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The rediscovery of *Danielssenia intermedia* Wells 1965 (Copepoda, Harpacticoida): a missing link between the 'danielsseniid' genera and *Paranannopus* Lang 1936 (Paranannopidae)

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Danielssenia intermedia Wells 1965, originally described from a single male specimen from the Fladen ground in the North Sea, is redescribed on the basis of new material of both sexes from off Cullercoats, also in the North Sea. Although *D, intermedia* has many similarities to the genera *Danielssenia* Boeck and *Psammis* Sars, it must be placed in a new genus *Fladenia* based on distinctive features of the female antennule, the mandible, maxilliped, first and fifth legs and the sexual dimorphism of both rami of legs 2–4. The characteristics of *Fladenia* are such that it serves to link the other genera of the danielsseniid complex with *Paranannopus* Lang. The proposal that all these genera should be placed in the family Paranannopidae Por is reinforced by close similarities in the structure of the female genital field.

KEYWORDS: Copepoda, Harpacticoida, *Fladenia* gen. nov., *Danielssenia, Psammis, Paranannopus*, Paranannopidae.

Introduction

Wells (1965) described *Danielssenia intermedia* from a single male specimen recovered from core samples taken at 146 m depth on the Fladen ground in the northern North Sea in sediment made up of approximately 20% fine sand and 80% silt and clay (McIntyre, 1961). From features which could be discerned in the whole mount, Wells (1965) was unable to assign it, with certainty, to either *Danielssenia* Boeck 1872 or *Psammis* Sars 1910, as they were then constituted. His decision 'to place it in the former genus was based almost solely on the structure of the fifth leg with some supporting evidence from the setation of the swimming legs', but he suggested that the discovery of the female of this species would be most useful in resolving its taxonomic position.

Recently, Dr R. Hamond sent us a small number of 'Danielssenia-like' forms which he collected from a soft, grey mud bottom at 91 m off Cullercoats in the North Sea. These proved to include some specimens of *Danielssenia typica* Boeck 1872 and a number of females and males of a species in which the characteristics of the males agreed with the type specimen of *D. intermedia*.

Lang (1944) placed the genera *Danielssenia* and *Psammis* along with *Thompsonula* T. Scott 1905 in the subfamily Thompsonulinae of the family Tachidiidae Sars, Lang. Since that time three further genera, *Paradanielssenia* Soyer 1970, *Leptotachidia* Becker 1974 and *Micropsammis* Mielke 1975 (see Bodin, 1988), have been described which are related in some way to *Danielssenia* and, therefore, have been placed in the same subfamily. Recently, however, Huys and Gee (1990) raised the subfamily to full family rank and redefined the Thompsonulidae to include only the genus *Thompsonula* and a new genus *Caribbula*. In the same paper they indicated that the systematic position and affinities of the 'danielsseniid genera' were uncertain, but suggested that they may be closely related to the two genera at present constituting the family Paranannopidae as defined by Por (1986).

In this paper not only do we show that the discovery of the female of *D. intermedia* Wells necessitates the erection of a new genus, but also that its characteristics strengthen the argument that the 'danielsseniid genera' should be placed in the Paranannopidae.

Methods

The habitus was drawn and body length measurements made from whole specimens mounted in lactic acid. Specimens of both sexes were dissected in lactophenol, the parts mounted in polyvinyl lactophenol, and all drawings prepared using a camera lucida on an Olympus BH-2 interference microscope.

In this paper the terminology of Lang (1948, 1965) is adopted except that (1) following Mielke (1984), the terms pars incisiva, pars molaris and lacinia mobilis are omitted in the description of the mandibular gnathobase; (2) the terminology applied to the segments of the mandible and maxilliped follows that of Boxshall (1985); (3) the terminology for caudal ramus structure follows that of Huys (1988). Abbreviations used in the text and figures are: P1–P6 for swimming legs 1–6; exopod (endopod)-1 (-2, -3) to denote the proximal (middle, distal) segment of a ramus. Body length was measured from the base of the rostrum to the posterior margin of the anal somite.

Systematics

Genus *Fladenia* gen. nov.

Synonyms: Danielssenia Boeck (part.)

Diagnosis. Body rounded anteriorly; prosome slightly dorsoventrally flattened; urosome narrower than prosome; P1 bearing somite incorporated in cephalothorax; female genital double-somite with lateral and ventral cuticular ridge; hyaline frill including pseudoperculum minutely dentate; anal somite deeply divided; seta I of caudal ramus minute. Female genital field with genital slit, rectangular copulatory pore, paired seminal ducts and single ovoid seminal receptacle anterior to copulatory pore; vestigial P6 with one seta and two denticles; two large flap-pores just posterior to genital field. Rostrum, large, hyaline, semi-circular with four sensilla. Female antennula 5-segmented; segment II with two large posteriorly directed pinnate setae; segment III and V with aesthetasc; segment IV with pectinate spines. Antenna with well-developed coxa; allobasis with large pinnate seta; 3-segmented exopod with one, one, three setae on proximal to distal segments. Mandibular gnathobase with slender teeth and a pinnate seta at distal corner; basis with four setae; endopod 1-segmented, twice as long as exopod and with three lateral setae; exopod 2-segmented, proximal segment with two lateral setae. Maxillula without coxal epipodite; both rami 1-segmented, equal in length, with three setae. Maxilla with three endites, each with three spines; endopod 1-segmented with four setae, Maxilliped prehensile, well-developed; syncoxa with one small and one large pinnate seta; basis with moderately small pinnate seta; endopodal claw as long as basis, with two accessory setae. P1 exopod 3-segmented, distal outer spine on exopod-3 always shorter than middle outer spine; endopod non-prehensile, 2-segmented, inner seta of endopod-2 implanted near base of segment. P2–P4 intercoxal plate U-shaped with spinules on free margin; both rami 3-segmented, exopod-1 with inner seta, endopod-1 with inner spine. Female P5s separated medially; baseoendopod and exopod fused but identifiable; endopodal and exopodal lobes equal in length, well separated; endopodal lobe with four setae and a marginal pore.

Sexual dimorphism in body size, antennula, P2, P3, P4, P5, P6 and urosome. Male antennula 7-segmented, sub-chirocer with segment V moderately swollen and geniculation between segments V and VI; segment II small with one seta; segments V and VII with aesthetasc. P2–P4 exopod-3 inner setae more strongly developed than in female. P2 endopod-2 with apophysis reaching mid-point of terminal segment; endopod-3 two terminal setae very reduced, others enlarged compared to female. P3 endopod-2 with hooked apophysis; endopod-3 with one additional inner seta. P4 endopod-3 with one additional seta. P5s fused medially; baseoendopod and exopod fused; endopodal lobe reduced, with two setae; exopodal lobe with five setae of which second inner minute. P6 a single plate with three setae on each side.

Females with one egg sac, males with one spermatophore.

Habitat. Marine muddy sediments, 90–150 m.

Type species. *Fladenia intermedia* (Wells 1965) by monotypy.

Etymology. Generic name derived from the type locality, the Fladen ground in the North Sea. Gender feminine.

Fladenia intermedia (Wells)

(Figs 1–11)

Synonyms: Danielssenia intermedia Wells 1965.

Material examined. (1) Holotype; a male, whole mount, mud (20% sand, 80% silt and clay), Fladen ground, North Sea, 58°20′N, 00°30′E, 146 m, British Museum of Natural History Reg. No. 1965.3.26.2.

(2) Three adult females, 3 adult males, soft dark grey mud at 91·5 m depth, North Sea off Cullercoats, 55°07′N, 01°07′E, collected by Dr R. Hamond, British Museum (Nat. Hist), Reg. No. 1990.136.141.

(3) Seven adult females (3 dissected), 4 juvenile females, 6 adult males (2 dissected) from same locality.

Description of female

Body (Fig. 1). Length 0·78–0·99 mm (mean 0·89 mm); maximum width in region of first free-prosomite; prosome slightly dorsoventrally flattened; clear distinction between prosome and urosome. Cephalothorax rounded anteriorly, about as long as first two free-prosomites; posterior border of cephalic shield smooth but dorsal and lateral surface with numerous pores and sensilla; hyaline frill with numerous canals. Free-prosomites with well-developed epimeral plates and with pores and sensilla on dorsal surface; first and second free-prosomites with small row of spinules on lateral anterior border (Fig. 1b) and a canulate hyaline frill; second and third free-prosomites with row of spinules on posterior dorsal border. All urosomites, except anal somite with wide, minutely dentate, hyaline frill (Fig. 2). Urosomite-1 (bearing P5) with row of spinules on dorsal posterior border (Figs 1a, 2a) and two small rows of ventrolateral surface (Fig. 2b). Genital double somite (Fig. 2) completely fused dorsally but with cuticular ridge laterally and ventrally; with a row of spinules on ventral anterior face

