

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/5424849>

# A revision of the family Dissonidae Kurtz, 1924 (Copepoda : Siphonostomatoida)

Article in *Systematic Parasitology* · June 2008

DOI: 10.1007/s11230-008-9132-z · Source: PubMed

CITATIONS

16

READS

340

6 authors, including:



**Susumu Ohtsuka**

Hiroshima University

261 PUBLICATIONS 3,318 CITATIONS

[SEE PROFILE](#)



**B.A. Venmathi Maran**

Universiti Malaysia Sabah (UMS)

121 PUBLICATIONS 897 CITATIONS

[SEE PROFILE](#)



**Jean-Lou Justine**

Muséum National d'Histoire Naturelle

539 PUBLICATIONS 8,045 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Cobia breeding [View project](#)



Marine symbiosis [View project](#)

## A revision of the family Dissonidae Kurtz, 1924 (Copepoda: Siphonostomatoida)

Geoff A. Boxshall · Ching-Long Lin · Ju-Shey Ho ·  
Susumu Ohtsuka · B. A. Venmathi Maran ·  
Jean-Lou Justine

Received: 23 July 2007 / Accepted: 24 July 2007  
© Springer Science+Business Media B.V. 2008

**Abstract** Two new species of the parasitic copepod genus *Dissonus* Wilson, 1906 are described: *D. excavatus* n. sp. from the gills of a labrid, *Bodianus perditio*, and a lutjanid, *Macolor niger*, collected off New Caledonia and Taiwan, and *D. inaequalis* n. sp. from a hemiscylliid elasmobranch, *Chiloscyllium punctatum*, collected off Sarawak (Malaysia) and the Philippines. Material of *D. heronensis* Kabata, 1966 is described from a balistid host, *Pseudobalistes fuscus*, off New

Caledonia, and this constitutes a new host record for this parasite. *D. manteri* Kabata, 1966 was collected from four serranid host species off New Caledonia and from one of the same hosts off Taiwan. Two of the hosts from New Caledonia, *Plectropomus laevis* and *Epinephelus cyanopodus*, represent new host records. *D. pastinum* Deets & Dojiri, 1990 was recognised as a new synonym of *D. nudiventris* Kabata, 1966, so the total number of valid species is now twelve. Material from museum collections of *D. nudiventris*, *D. similis* Kabata, 1966 and *D. spinifer* Wilson, 1906 was re-examined and provided new information which is utilised in a key to all valid species of *Dissonus*.

---

G. A. Boxshall (✉)  
Department of Zoology, Natural History Museum,  
Cromwell Road, London SW7 5BD, UK  
e-mail: gab@nhm.ac.uk

C.-L. Lin  
Department of Aquatic Sciences, National Chiayi  
University, Chiayi 60083, Taiwan

J.-S. Ho  
Department of Biological Sciences, California State  
University, Long Beach, CA 90840-3702, USA

S. Ohtsuka · B. A. Venmathi Maran  
Takehara Marine Station, Setouchi Field Science Center,  
Graduate School of Biosphere Science, Hiroshima  
University, Takehara 725-0024, Japan

J.-L. Justine  
Équipe Biogéographie Marine Tropicale, Unité  
Systématique, Adaptation, Évolution (CNRS, UPMC,  
MNHN, IRD), Institut de Recherche Pour le  
Développement, BP A5, 98848 Noumea Cedex, Nouvelle  
Calédonie

### Introduction

The family Dissonidae Kurtz, 1924 exhibits the most plesiomorphic body form of all the caligiform families within the order Siphonostomatoida and has been regarded as a basal family within this lineage (Kabata, 1979). It is characterised by the possession of a flattened caligiform cephalothorax incorporating only the first pedigerous somite, the second and third pedigerous somites being free. As in the caligids and trebiids, the expanded lateral zones of the dorsal cephalothoracic shield are provided with a characteristic marginal membrane, as are the frontal plates. This family also retains the biramous

condition in the fourth leg, as in the Trebiidae Wilson, 1905, and the two most basal genera within the Caligidae Burmeister, 1835, *Avitocaligus* Boxshall & Justine, 2005 and *Euryphorus* Milne Edwards, 1840 (see Boxshall & Justine, 2005). The family contains just the type-genus, *Dissonus* Wilson, 1906, and eleven species are currently recognised (Tang & Kalman, 2005). The single male described as *Dissonus* sp. by Pillai (1968) does not belong to *Dissonus* as currently recognised.

The Dissonidae has been widely attributed to Yamaguti (1963) (e.g. Kabata, 1965; Pillai, 1985; Boxshall & Halsey, 2004); however, Kurtz (1924) proposed the Dissoninae as a new subfamily of the Caligidae. As the first to accord family-group status to this taxon, 'Kurtz, 1924' is the correct authority for the family name. A further nomenclatural correction to be noted relates to the new genus of syringophilid quill mite established by Skoracki (1999) under the name *Dissonus*. Skoracki (1999) was unaware that this name was pre-occupied by *Dissonus* Wilson, 1906. The homonym, *Dissonus* Skoracki, 1999, has been replaced by *Neoaulonastus* Skoracki, 2004 (Skoracki, 2004).

The species of *Dissonus* are known to parasitise a wide range of fishes including both elasmobranchs and actinopterygians (Kabata, 1966; Deets & Dojiri, 1990; Tang & Kalman, 2005). All species have thus far been reported only from the Indo-Pacific, from Madagascar in the west to New Caledonia in the east. The material reported here comes from various localities including off Taiwan, the Philippines, Sarawak (Malaysia) and New Caledonia. The material from off New Caledonia and Sarawak was made available for study by Jean-Lou Justine (IRD, Nouméa) and by Janine Caira (University of Connecticut, USA), respectively. In both cases the material was collected during major surveys for metazoan parasites of marine fishes. Access to such a large amount of material has enabled us to address questions relating to variability for the first time in this genus.

