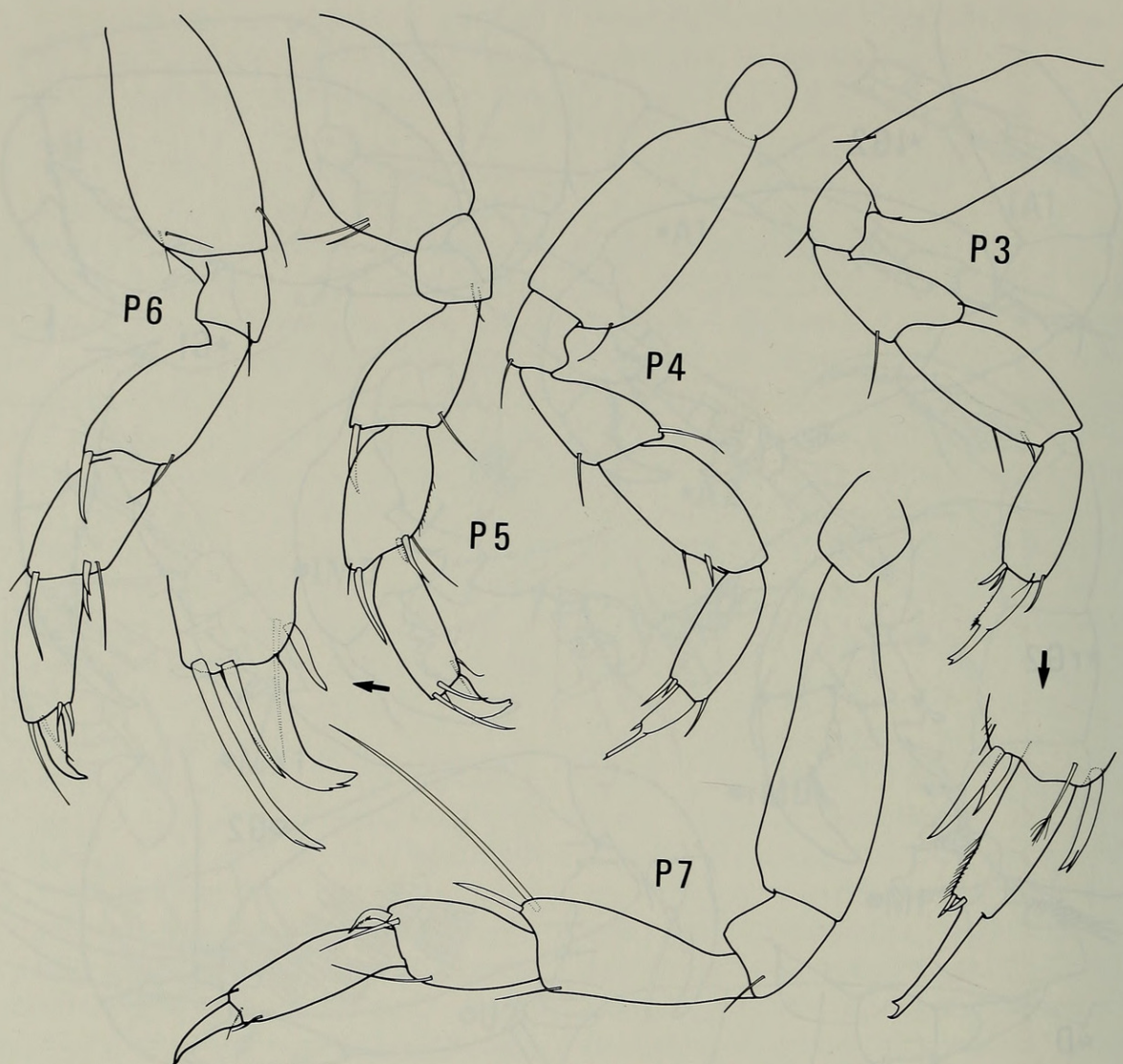


Fig. 8. *Ingolfiella bassiana*, holotype, male, 1.8 mm, NMV J13119; southwest of Cape Otway, Bass Strait, Australia. For Abbreviations see Fig. 1.

oblique proximal teeth. Pleopods without distal setae. Uropod 1 peduncle without lateral plumose seta. Uropod 2 peduncle without proximoventral hook, with 4 mesial transverse rows of (proximal to distal) 9, 15, 12, 8 spines.

Etymology.—For Bass Strait.