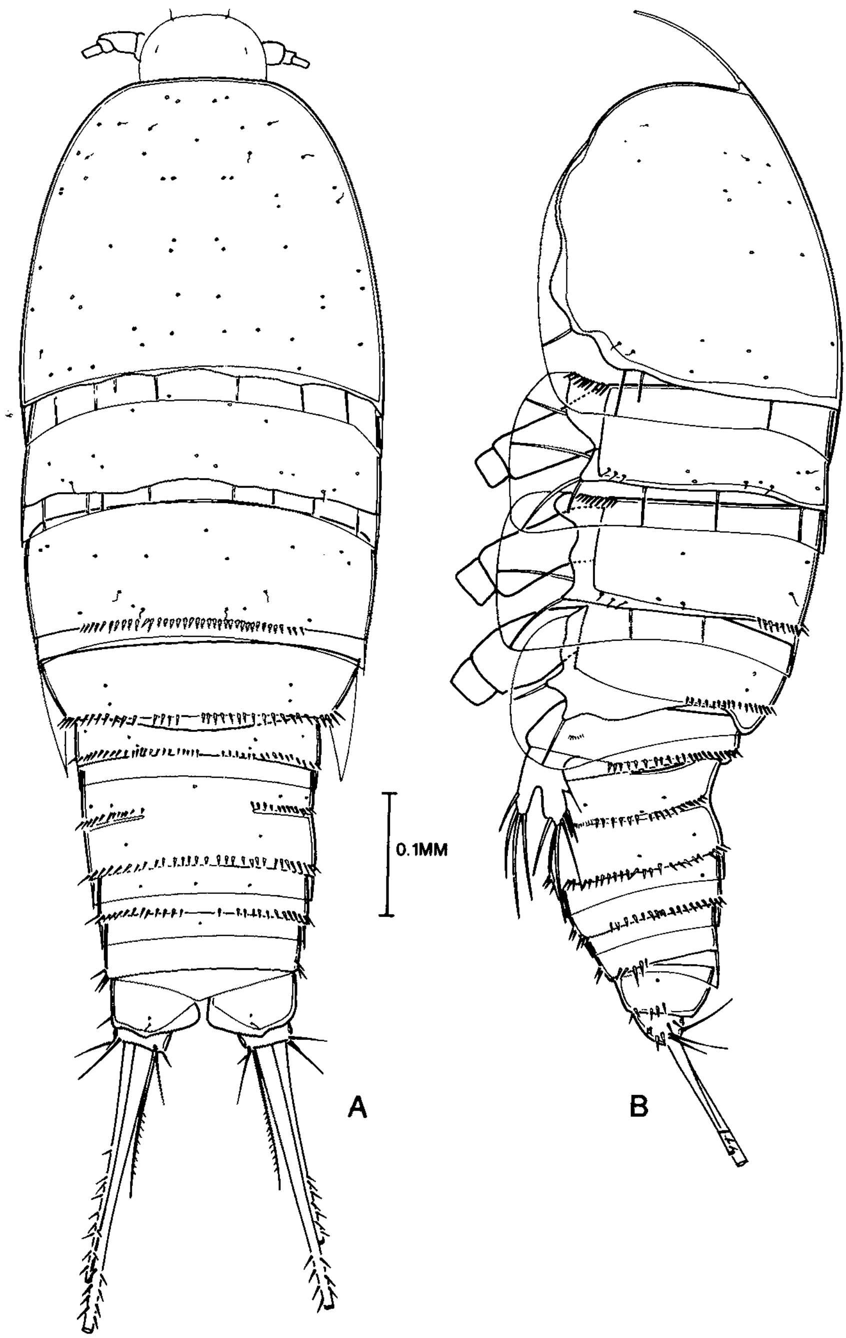

FIG. 1. *Fladenia intermedia*. Habitus of female **A**, dorsal; **B**, lateral.

(Fig. 2b), mid-laterally and all round posterior border; surface pore pattern as in Fig. 2a,b. Genital field (Fig. 3a) with small copulatory pore posterior to genital slit; paired seminal ducts and single large ovoid or dumbbell-shaped seminal receptacle anterior to copulatory pore and under genital plate; vestigial P6 with one pinnate seta and two

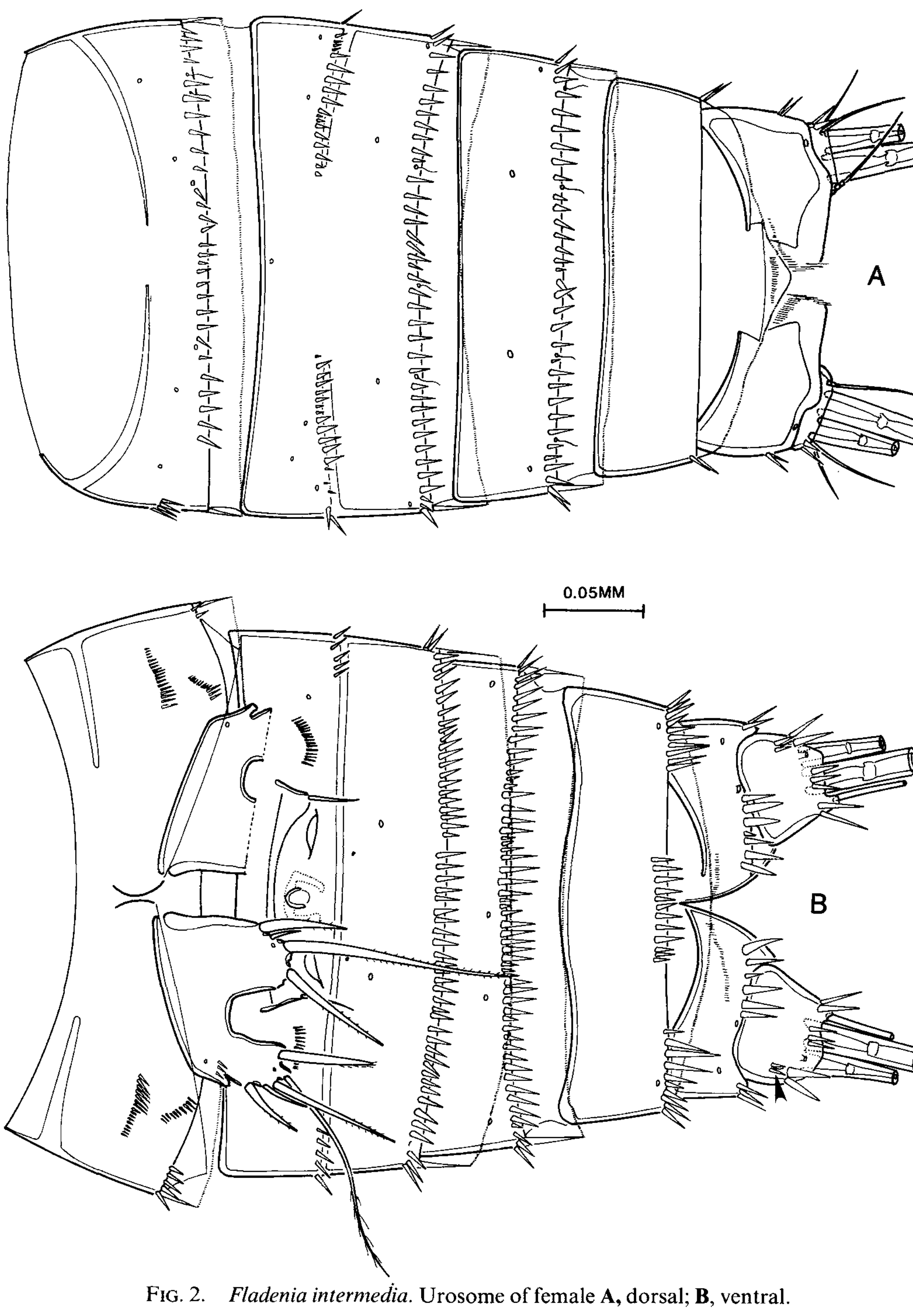

FIG. 2. *Fladenia intermedia*. Urosome of female **A**, dorsal; **B**, ventral.

small teeth distally; two large flap pores immediately posterior to genital field. Urosomite-4 with surface pores and continuous row of spinules around posterior border. Urosomite-5 with only one pair of pores and three short rows of spinules on ventral posterior border (Fig. 2b); dorsal hyaline frill expanded posteriorly into