## Materials and methods

Parasites were removed from the fish hosts under a dissecting microscope and preserved in 70% ethanol. Parasites were cleared in a drop of lactic acid or in lactophenol, and dissected using electrolytically-sharpened tungsten needles. Whole animals and

dissected appendages were examined as temporary mounts using a Leitz Diaplan microscope or an Olympus BH2 microscope equipped with differential interference contrast, and drawings were made using a camera lucida. Measurements are given in millimetres, unless otherwise indicated, and as the mean, with the range in parentheses. Material for SEM was washed in distilled water, dehydrated through a graded acetone series, critical point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with palladium. Coated material was examined using a Phillips XL30 Field Emission Scanning Electron microscope operating at 5 KV. Morphological terminology follows Boxshall (1990) and Huys & Boxshall (1991).

Type-material is deposited in the following museums as specified by agreements and collecting permits issued to the collectors: these are the Natural History Museum, London, (BMNH), the Muséum National d' Histoire Naturelle, Paris (MNHN), the Muzium Zoologi, Universiti Malaya, Kuala Lumpur, Malaysia (MZUM), the Sarawak Biodiversity Centre, Kuching, Sarawak, Malaysia (SBC), the US National Parasite Collection (USNPC), and the US National Museum, Smithsonian Institution (USNM).

## Family Dissonidae Kurtz, 1924

### Genus *Dissonus* Wilson, 1906<sup>1</sup>

Syn. *Caligotrogus* Ummerkutty, 1970

### *Dissonus excavatus* n. sp.

*Type-host*: Golden-spot hogfish *Bodianus perditio* (Quoy & Gaimard) (Table 1).

*Additional host*: Black and white snapper *Macolor niger* (Forsskål) (Table 1).

*Site*: Gills.

*Type-locality*: Récif To (22°29'S, 166°26'E), off Nouméa, New Caledonia.

*Additional locality*: Off Taiwan (Table 1).

*Material examined*: 3♀♀, 1♂ from gills of *Bodianus perditio* (JNC582A), Récif Le Sournois (22°31'S, 166°26'E), New Caledonia (NC), 01 July 2003; 1♀ from gills of *B. perditio* (JNC584B), Récif Le Sournois (NC), 01 July 2003; 6♀♀, 1♂ from gills of *B. perditio* (JNC870A), Passe de Dumbéa (22°21'S,

<sup>1</sup> Not *Dissonus* Skoracki, 1999.

**Table 1** Body lengths of *Dissonus excavatus* n. sp. from different hosts and localities

Host species	Locality	Female BL (mm) mean (range)	Male BL (mm) mean (range)
<i>Bodianus perditio</i>	New Caledonia	2.75 (2.58–2.90) (N = 12)	2.91 (2.74–3.08) (N = 2)
<i>Bodianus perditio</i>	Taiwan	2.84 (2.44–3.02) (N = 10)	2.81 (2.74–2.86) (N = 4)
<i>Macolor niger</i>	New Caledonia	3.12 (2.91–3.26) (N = 20)	3.35 (3.14–3.48) (N = 12)

BL, Body length

166°15'E) (NC), 02 Oct. 2003; 5♀♀ from gills of *B. perditio* (JNC1088B), Récif To (22°29'S, 166°26'E) (NC), 28 Apr 2004; 1♀ from gills of *B. perditio* (JNC1469B), Récif Le Sournois (NC), 08 Mar 2005; 2♀♀ from gills of *B. perditio* (JNC1526), Récif Aboré (22°21'S, 166°16'E) (NC), 26 Apr 2005; 23♀♀, 11♂♂ from gills of *Macolor niger* (JNC1716), Passe de Dumbéa (NC), 16 Jan 2006; 22♀♀, 5♂♂ from gills of *M. niger* (JNC1717), Passe de Dumbéa (NC), 16 Jan 2006. Taiwanese material: 23♀♀, 4♂♂ paratypes from gills of *B. perditio*, Tai-Dong, Taiwan, 17 Aug. 2005.

**Type-material:** Holotype female, 8 paratype females and 1 paratype male, MNHN-Cp2432 (holotype) and MNHN-Cp2433 – Cp2435 (paratypes); 9 paratype females and 1 paratype male, BMNH 2007.306–315. The Taiwanese paratypes (11 females and 3 males, USNM 1102748–1102751); personal collection of C.-L.Lin (12 females and 1 male). Additional material from *Macolor niger*, MNHN Cp2436 (23 females and 11 males) and BMNH 2007.316–325 (22 females and 5 males).

**Etymology:** The new species is characterised by the strongly indented margin of the distal exopodal segment of the first leg. The specific name, *excavatus*, refers to this distinctive notched margin.

**Remarks on prevalence:** Off New Caledonia, the prevalence on *M. niger* was 100% (2/2), and 33% on *B. perditio* (6/18). Specimens of *B. perditio* harbouring this species tended to be larger than those without it [fork length (FL) 370–450, mean 430 mm, and weight 1,028–1,900, mean 1,538 g (n = 6) compared with FL 228–440, mean 311 mm, and weight 228–1,580, mean 650 g (n = 12)].