Remarks.—The possession of triangular pleopods and a basofacial hook on uropod 2 allies *I. bassiana* to the five West Indian and Canary Islands species in the subgenus *Gevgeliella* discussed by Ronde-Broekhuizen & Stock (1987). All differ from the type species *I. petkovskii* Karaman, 1957, and the two other Mediterranean species of *Gevgeliella* (*I. catalanensis* Coineau, 1963 and *I. vandeli* Bou, 1970) which do not have

these characters. The complexity of the palmar spines on male gnathopod 2 and apical setae on pleopods 1 and 2 distinguish *I. bassiana* from all of these species.

Stock (1979) has suggested that the reversed seta on gnathopod 1, the apical setae on pleopod 1 and the basofacial hook on uropod 2 are all male characters of *Gevgeliella*. Our holotype has all of these characters and paired penial processes. Our “female” specimens do not, thus confirming Stock’s presumptions.

The complex nature of the mesial spines on uropod 2 (shown here in female) have been illustrated (for *I. fuscina*) previously only by Dojiri and Sieg (1987). Males of *I. bassiana* possess a long plumose seta on the

peduncle of uropod 1, a character never before reported.

Discussion

Sexual dimorphism and subgenera. — Sexual dimorphism was used to help define two of the five subgenera recognized by Stock (1976). It was not used to define the three other subgenera because the data were, and still are, not available. In the absence of information about sexual dimorphism, differences between some subgenera are unconvincing (for example, between *Ingolfiella* and *Hansenliella*). Dojiri & Sieg (1987) also questioned the value of subgenera for the same reason. Stock (1976) used only two dimorphic characters, gnathopod 2 and pleopod 1. We have examined 8 characters which show sexual dimorphism, and surveyed the literature for 25 species. For about half of these species males are not known or cannot be distinguished within the available material. Most of these species fall into subgenera for which sexually dimorphic characters are not considered to be diagnostic.

Some characters are unique or not widely distributed and thus of little phylogenetic value. These apomorphic forms include:

1. Complex palmar spines in the male gnathopod 2 (only *I. bassiana*);

2. Loss of pleopods 2 and 3 in males and 1 to 3 in females (only *I. thibaudi* Coineau, 1968 and *I. catalanensis* Coineau, 1963, Ruffo, pers. comm);

3. Complex distal seta on the peduncle of male uropod 1 (in *I. fuscina* Dojiri & Sieg, 1987 and *Troglroleleupia eggerti* Ruffo, 1951);

4. Row of stout ventral setae in "female" uropod 1 (only *I. bassiana*).

Other characters are more widespread and may indicate phylogenetic affinities. These include:

5. Reversed seta on carpus of gnathopod 2 (occurs in all species assigned to *Gevgeliella* and *Troglroleleupia eggerti*);

6. Male pleopod 1 digitiform (most species of *Trianguliella* and *G. catalanensis*;

7. Male apical setae on pleopod 1 (all species for which males are known);

8. Uropod 2 with male peduncular basofacial hook (most, but not all species of *Gevgeliella*, *I. bassiana*, *Trianguliella berisfordi* and *Troglroleleupia eggerti*).

Among the widespread sexually dimorphic characters there is overlap between genera and subgenera and the existing arrangement is not well supported by this investigation. Until more males are known and more species are discovered subgeneric classification within the Ingolfiellidae is unstable.

It is probable that some form of sexual dimorphism is plesiomorphic in ingolfiellideans (Dojiri and Sieg 1987). When the plesiomorphic type is established and the derived types are understood, then these forms may be used to define species groups.

Subordinal status. — Recently Bowman & Abele (1982), based on the extensive arguments of Dahl (1977), abandoned the suborder Ingolfiellidea and placed both of its families in the suborder Gammaridea. Dahl looked at several characters from earlier works by Hansen (1903), Ruffo (1951), and Siewing (1963). He concluded that of these characters only the "eye-lobe" could be used to define the group at the subordinal level.

The presence of an "eye-lobe" in ingolfiellideans was first noted by Hansen (1903). Dahl (1977) seemed unconvinced that this structure, a small scale on the side of the head of some species, is a rudimentary stalked eye. He noted: "Its functional significance is unknown, and it contains no dioptric and apparently also no nervous elements. Its location, however, corresponds well with that of the lobate rudiment of the compound eye in *Gammarus* . . ." Bowman (1984), citing Dahl, was equally equivocal: "Whether these lobes represent eyestalks is questionable."