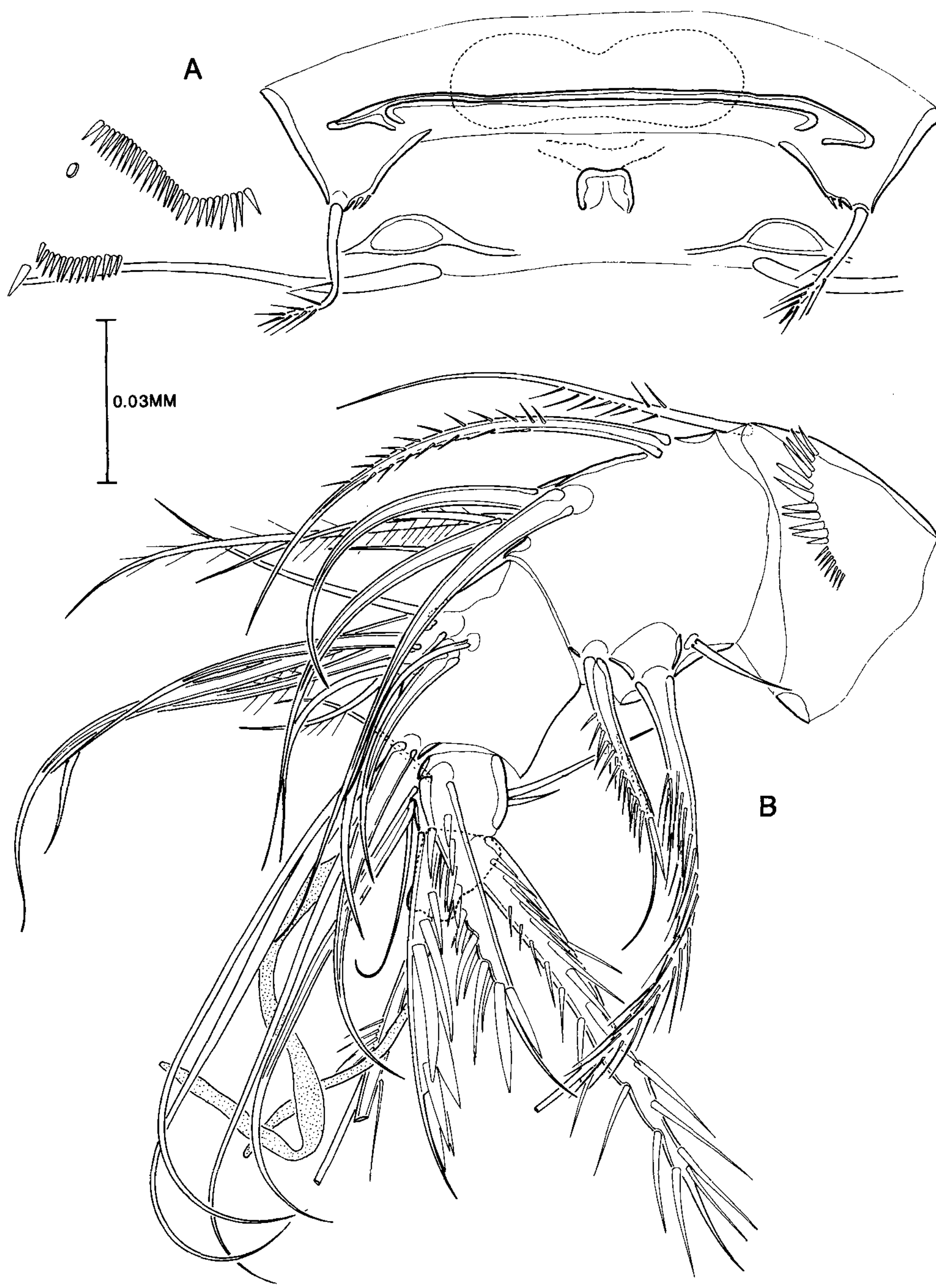

FIG. 3. *Fladenia intermedia*. Female. **A,** Genital field; **B,** antennula.

pseudoperculum. Anal somite deeply divided with rows of hairs on inner surface and a lateral and ventral row of spinules on posterior border. Caudal rami slightly broader than long but almost completely obscured by posterior border of anal somite dorsally; small row of two or three spinules medially on outer ventrolateral margin associated

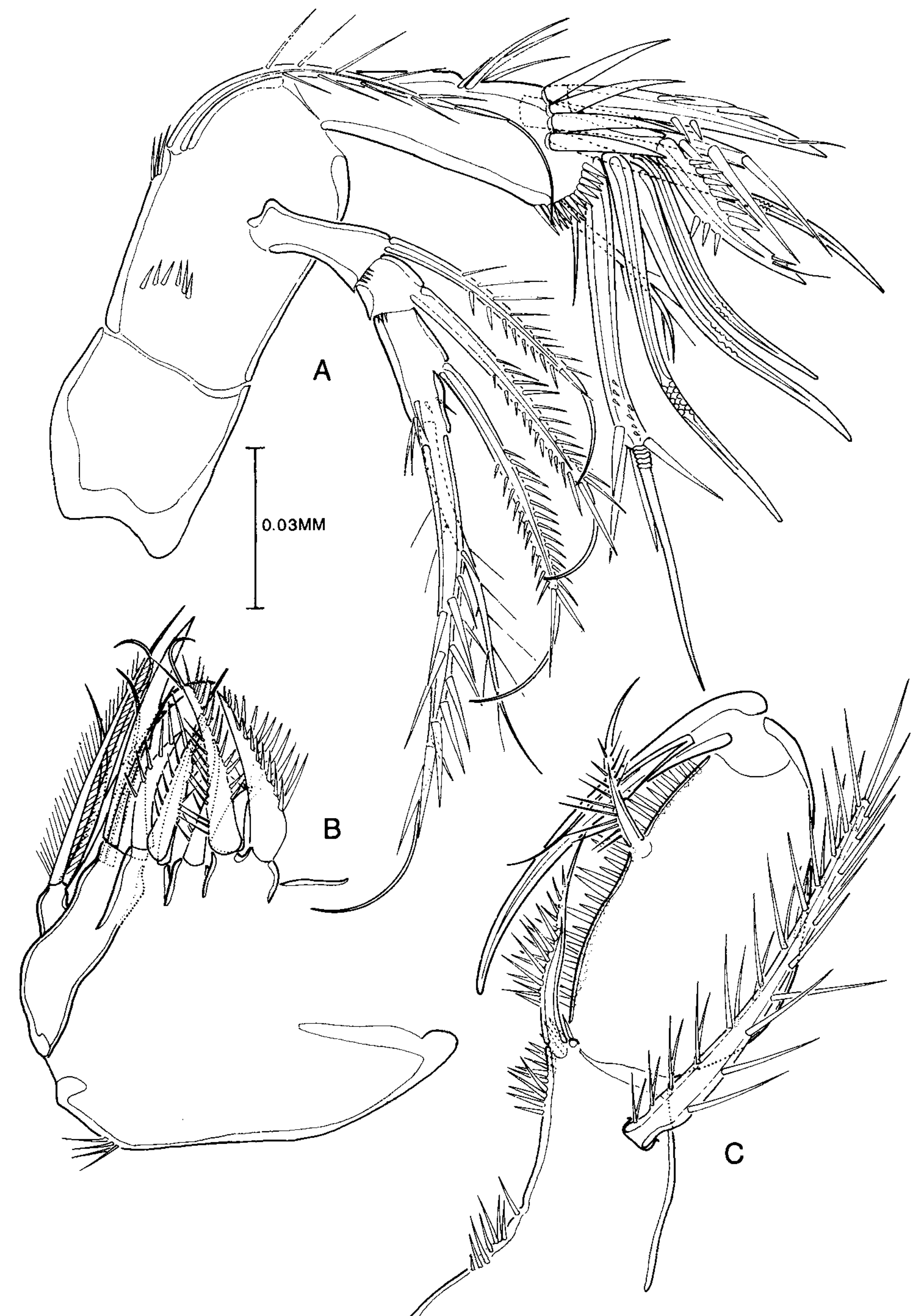

FIG. 4. *Fladenia intermedia*. **A,** Antenna; **B,** maxilla; **C,** maxilliped.

with minute seta I (arrowed in Fig. 2b); another lateral row of large spinules at outer distal corner at base of setae II and III; large terminal setae IV and V spinulose for most of length and with small row of spinules at base on ventral margin of ramus; few large spinules at base of moderately developed, pinnate seta VI situated at inner distal corner of ramus; tri-articulate seta VII on inner dorsolateral margin of ramus.

Rostrum (Fig. 1a). Large, slightly recurved, hyaline, rounded anteriorly and parallel-sided, with four small sensilla.

Antennula (Fig. 3b). Short, stout, 5-segmented. Segment I short, almost triangular, with row of spinules on dorsal surface and a pinnate seta at anterior distal corner. Segment II almost square, with 10 setae; one pinnate seta proximally on anterior margin, six setae at anterior distal corner and three setae on posterior margin, two of which are strongly pinnate and posteriorly directed. Segment III with 13 setae; nine medially on anterior margin and four setae and an aesthetasc at anterior distal corner. Segment IV small, square, with eight setae; one large pectinate seta and three plain setae proximally on anterior margin, two large pectinate setae in distal margin and two simple setae on posterior margin. Segment V with six setae and an aesthetasc; one pinnate seta one plain seta and aesthetasc on distal margin and four small setae on posterior margin (not shown in Fig. 3b).

Antenna (Fig. 4a). Antenna with well-developed coxa. Allobasis with row of setules at base of strongly pinnate abexopodal seta which reaches beyond distal margin of endopod; row of spinules near base of exopod. Exopod 3-segmented; exopod-1 and -2 each with a strongly pinnate seta; exopod-3 with a distal row of spinules, a lateral and two terminal pinnate setae. Endopod with a median row of setules on anterior margin, a row of very large, strong spinules subterminally and a row of small spinules on distal margin; segment bears, subterminally, two pectinate spines and a geniculate seta and, terminally, one pectinate spine, four geniculate setae (of which one has spinules around the geniculation), one pinnate seta and a small naked seta.

Mandible (Fig. 5a). Gnathobase with relatively long, slender, teeth of which two tricuspid, three bicuspid, five unicuspid and two minutely dentate; one pinnate seta at distal corner. Basis about as long as maximum width, with setules on surface and four setae on distal margin, inner seta with long sparse pinnules, second inner plumose, second outer with long proximal and short distal pinnules, and outer seta with pinnules gradually shortening distally. Endopod 1-segmented, twice as long as exopod, with three lateral pinnate setae and four terminal simple setae. Exopod 2-segmented; proximal segment with a distal row of stout spinules and two lateral pinnate setae; distal segment with two pinnate and one simple setae.