## Description (Figs. 1–3)

### Adult female

Body (Fig. 1A) dorsoventrally flattened, comprising caligiform anterior cephalothorax, incorporating first

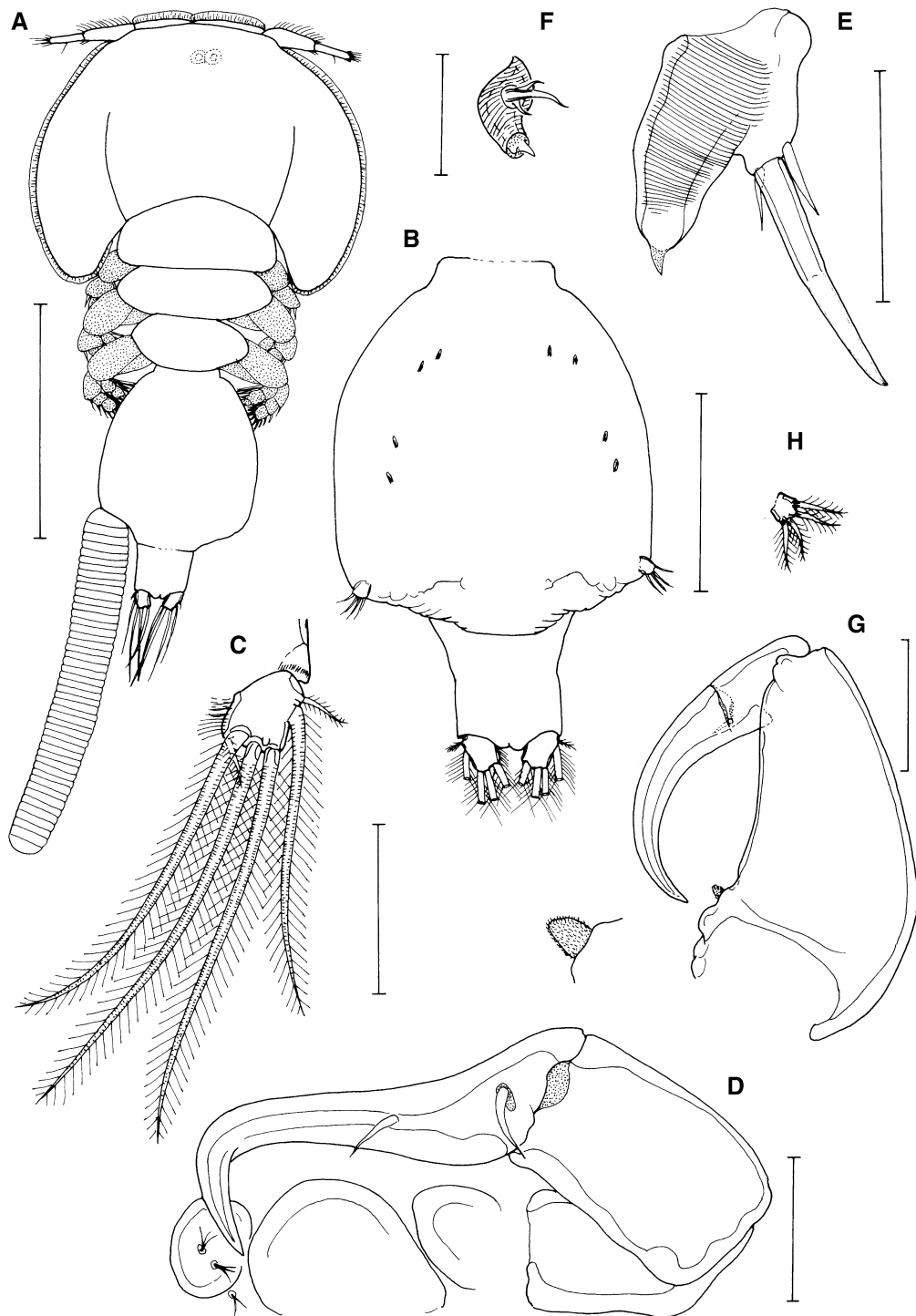
pedigerous somite only, 3 free pedigerous somites, genital complex and free 1-segmented abdomen. Body length 2.84 (2.44–3.02, based on 10 specimens). Paired frontal plates present between antennules, lacking lunules. Dorsal cephalothoracic shield expanded laterally; lateral zones provided with marginal membrane along entire free margin. Nauplius eye present close to frontal margin of dorsal cephalothoracic shield. Genital complex (Fig. 1B) just wider than long with length 0.82 (0.70–0.90, based on 10 specimens) and width 0.87 (0.78–0.96), with evenly rounded margins. Paired oviduct openings on ventral surface adjacent to posterior margin of complex; paired copulatory pores located anterior to oviduct openings. Ventral ornamentation of genital complex comprising 4 bifid anterior spinules arranged transversely in 2 pairs, plus 4 bifid spinules located laterally. Abdomen (Fig. 1B) just wider than long; length 0.25 (0.20–0.28, based on 10 specimens) and width 0.27 (0.24–0.30). Caudal rami (Fig. 1C) with 2 short and 4 long plumose setae. Egg-sacs uniseriate, c.1.70 in length, containing approx. 50 eggs.

Antennule (Fig. 2A) 2-segmented, slender; first segment tapering distally, with 25 plumose setae arrayed on ventral surface by anterior and distal margins, plus 2 dorsal surface setae; second segment cylindrical with 11 setae (5 plumose and 6 naked) and 2 aesthetascs, plus 1 plumose seta midway along posterior margin.