Only three of seven peracaridan orders contain species with unambiguous eyestalks. In the Mysidacea (numerous species) the eyestalks carry well developed terminal

eyes. In the Spelaeogriphacea, where only two living species are known (*Spelaeogriphus lepidops* and *Potiicoara brasiliensis*), the lobe has no pigment or optic structure (Gordon 1957, Pires 1987). In Mictacea one of the three species known (*Mictocaris halope*) has pyriform eyestalks lacking visual elements (Bowman & Iliffe 1985). In the only pancaridan order, four of the six Thermosbaenacea genera have plate-like eyestalks but lack pigment (Bowman & Iliffe 1986, 1988). Eyestalks in the syncarid family Anaspididae are similar to those in peracaridans. The spelaeogriphaceans, the thermosbaenaceans and the mictacean are troglobitic so it is not surprising that they are blind. What is notable is that the eyestalks in all these groups attach obliquely above the first antenna near the base of the rostrum, a position and attitude very different from that of the ingolfiellidean scale.

It seems probable that the hinged ingolfiellidean "eye-lobe" is the anterolateral margin of the head, often produced at this point in amphipods, whether it bears a sessile eye or not. A similar situation is seen in the tanaidacean genus *Heterotanais* in which the eyes occur on hinged lobes (Sars 1896). These are in the same position, ventral to the antennae, as the normally sessile eyes of other tanaidaceans.

We think that the so-called "eye-lobe" of ingolfiellideans is not homologous to that of other peracaridans or of other malacostracans. The "eye-lobe" therefore is not of subordinal importance.

Dahl (1977) did not take into account the single species of the second ingolfiellidean family, *Metaingolfiella mirabilis* (Ruffo, 1969). The plesiomorphic characters of this species provide further evidence for the placement of the group within the Gammaridea. The pleopods of *M. mirabilis* are biramous, typical of most Gammaridea, and quite unlike the reduced form of the Ingolfiellidae. On pereopods 3 and 4 the unguis is undifferentiated, as in Gammaridea, and not specialized as in Ingolfiellidae. The

mandibular molar is a fixed process, not articulating as in Ingolfiellidae. The existence of *Metaingolfiella* removes any argument for retaining a separate suborder.

Relationships within the Gammaridea. — Many of the unusual characters of the ingolfiellideans are associated with their interstitial way of life and are paralleled by other crustaceans in similar habitats. The maxilliped, gnathopods 1 and 2, and the telson may help place the group within the Gammaridea.

In considering the polarity of character states in the following discussion we have used the isopods for outgroup comparison. Most peracaridan groups, including the isopods, have a maxilliped with a basal endite and a palp of five articles, a condition which we consider plesiomorphic among peracaridans. This state also occurs in ingolfiellideans and in all members of the gammaridean families Cressidae, Leucothoidae, Pagetinidae, Stenothoidae and Thaumatesonidae. This is in contrast to the more widely held view that a maxilliped with both basal and ischial endites (the usual gammaridean state) is plesiomorphic (Bousfield 1979). The small ischial endite which occurs in some of these families is thus a developing rather than a reducing condition.

Carpochelate gnathopods are an important character defining the ingolfiellideans. A similar condition is known in leucothoids, some corophioids, the deep sea pardaliscid *Eperopeus abyssicola* Mills, 1967, and is widespread among the hyperiideans. There can be little doubt that carpocheley has arisen more than once, but the leucothoids are the only group which share the primitive maxilliped with the ingolfiellideans.

The telson is entire in all peracaridan groups. The only exception is some Amphipoda. We consider it to be the plesiomorphic condition among the isopods and the amphipods. It is entire in the ingolfiellideans, leucothoids, corophioids and representatives within other families. We rec-

ognize that within the Amphipoda the entire telson has been secondarily derived many times. This contrasts with the view of Bousfield (1979) that the laminate cleft telson is plesiomorphic.

The evidence for phylogenetic relationships of the ingolfiellideans within the Gammaridea is meager. The ingolfiellideans and the leucothoids are the only living amphipods without an ischial endite on the maxilliped. This is the usual form in all other peracaridans, and indicates that the evolution of ischial endites occurred after the amphipods arose as a distinct group. The ingolfiellideans and the leucothoids both have carpochele gnathopods. These observations may be interpreted as a phylogenetic link between the ingolfiellideans and the leucothoids and may indicate that both groups were derived early and close from the amphipodan stem.

Acknowledgments

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