Maxillula (Fig. 5b). Precoxa with a row of spinules on outer margin; arthrite with two surface setae and nine elements on distal margin, three pairs of dentate spines, one pair of stout, pinnate setae and a small naked seta. Coxal epipodite absent; coxal endite with a median lateral row of spinules and six setae on distal margin, of which one is strongly pinnate. Basis with row of spinules on lateral and distal margin and six setae. Exopod 1-segmented with two rows of spinules and three plumose setae. Endopod only as long as exopod but inwardly directed, 1-segmented with a row of spinules, two simple setae and one large pinnate seta.

Maxilla (Fig. 4b). Syncoxa with row of spinules on outer margin; three endites, inner and middle endites each with three strongly pinnate spines (two spines on middle endite not shown in Fig. 4b), outer endite with two strongly pinnate spines and a seta. Basal endite with a large recurved spine and three setae. Endopod 1-segmented with four setae of which one finely plumose.

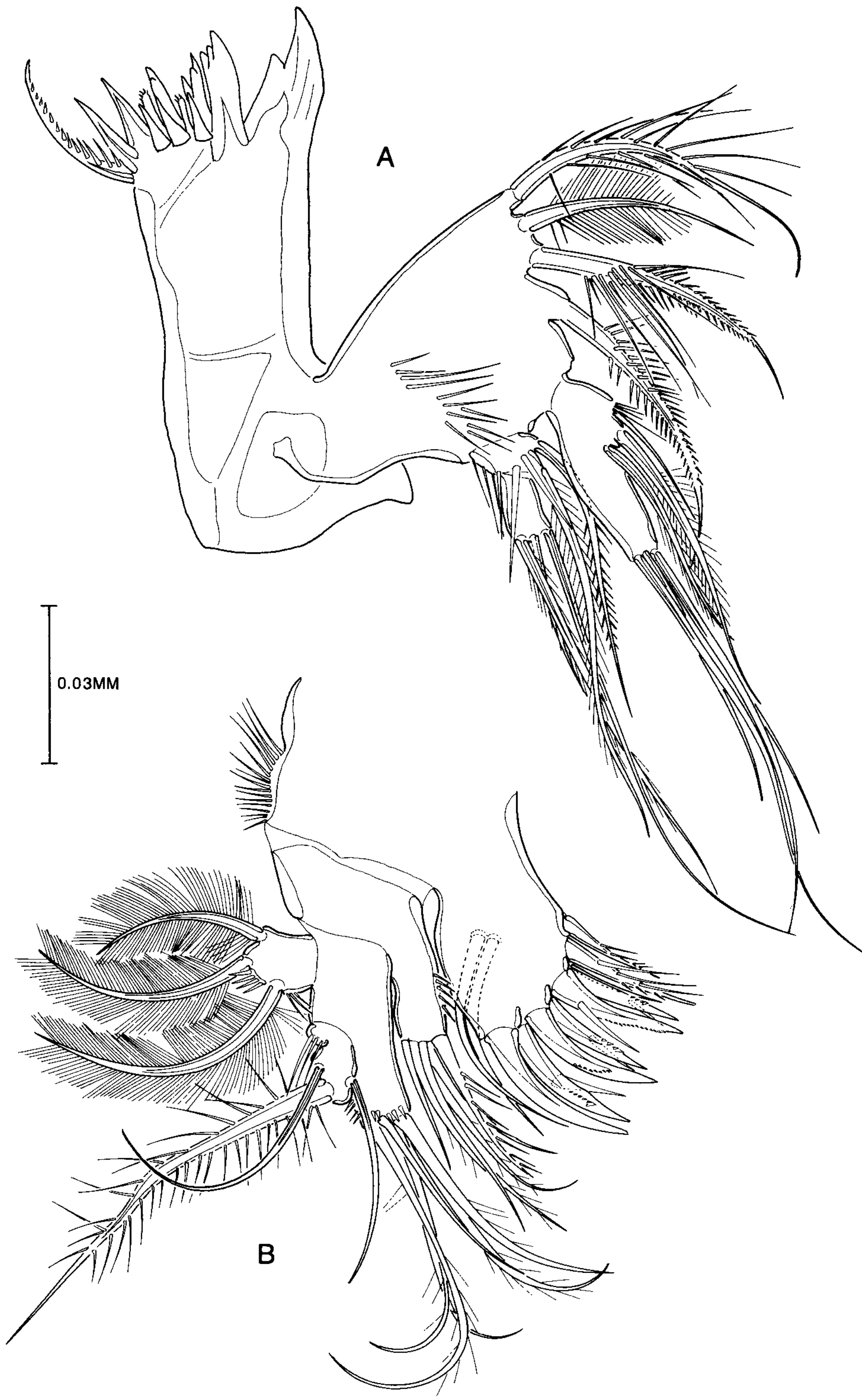

FIG. 5. *Fladenia intermedia*. **A,** Mandible; **B,** maxillula.

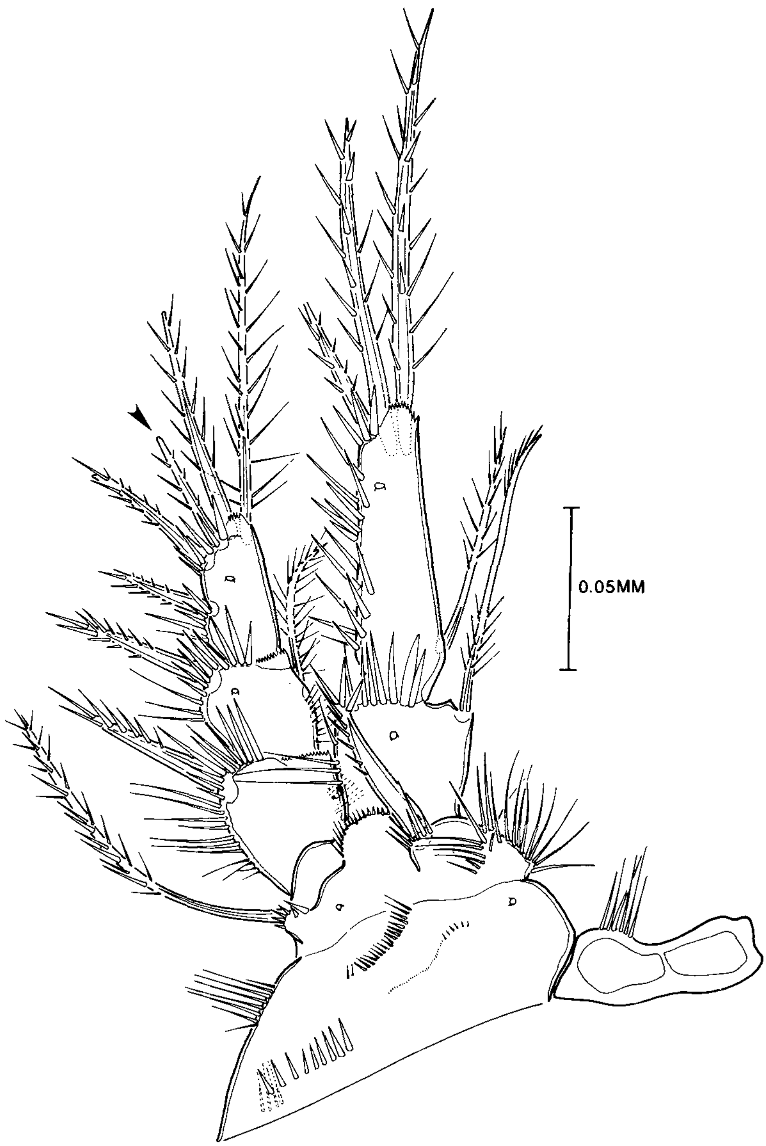

FIG. 6. *Fladenia intermedia*. P1.

Maxilliped (Fig. 4c). Coxa with a proximal and distal row of spinules on outer margin; small tripinnate seta at outer distal corner and large, tripinnate seta distally on posterior face. Basis oval, twice as long as broad, with row of stout spinules and a moderately small pinnate seta on palmar margin. Endopodal claw without teeth, as long as basis, and with one long and one short accessory seta.