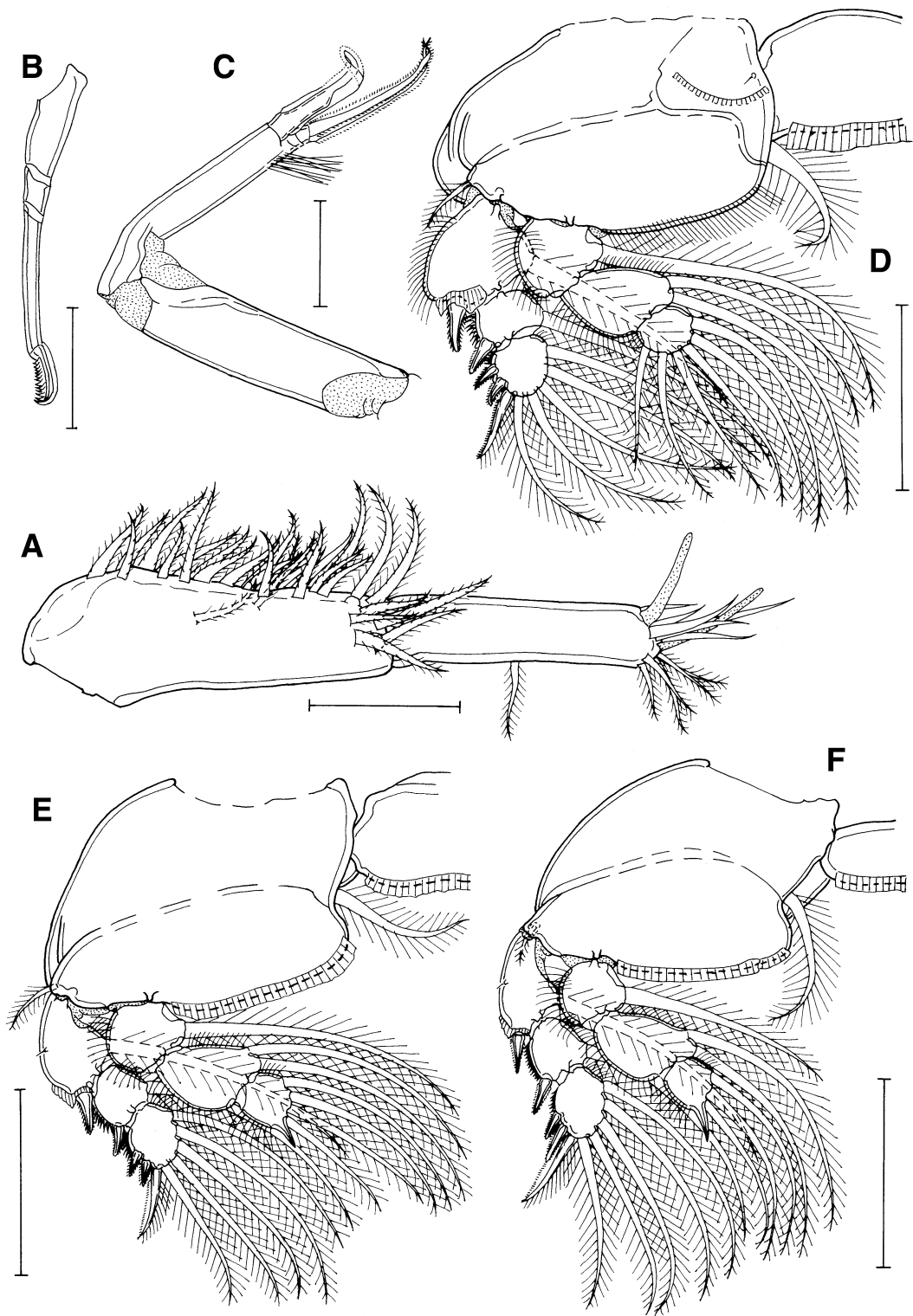
Antenna (Fig. 1D) uniramous, 3-segmented: proximal segment unarmed; middle segment unarmed; distal segment forming laterally-directed subchela armed with 2 naked setae. Postantennal process represented by small raised region under subchela, with 3 multisetulate sensory papillae located adjacent.

Oral cone with opening formed by both labrum and labium. Mandible stylet-like (Fig. 2B), bearing row of 12 similar teeth on one side near apex.

Maxillule (Fig. 1E,F) forming a small lobe with striated surface bearing 3 unequal naked setae anteriorly representing papillate palp, and with



**Fig. 1** *Dissonus excavatus* n. sp., adult female. A, habitus, dorsal view; B, genital complex and free abdomen, ventral view showing surface spinules; C, caudal ramus, ventral; D, antenna, ventral view *in situ*; E, maxillule, dissected out and drawn in medial view; F, maxillule *in situ*, ventral view; G, maxilliped (proximal segment not shown), posterior view, with inset showing sensory process in myxal region; H, detail of fifth leg enlarged from B. Scale-bars: A, 1 mm; B, 0.5 mm; C, G, 200  $\mu$ m; D-F, 100  $\mu$ m



**Fig. 2** *Dissonus excavatus* n. sp., adult female. A, antennule, antero-ventral view; B, mandible; C, maxilla, ventral view; D, leg 2, ventral view; E, leg 3, ventral view; F, leg 4, ventral view. Scale-bars: A, 100  $\mu\text{m}$ ; B, 50  $\mu\text{m}$ ; C-F, 200  $\mu\text{m}$



tapering posterior extremity carrying a tiny spinous process.

Maxilla (Fig. 2C) comprising slender, unarmed syncoxa and slender basis terminating in 2 slightly curved processes; both ornamented with slightly twisted rows of finely serrated membrane. Tuft of long setules present proximal to longer process.

Maxilliped (Fig. 1G) slender, with robust protopod (corpus); distal subchela incorporating endopodal segments and claw. Myxal margin of corpus with raised area proximally bearing stout micro-spinulate sensory element (inset in Fig. 1G). Subchela with partial suture line marking plane of fusion between endopod and claw; single seta located near inner concave margin; tip of subchela sclerotised.

Sternal furca absent.

Swimming legs 1 to 4 biramous; rami of first leg 2-segmented; rami 3-segmented in legs 2 to 4. Intercoxal sclerite ornamented with marginal membrane along posterior margin present in legs 1 to 4. Spine and seta formula as follows:

	Coxa	basis	exopodal segments	endopodal segments
leg 1	0-0	1-1	I-0; IV,3	0-0; 3
leg 2	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 6
leg 3	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 4
leg 4	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 3

Leg 1 (Fig. 3A) ornamented with strong sclerotised flanges on anterior surface of basis and first endopodal segment; ornamented with fine spinule rows along outer margin of second endopodal segment and inner margin of first exopodal segment. Distal exopodal segment armed with 2 short spines proximally and 2 long spines distally on outer margin; outer margin of segment indented at level of first spine. Distal endopodal segment drawn into distal tooth-like process, and with 2 smaller denticles subdistally on lateral margin. Leg 2 (Fig. 2D) ornamented with strong sclerotised flange on anterior surface of coxa and row of fine spinules along free posterior margin of basis. Legs 3 (Fig. 2E) and 4 (Fig. 2F) each with marginal membrane along free posterior margin of basis.

Fifth leg (Fig. 1H) represented by small exopodal lobe bearing 4 plumose setae. Leg 6 represented by unarmed genital operculum in female.

### Male

Body form (Fig. 3B) and expressed segmentation similar to that of female. Body length 2.81 (2.74–2.86, based on 4 specimens). Genital complex (Fig. 3C) longer than wide with length 0.85 (0.82–0.90, based on 4 specimens) and width 0.53 (0.52–0.54), with evenly convex lateral margins. Paired genital openings on ventral surface close to posterior margin. Ventral ornamentation of genital complex comprising 4 bifid anterior spinules arranged transversely in 2 pairs, plus 4 bifid spinules located laterally and positioned in oblique line between anterior spinules and leg 5. Abdomen (Fig. 3C) just wider than long; length 0.22 (0.20–0.26, based on 4 specimens) and width 0.28 (0.28–0.28).

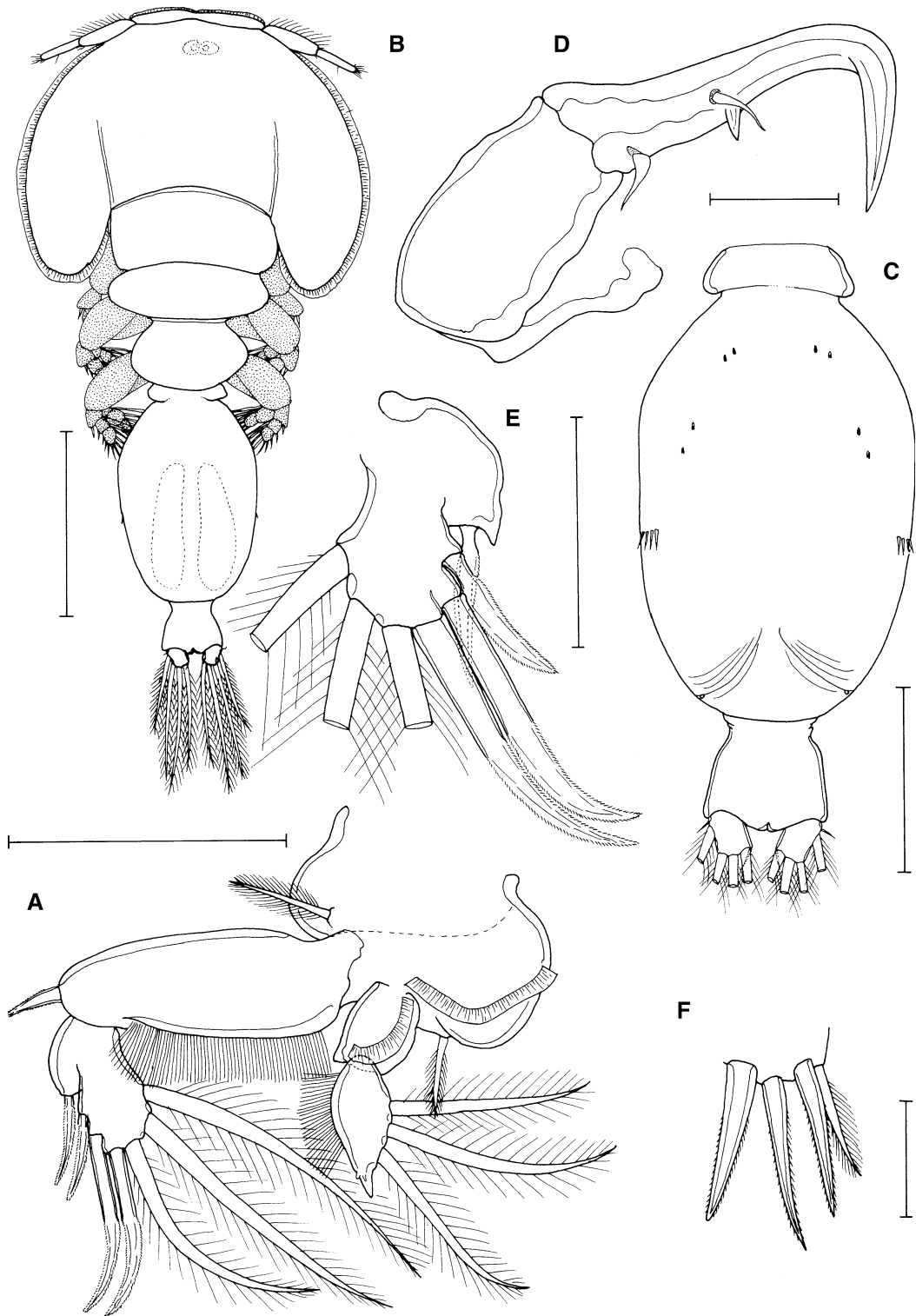
Most limbs as in female, except antenna, leg 1 and legs 5 and 6. Antenna (Fig. 3D) 3-segmented: proximal segment unarmed; middle segment unarmed; distal segment forming double-clawed subchela armed with 2 naked setae; accessory claw small, located about mid-length and directed posteriorly. Postantennal process as in female.

Leg 1 (Fig. 3E) similar to that of female except indentation on outer margin of distal exopodal segment is more pronounced and proximal spine carried at this level lying posteriorly and is largely concealed behind other outer spines.

Leg 5 (Fig. 3C,F) represented by row of 4 spiniform setal elements located laterally on genital complex about at mid-length. Leg 6 (Fig. 3C) represented by paired genital opercula and carrying rounded spine.