P1 (Fig. 6). Intercoxal plate small, well-developed, with a row of setules on each side. Coxa with a pore at inner distal corner, a row of setules on outer margin, three rows of spinules on anterior face and one short row on posterior face at outer proximal corner. Basis with bilobed inner margin, proximal lobe with a row of setules, distal lobe with a

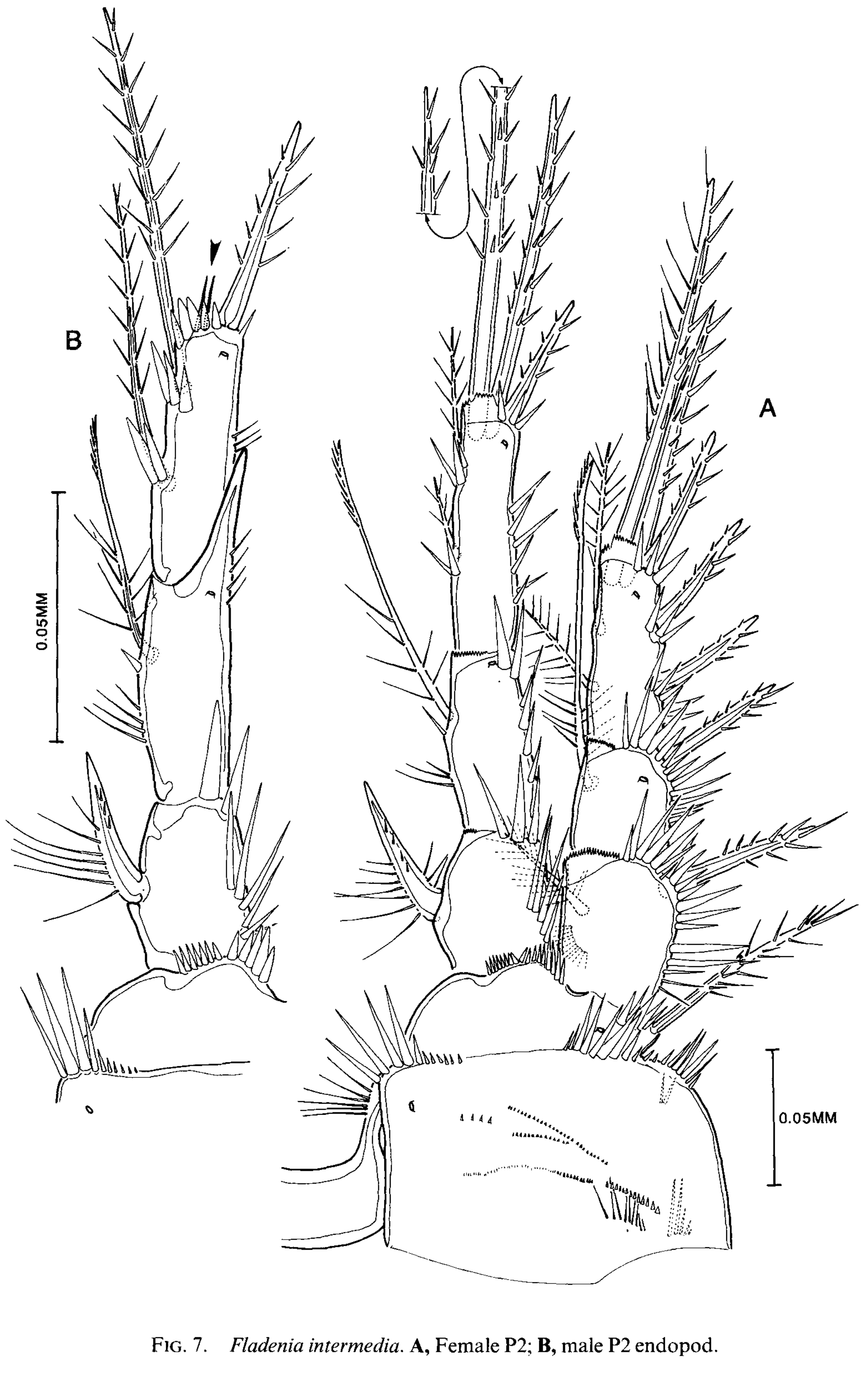

FIG. 7. *Fladenia intermedia*. **A,** Female P2; **B,** male P2 endopod.

FIG. 8. *Fladenia intermedia*. **A,** Female P3; **B,** male P3 endopod.

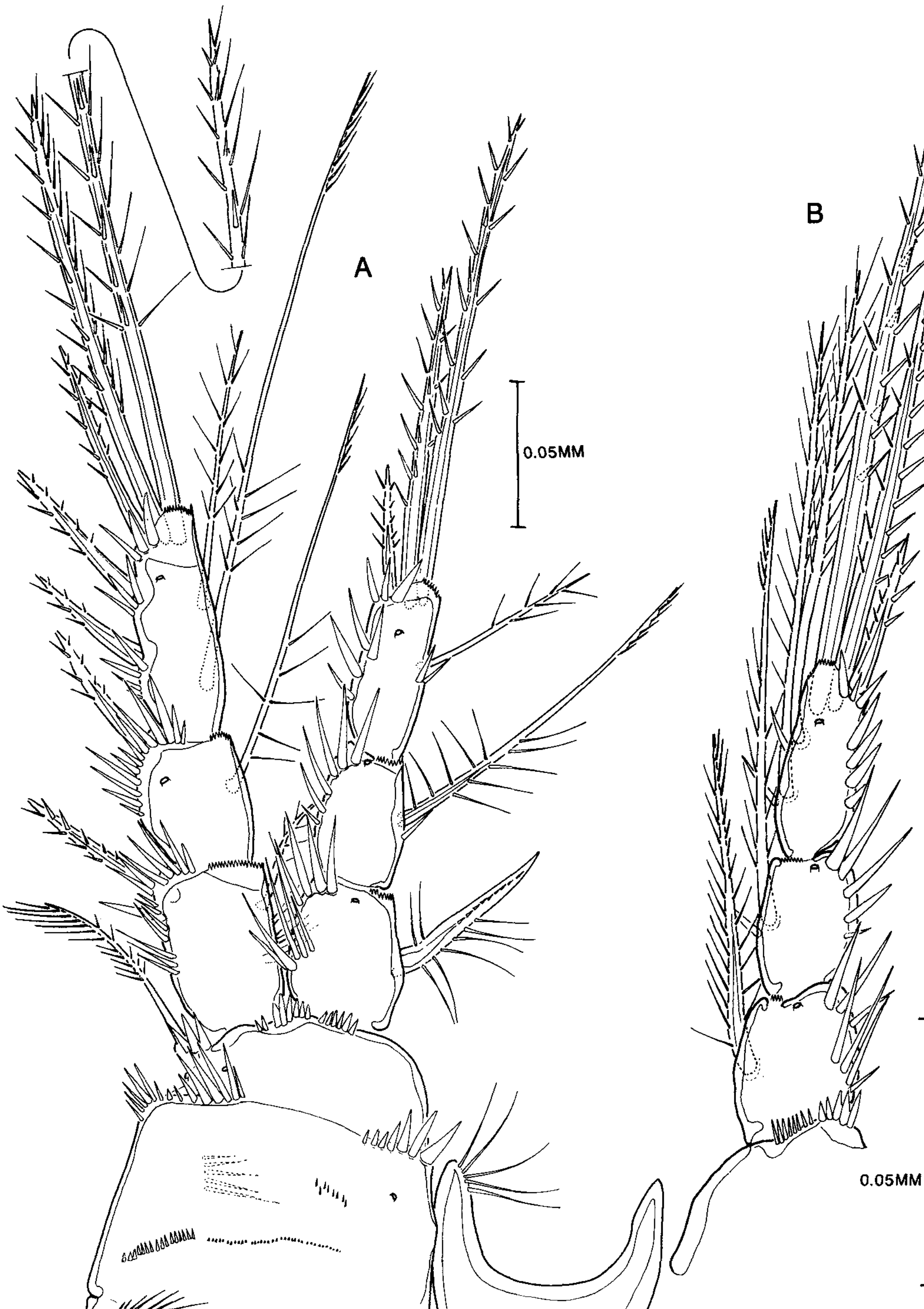

FIG. 9. *Fladenia intermedia*. **A**, Female P4; **B**, male P4 endopod.

row of spinules around base of ventrally directed pectinate inner spine; row of spinules on median distal margin and at base of long, tripinnate, outer seta; a pore near base of outer seta on anterior face. Exopod 3-segmented; all segments with finely dentate hyaline frill, row of spinules around outer margin and strongly pinnate outer spines; proximal and middle segments with short row of setules on inner margin, middle and distal segments with a pore on anterior face; exopod-3 with distal outer spine (arrowed in Fig. 6) always shorter than middle outer spine, inner terminal seta tripinnate. Endopod slightly longer than exopod; 2-segmented, both with row of spinules on outer and distal margin and a pore on anterior surface; endopod-1 as broad as long, inner seta with comb tip; endopod-2 three times longer than broad, inner seta implanted in proximal one-fifth of segment, two terminal setae tripinnante.

P2–P4 (Figs 7a, 8a, 9a). Intercoxal plate well-developed, with U-shaped distal margin (Fig. 9a) bearing two groups of setules. Anterior face of coxa with a pore at inner distal corner, a short row of setules at outer proximal corner and two or three rows of microspinules medially; posterior face with a short row of setules at proximal and distal outer corner; distal margin with a row of spinules at inner and outer corner. Basis with row of spinules on median distal margin and a pore and row of spinules at base of tripinnate outer seta. All rami 3-segmented, each segment with a dentate hyaline frill, one pore on anterior surface (except exopod-1) and a row of spinules on outer and distal margin; endopod longer than exopod in P2, same length in P3 and shorter than exopod in P4; endopod-1 with pinnate spine on inner margin; exopod-2 and endopod-2 inner seta with comb tips; exopod-3 and endopod-3 inner setae small (except in P4 exopod-3 where proximal inner seta long with comb tip), terminal setae tripinnate.

Setal formula of swimming legs as follows:

	Exopod	Endopod
P1	0.1.023	1.121
P2	1.1.223	1.1.221
P3	1.1.223	1.1.2(3)21
P4	1.1.223	1.1.1(2)21

Figures in parentheses refer to the male condition.

P5 (Fig. 10a). Element of each side not fused medially. Baseoendopod and exopod fused (althouth a partial cuticular break present on both anterior and posterior faces at base of exopodal lobe and on posterior face only at base of endopodal lobe), both lobes distinct, well separated and equal in length. Baseoendopod with a pore and two rows of setules at outer corner. Endopodal lobe with a surface pore on each face, a marginal pore at outer distal corner (arrowed in Fig. 10a) and four minutely tripinnate setae on distal margin, of which second inner is small. Exopodal lobe with a surface pore on each face and a short spinule row at base of inner and three outer setae; distal margin with five setae, innermost with a few pinnules at tip, second inner slender with fine pinnules, three outer stout with short pinnules.

Description of male

As in female except for following features

Body (Fig. 11b, c). Length 0·47–0·62 mm (mean 0·525 mm, $n = 6$); urosomites-2 and -3 not fused; spinules in ventral rows on urosome more strongly developed than female and arranged in groups of varying length.

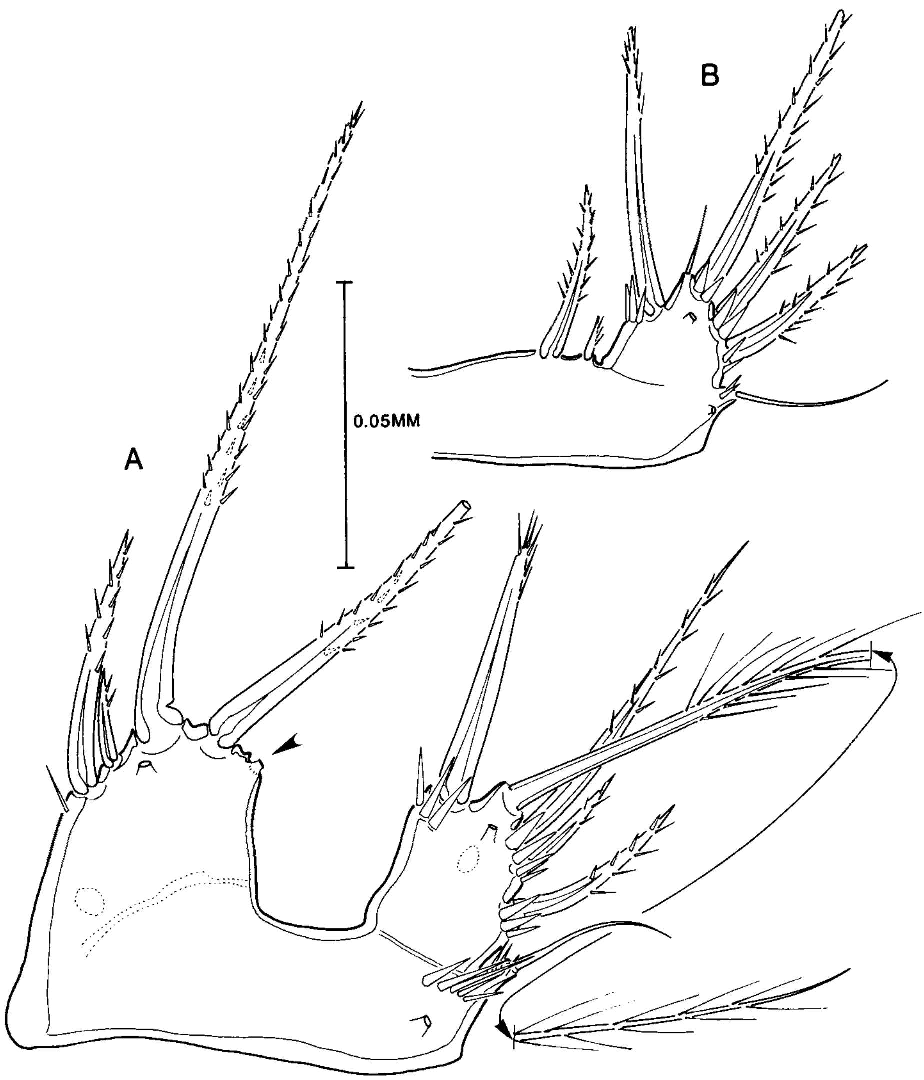

FIG. 10. *Fladenia intermedia*. **A,** Female P5; **B,** male P5.

Antennula (Fig. 11a). Seven-segmented, sub-chirocer with principal articulation between segments V and VI. Segment I with row of spinules on dorsal surface and a pinnate seta at anterior distal corner. Segment II short with a pinnate seta at anterior distal corner. Segment III square with 12 setae, nine (of which one is pinnate) at anterior distal corner and three on posterior margin, of which two large, strongly pinnate and directed posteriorly, Segment IV small and square, with 10 setae at anterior distal corner (the five ventral setae not drawn in Fig. 11a). Segment V moderately swollen with convoluted anterior face bearing three of more rows of denticles; 11 setae on anterior margin, four simple and four pinnate setae proximally (not drawn in Fig. 11a) and three long simple setae and an aesthetasc distally. Segment VI with three setae. Segment VII with four setae and a small aesthetasc.

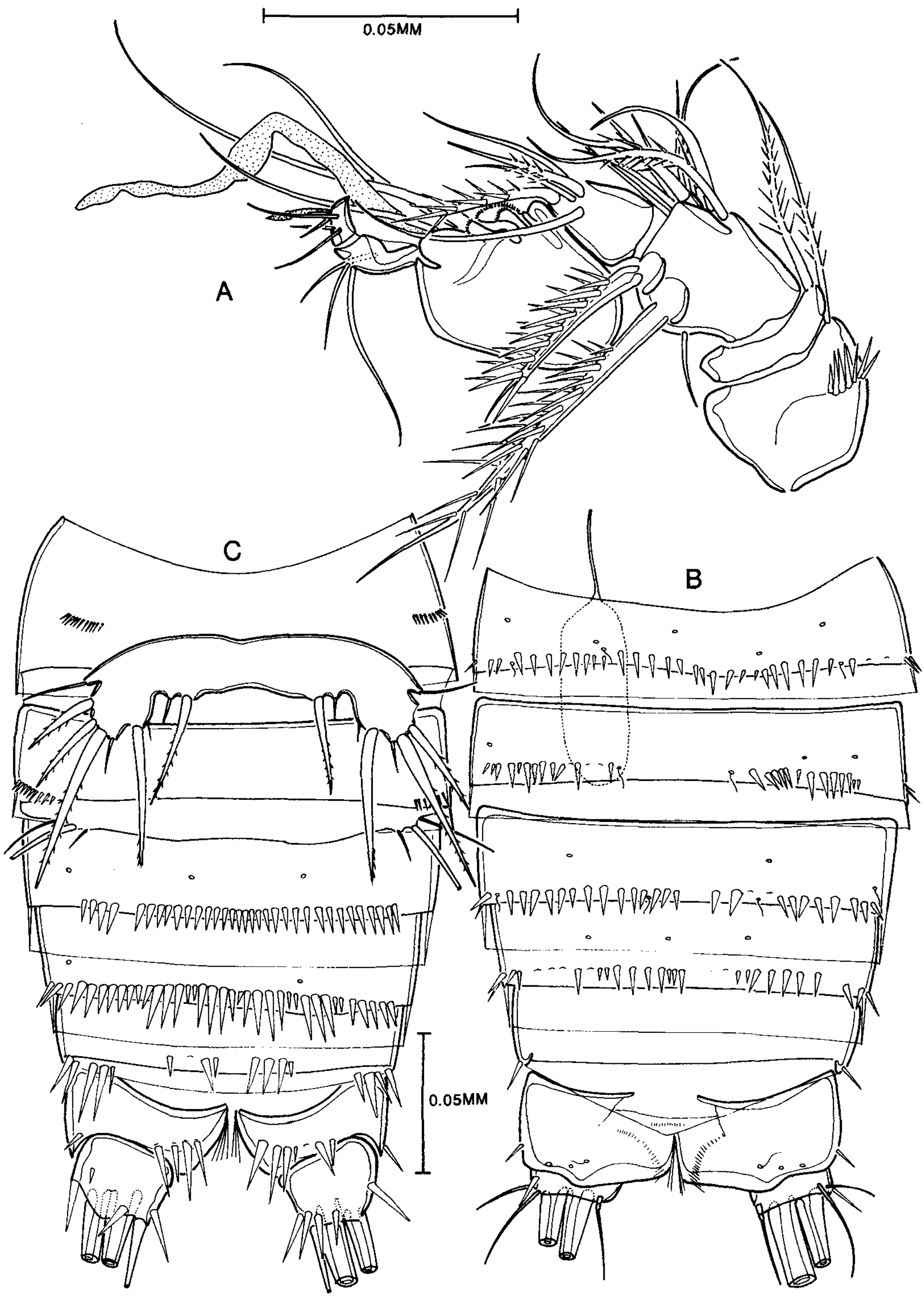

FIG. 11. *Fladenia intermedia*. Male. **A,** Antennula; **B,** urosome dorsal view; **C,** urosome, ventral view.