### Remarks

The new species shares the lack of a sternal furca or sternal stylet with five other congeners: *D. glaber* Kurtz, 1924, *D. spinifer* Wilson, 1906, *D. heronensis* Kabata, 1966, *D. furcatus* Kirtisinghe, 1950 and *D. similis* Kabata, 1966. It also shares with all of these, except *D. glaber*, the possession of an ornamentation of spinules on the ventral surface of the genital complex in both the female and the male. The description of *D. furcatus* (Kirtisinghe, 1950) lacks sufficient detail to allow comparison between appendages, but it is characterised by an elongate abdomen, more than twice as long as wide, in both



**Fig. 3** *Dissonus excavatus* n. sp., adult female. A, first leg, ventral. Adult male. B, habitus, dorsal; C, genital complex and free abdomen, ventral view showing surface spinules; D, antenna, ventral view *in situ*; E, distal exopodal segment of leg 1, showing posteriorly displaced proximal spine; F, leg 5, ventral *in situ*. Scale-bars: A, 200  $\mu$ m; B, 1 mm; C, 0.5 mm; D-E, 100  $\mu$ m; F, 50  $\mu$ m



sexes. This serves to distinguish Kirtisinghe's species from *D. excavatus* n. sp. in which the abdomen is wider than long in both sexes.

The pattern of ventral spinulation allows the new species to be distinguished from *D. spinifer* and *D. similis*. It has only eight ventral spinules on the genital complex in both sexes, whereas these two species have numerous spinules. *D. spinifer* has longitudinal rows of bifid and simple spinules extending almost to the posterior margin of the ventral surface (see below) and *D. similis* has extensive areas of spinulation over the anterior half of the ventral surface (Kabata, 1966).

Finally, the new species differs from *D. heronensis* in the relative lengths of the outer margin spines on the distal exopod segment of leg 1: in the latter all four spines are of similar length, although the second spine is the shortest, whereas in *D. excavatus* the two proximal spines are markedly shorter than the two distal spines (cf. Figs. 3A, 7A). In addition, in the new species the terminal exopodal segment is modified: the outer margin is strongly indented and, in the male, the outer spine is located posterior to, and largely concealed by, the other outer spines (Fig. 3E). Other differences between these two species include the form of the maxillule in *D. excavatus* in which the largest of the three setae on the prominent anterior papilla is thickened proximally and extends way beyond the apex of the posterior process (cf. Fig. 1E and 6D). In the male leg 6 is represented by a tiny, knob-like setal vestige in *D. excavatus*, whereas in *D. heronensis* it carries one short and two long setae. In *D. excavatus* the myxal margin of the corpus of the maxilliped has a raised area proximally bearing a micro-spinulate sensory element, whereas in *D. heronensis* the myxal region of the corpus has a well-developed crescentic ridge (cf. Figs. 1G, 6E).

The new species is the first to be reported from a member of the family Labridae. It has a wide distribution on the golden-spot hogfish *Bodianus perditio* from Taiwan to New Caledonia. It is also the first to be reported from a snapper (family Lutjanidae) and is currently known only from the black and white snapper *Macolor niger* off New Caledonia. Specimens of both sexes of *D. excavatus* n. sp. are larger on the lutjanid host than on the labrid (Table 1), with a mean female body length of 3.12 mm compared to 2.84 mm (Taiwan) and 2.75 mm (New Caledonia) in the latter. The mean male body length is 3.35 mm on the lutjanid

compared to 2.91 (New Caledonia) and 2.81 mm (Taiwan) in the labrid. The mean body lengths of both sexes are very similar in the material from *B. perditio* collected off Taiwan, but, unusually, the male is larger than the female in the material from both hosts off New Caledonia, especially so in *M. niger*.

This copepod was not found on three other species of *Bodianus* examined (*B. loxozonus* Snyder, *B. axillaris* (Bennett) and *B. busellatus* Gomon). It was also not found on twelve other species of labrids examined (*Cheilinus chlorourus* (Bloch), *C. trilobatus* Lacépède, *C. undulatus* Rüppell, *Choerodon fasciatus* (Günther), *C. graphicus* (De Vis), *Coris aygula* Lacépède, *Epibulus insidiator* (Pallas), *Oxycheilinus diagrammus* (Lacépède), *O. unifasciatus* (Streets), *Stethojulis strigiventer* (Bennett), *Thalassoma lutescens* (Lay & Bennett) and *T. nigrofasciatum* Randall). Among the lutjanids, it was found only on *M. niger* and not in other species such as *Aprion virescens* Valenciennes, *Etelis carbunculus* Cuvier, *E. coruscans* Valenciennes, *Lutjanus argentimaculatus* (Forsskål), *L. fulviflamma* (Forsskål), *L. gibbus* (Forsskål), *L. kasmira* (Forsskål) and *L. vitta* (Quoy & Gaimard).

*B. perditio* is one of the largest labrids in New Caledonia, and the largest specimens tended to be more infested than smaller ones; the specimens of *M. niger* examined were among the biggest lutjanids examined (FL 520–560 mm, W 2,900–3,200 g), it might be that this copepod preferentially selects large hosts. However, it is interesting to note (Lim & Justine, 2007) that the ancycrocephalid monogenean *Haliotrema banana* Lim & Justine, 2007 was found, among labrids, only in *B. perditio*, as was the case for *D. excavatus*. Monogeneans are rare on labrids and *B. perditio* thus has an outstandingly rich gill parasite fauna.

### *Dissonus inaequalis* n. sp.

*Type-host*: *Chiloscyllium punctatum* Müller & Henle.

*Additional host*: *Chiloscyllium* cf. *punctatum*.

*Site*: Gills and nasal bulbs.

*Type-locality*: South China Sea (02°54'N, 112°06'E), off Mukah, Sarawak, Malaysia.

*Additional locality*: Off Iloilo, Philippines.