P2. Coxa and basis as in female. Exopod as in female except that both inner setae on exopod-3 more strongly developed. Endopod (Fig. 7b) modified; outer distal corner of endopod-2 with apophysis reaching mid-point of endopod-3 and with outer marginal spinules very reduced; endopod-3 with two inner setae and outer terminal seta much more strongly developed than in female and two terminal setae (arrowed in Fig. 7b) reduced to minute simple setae, outer marginal spinules of segment very reduced.
P3. Coxa and basis as in female. Exopod as in female except that both inner setae of exopod-3 much more strongly developed. Endopod (Fig. 8b) modified; endopod-2 with hooked apophysis at outer distal corner reaching almost to mid-point of endopod-3 and outer marginal spinules reduced; endopod-3 with three inner setae, all much more strongly developed than two inner setae in female.
P4. Coxa and basis as in female. Exopod as in female except that distal inner seta on exopod-3 more strongly developed. Endopod-1 (Fig. 9b) with a long pinnate inner seta rather than a spine; endopod-3 with two inner setae, both more strongly developed than single inner seta of female.
P5 (Fig. 10b). Both limbs fused medially to form a single plate; exopod and baseoendopod fused. Baseoendopod with a short row of spinules and a pore at outer distal corner; endopodal lobe very reduced with two pinnate setae, of which outer very small; exopodal lobe with a pore on anterior face, five setae as in female except that second inner seta minute and naked.
P6 (Fig. 11c). A single symmetrical plate with three setae on each side.

Discussion

There is no doubt that our specimens are conspecific with Wells' description (1965) of the holotype of *D. intermedia*, and the few discrepancies that do exist are due to inaccuracies in the original description. The most significant of these is Wells' statement that the baseoendopod and exopod of the P5 are separate, whereas in our male specimens they are fused, albeit with a partial suture on the anterior face. However, the holotype is a whole-mounted specimen in which such details of the P5 are impossible to see.

Wells was clearly puzzled by his specimen, which he thought had a maxilliped like *Psammis*, a P5 like *Danielssenia* but tending towards the *Psammis* condition, a swimming leg setal pattern containing features of both but with a P2 endopod which was unlike the male condition in either genus. He placed it in the genus *Danielssenia* based on the structure of the P5 and on the setation of the distal segment of the endopod of P1 which he thought was more akin to this genus than *Psammis*. The discovery of the female and additional males of *D. intermedia* has resolved the problem by making it clear that this species should be placed in a new genus *Fladenia*. However, before this can be justified it is necessary to reconsider the composition of the above-named genera.

Lang (1944) established two species-groups within the genus *Danielssenia*, the *Typica* group embracing (Lang 1948), *D. typica*, *D. fusiformis* (Brady and Robertson 1875), *D. robusta* Sars 1921 and *D. perezi* Monard 1935, and the *Sibirica* group containing *D. sibirica* Sars 1898 and *D. stefanssoni* Willey 1920. These were still the only known species in 1965, but since then seven other species have been added to the *Typica* group (see Bodin, 1988). We have made a preliminary re-examination of the type material of most of these species which reveals that *D. perezi*, *D. paraperezi* Soyer 1970, *D. minuta* Coull 1969 and *D. eastwardae* Coull 1971 all have aesthetascs on the mouthparts. In subsequent papers we will show that these species and, for other reasons, *D. sibiraca, D. stefanssoni* and *D. spinipes* Wells 1967, should be placed in several new genera. Therefore, in the following discussion, we have characterized the genus *Danielssenia* Boeck as containing the species *D. typica* (with which Gee, 1988a, synonymized *D. fusiformis*), *D. quadriseta* Gee 1988, *D. reducta* Gee 1988 and probably *D. robusta* and *D. similis* Tschislenko 1978, although we have been unable to examine material of these two species.

By 1965 three species had been assigned to the genus *Psammis*: *P. longisetosa* Sars 1910, *P. borealis* Klie 1939 and *P. kliei* Smirnov 1946, but of these *P. borealis* almost certainly belongs to the subfamily Pseudotachidiinae in the Thalestridae, and the description of *P. kliei* is too incomplete to be certain of its affinities with *P. longisetosa*. Since then two further species have been added to the genus, *P. longifurca* Bodin 1968 and *P. longipes* Becker 1974, but again the material of the single female of *P. longifurca* is too incomplete to be certain that it belongs to this genus. Therefore, for the purposes of the following discussion, the genus *Psammis* is characterized from *P. longisetosa* (for which both sexes are known) and *P. longipes* (known only from the female).

Also, since Wells (1965) described *D. intermedia*, three new genera have been established, *Paradanielssenia, Micropsammis* and *Leptotachidia*, which have affinites with *Danielssenia*. They are distinguished from *Danielssenia* and *Psammis* by the presence of claviform sensory aesthetascs on the oral appendages and by the sexually dimorphic characters of the swimming legs (Soyer, 1970; Becker, 1974; Mielke, 1975). However, as *D. intermedia* has no aesthetascs on the oral appendages and the sexual dimorphism of the swimming legs is more complex, it cannot be placed in any of these genera.

In Table 1 is a list of the characteristics by which *Danielssenia* and *Psammis*, as defined above, differ from each other and/or from *D. intermedia*. Whilst it is clear that *D. intermedia* has characters which are found in one or other of the two genera, it has been placed in the new genus *Fladenia* on the basis of the following unique characters: a 5-segmented female antennula; a mandibular exopod only half as long as the endopod; the endopodal claw of the maxilliped with two accessory setae; P1 exopod-3 with the distal outer spine shorter than the middle outer spine; P1 endopod-2 with the inner seta implanted near the base of the segment; P2–P3 endopod-1 with an inner spine rather than a seta; fusion of the P5 baseoendopod and exopod in both sexes and of each P5 element medially in the male; the female P5 baseoendopod with four setae; the male P6 with three setae. *Psammis*, on the other hand, is characterized as follows: the mandibular gnathobase with a naked seta and the exopod and endopod with only one lateral seta; the maxilliped basis with a very large palmar seta; P2 endopod-1 with an apophysis at the outer distal corner; P2 endopod-2 with two inner setae; P5 baseoendopod and exopod fused only in the female. *Danielssenia* is unique in that the mandibular gnathobase has short, bluntly rounded teeth and the basis has only three setae; there is no inner seta on P2–P4 exopod-1; the P5 baseoendopod and exopod not fused in either sex. When considering the above characterizations it should be borne in mind that *Fladenia* is a monotypic genus and some of its characteristics (e.g. the form of setae on the swimming legs) may turn out to be specific, rather than generic. Variation akin to this is found between the two species definitely belonging to *Psammis* in which *P. longisetosa* adults have only one seta on the maxilliped basis (although Gee, 1988b, has shown that two are present in the copepodites) whereas *P. longipes* adults have two basal setae.

However, the discovery of the female of *D. intermedia* has enabled us to determine more fully the sexually dimorphic characters of this taxon, and it is on the basis of these

Table 1. A comparison of characteristic features of the genera *Danielssenia* and *Psammis* with those of *Danielssenia intermedia*, assigned to the new genus *Fladenia*

Characters	*Danielssenia*	*Psammis*	*D. intermedia*
Female antennula segments	4	4	5
Antenna exopod-1 setae	1	2	1
Mandible			
Gnathobase teeth	Short and blunt	Long and fine	Long and fine
Gnathobase seta	Pinnate	Naked	Pinnate
Basis setae	3	3–4	4
Exopod: endopod length	Equal	Equal	Half
Lateral setae on exopod/endopod	2/3	1/1	2/3
Maxilliped			
Syncoxa setae.	2	1–2	2
Basis seta length.	Short	Long	Short
Endopodal claw accessory setae.	1	1	2
P1			
Exopod-3 length of distal outer seta relative to middle seta	Longer	Longer	Shorter
Endopod-2 position of inner seta	Medial	Medial	Proximal
P2–P4 Exopod-1 inner seta	0	1	1
P2 endopod-1 apophysis	Absent	Present	Absent
P2 endopod-2 setae	1	2	1
P2–P3 endopod-1, inner element	Seta	Seta	Spine
P5			
Elements fused medially in F/M	No/No	No/No	No/Yes
Exopod and baseoendopod fused in F/M	No/No	Yes/No	Yes/Yes
Female baseoendopod setae.	5	5	4
Male P6 setae	2	2	3
Sexual dimorphism			
P2 exopod/endopod	No/Yes	No/Yes	Yes/Yes
P3 exopod/endopod	No/Yes	No/Yes	Yes/Yes
P4 exopod/endopod	No/No	No/No	Yes/Yes

features, combined with those outlined above, that we feel fully justified in placing it in a new genus. Firstly, *Fladenia* exhibits slight sexual dimorphism on the exopod of P2–P4 in that the inner setae of exopod-3 are more strongly developed in the male than in the female; a feature not found in any species of the other two genera. Secondly, whilst all three genera have an apophysis at the outer distal corner of the male P2 endopod-2, in *Fladenia* this reaches to only the mid-point of endopod-3, whereas in *Psammis* it reaches the distal margin and in *Danielssenia* far beyond the distal margin. Thirdly, the modifications of the setae in male P2 endopod-3 are distinctly different in the three genera; in *Fladenia* the terminal outer seta is considerably enlarged whereas in *Psammis* and *Danielssenia* it is reduced to a small hooked spine. Fourthly, P3 endopod-2 in males of all three genera has a small hooked apophysis at the outer distal corner, but only in *Fladenia* is there sexual dimorphism on endopod-3 of P3 in that the male has one more inner seta than the female. Lastly, there is no sexual dimorphism in the endopod of P4 in *Danielssenia* and *Psammis*, but in *Fladenia* the inner spine of endopod-1 of the female is transformed into a long seta in the male which also has an additional inner seta on endopod-3.

Whilst the form of sexual dimorphism of P2 endopod-2–3 and P3 endopod-2 exhibited by these three genera is also found to some degree in all the other 'danielsseniid' genera, sexual dimorphism of the exopod of P2–P4, endopod-3 of P3 and endopod of P4 is peculiar to *Fladenia*. However, an examination of the likely sexually dimorphic characters of the genus *Paranannopus* Lang 1936 reveals many similarities with *Fladenia*.

The problem with *Paranannopus* is that for no described species are both sexes known[1]. There are now five species known only from males and 17 species known only from females (see Bodin, 1988) but all the known males have more setae on exopod-3 of P2–P4 and endopod-2 of P4, and more segments in the endopod of P2–P3 than all the known females. This suggests that there is a high degree of sexual dimorphism in the swimming legs which has not been recognized previously as such. For instance, the only case in which both sexes have been found in one location is that of Wells (1965), who found seven females and two males of *Paranannopus* on the Fladen ground. Although he could find no differences between them in general body form or in the structure of the rostrum, antenna, mouthparts and caudal rami, he described them as two different species (the females as *P. triarticulatus* Wells 1965 and the males as *P. langi* Wells 1965) because the males had more setae than the females on exopod-3 of P2–P4 and endopod-2 of P4, and had more segments in the endopods of P2 and P3. He also described the male species as having one fewer setae on P1 endopod-2 than the female species. However, we have examined the holotype of *P. langi* and it clearly has one seta missing and agrees with the description of *P. triarticulatus* in all respects other than the setation and segmentation of P2–P4. We believe that a detailed re-examination of these two species will show them to be synonymous.

Therefore, if we accept these general differences between male and female species of *Paranannopus* as indicative of the sexually dimorphic characters of the genus, then they bear many resemblances to those outlined above for *Fladenia*. Both genera exhibit sexual dimorphism in the exopod of P2–P4 (a condition which Huys and Gee (1990) and Gee and Fleeger (1990) have shown to be quite rare within the Harpacticoida), male *Paranannopus* having more exopodal setae that the female, male *Fladenia* having only larger setae. Similarly, an increase in the number of elements in the endopod of the male P3 and P4 compared to the female is found in both genera, in *Paranannopus* an additional segment in P3 and additional setae in P4, but in *Fladenia* merely an increased number of setae. Further, in both genera the P5s are fused medially in the male, a condition which is also found in the females in *Paranannopus*.

In addition to the similarities in sexual dimorphism, there are other characters in which *Fladenia* shows greater affinities with *Paranannopus* than with *Danielssenia* and *Psammis*. In both the former genera the distal outer spine of P1 exopod-3 is shorter than the middle spine, whereas in the latter pair of genera is as long as or longer than the middle spine. Similarly, in *Fladenia* and *Paranannopus* the mandibular endopod is twice as long as the exopod rather than of equal length; the coxa of the maxillula has a

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[1] Schriever (1983) described a female of *P. langi* from the Iceland–Faroes ridge, but an examination of his type material showed that it is, in fact, a copodite V male, probably of a species other than *P. langi*. In a further paper (Schriever, 1985) he describes both sexes of *P. variabilis*, but again the female was described from a copepodite V male.

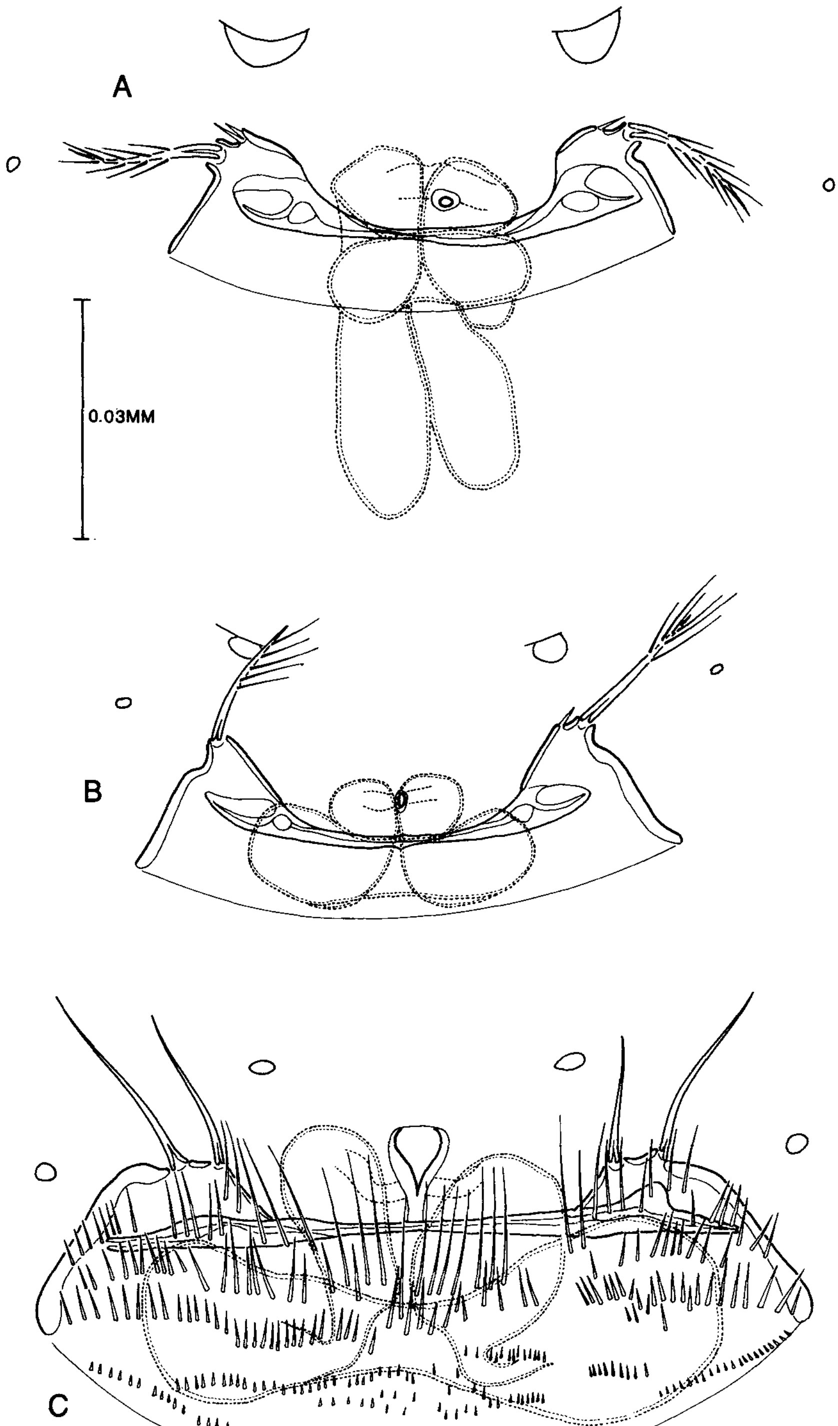

FIG. 12. Female genital field of **A**, *Danielssenia typica;* **B**, *Psammis longisetosa;* **C**, *Parananopus* sp.

normal pinnate seta rather than a pinnate spine; and the female antennula has more than four segments.

Thus, *Fladenia* appears to provide a link between *Paranannopus* and the known danielsseniid genera. That such a relationship exists is further strengthened by an examination of the characters which all the four genera have in common. They are remarkably similar in the structure and setation of the antennula (although in *Paranannopus* the fifth segment in the male is not swollen); the size and shape of the rostrum (except that in *Paranannopus* it is not hyaline and bears two setules which may or may not be plumose); the structure of the antenna and oral appendages, particularly the mandible and maxilliped; the form of the P1 with a non-prehensile two-segmented endopod; the deeply divided anal somite; and a minute seta I on the caudal ramus. The most significant similarity between all these genera, however, is in the structure of the female genital field (Figs 3a, 12). They all have a simple copulatory pore somewhat posterior to the genital slit and paired, swollen seminal ducts leading to a single, transverse, ovoid or dumbbell-shaped seminal receptacle lying anterior to the copulatory pore under the genital plate, a most unusual arrangement within the Harpacticoida. However, in *Danielssenia, Psammis* and *Fladenia* the vestigial P6 bears one pinnate seta (Figs 3a, 12a, 12b) whereas in the one speices of *Paranannopus* we have examined in detail, it has two naked setae, Fig. 12c).

In conclusion, the discovery and redescription of both sexes of *D. intermedia* Wells has shown that without doubt it belongs to a new genus. Further, the characteristics of this genus justify the proposal of Huys and Gee (1990) that the 'danielsseniid' genera should be removed to the family Paranannopidae. However, an in-depth examination of the other species of *Danielssenia* and of the genus *Paranannopus* (also thought to be an amalgam of several genera) remains necessary.

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