*Material examined*: 5♀♀, 6♂♂ from gills of male *Chiloscyllium* cf. *punctatum* (BO-278), South China Sea (02°54'N 112°06'E), off Mukah, Sarawak,

Malaysia, collected on 08 June 2002; 2♀♀, 2♂♂ from gills and nasal bulbs of female *C. punctatum* (BO-68), same locality data; 1♀ from gills of female *C. cf. punctatum* (BO-33), same locality data; 1♂ from gills of female *C. cf. punctatum* (BO-42), same locality data; 1♂ from nasal bulbs of male *C. cf. punctatum* (BO-274), same locality data; 2♀♀ from gills of female *C. cf. punctatum* (BO-280), same locality data; 1♂ from gills of male *C. cf. punctatum* (BO-281), same locality data; 10♀♀, 6♂♂ from gills and nasal bulbs of female *C. cf. punctatum* (BO-282), same locality data.

**Additional Material:** 3♀♀, 1♂ from gills of *C. punctatum*, off Iloilo, Philippines, 29 Sept. 2003.

**Type-material:** Holotype female, 3 paratype females and 3 paratype males, MZUM(P) 594(H) (holotype) and MZUM(P) 595(P)(a-d) and 596(P)(a-d) (paratypes); 3 paratype females and 3 paratype males, SBC P-00022-00027; 3 paratype females and 3 paratype males, USNPC 100096.00 to 100098.00; and 7 paratype females and 5 paratype males, BMNH 2007.326-337. One female from the additional Philippine material, BMNH 2007.338; the remaining Philippine material is stored in the personal collection of S. Ohtsuka.

**Etymology:** The name of the new species refers to the differences in size of the outer spines on the distal exopod segment of leg 1: the two distal spines on the outer margin differ markedly in size, whereas in those congeners for which this information is available, the distal two spines are usually of similar lengths.

## Description (Figs. 4, 5)

### Adult female

Body (Fig. 4A) segmentation typical for genus. Body length 1.86 (1.65–2.09, based on 12 specimens). Genital complex (Fig. 4B) 1.08 times longer than wide on average (L:W ratio range 1:0.99–1.15) with length 0.50 (0.45–0.59, based on 12 specimens) and width 0.47 (0.43–0.55), with evenly rounded margins. Paired oviduct openings on ventral surface adjacent to posterior margin of complex. Ventral ornamentation of genital complex comprising 8 bifid anterior spinules arranged transversely in 4 pairs, plus 4 bifid spinules located laterally and positioned in 2 pairs one posterior to other. Abdomen (Fig. 4B) about as long as wide; length 0.17 (0.15–0.21, based on 12

specimens) and width 0.17 (0.16–0.20). Caudal rami (Fig. 4B) with 2 short and 4 long plumose setae. Egg-sacs uniseriate, length c.0.97 (0.7–1.12), containing c.21 eggs per sac (range 14–25).

Antennule (Fig. 4C) 2-segmented, slender; first segment tapering distally, with 25 plumose setae arrayed on ventral surface by anterior and distal margins, plus 2 dorsal surface setae; second segment cylindrical with 10 setae and 2 aesthetascs, plus 1 seta midway along posterior margin.

Antenna (Fig. 4D) uniramous, 3-segmented: proximal and middle segments unarmed; distal segment forming laterally-directed subchela armed with 2 posteriorly-directed, naked setae. Postantennal process (Fig. 4D) represented by small raised region under subchela, with 3 setulate sensory papillae located adjacent.

Oral cone and mandible as in *D. excavatus* n. sp.

Maxillule (Fig. 4E) elongate, bearing 3 unequal naked setae anteriorly representing papillate palp, and with elongate posterior process carrying tiny, thin-walled, spinous process subapically.

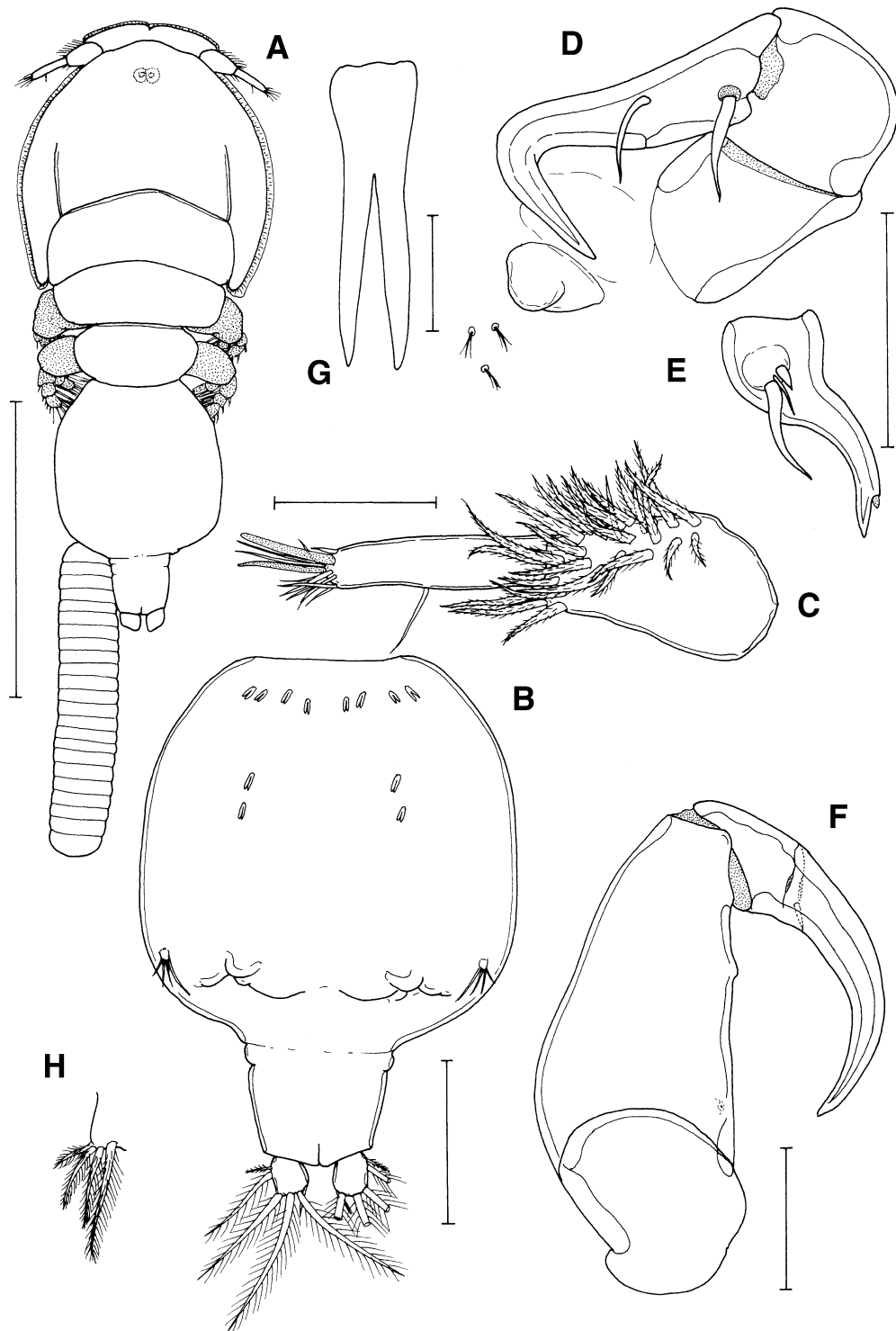
Maxilla as in *D. excavatus* n. sp.

Maxilliped (Fig. 4F) comprising robust protopod (corpus) and distal subchela incorporating endopodal segments and claw. Myxal margin of corpus with tiny proximal sensory process bearing pore and small swelling distally. Subchela with partial suture line marking plane of fusion between endopod and claw; single seta located near inner concave margin; tip of subchela sclerotised.

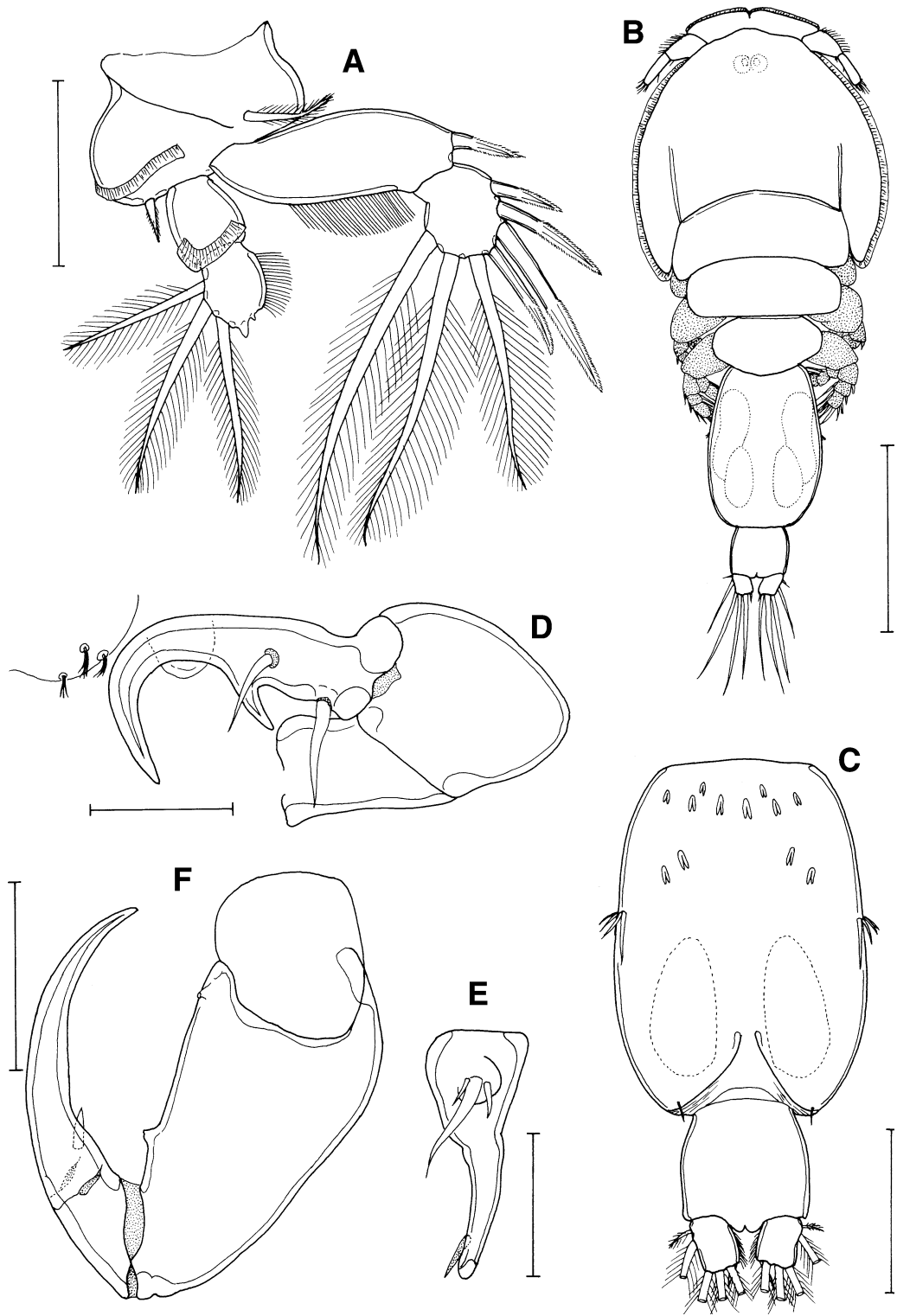
Sternal furca slender (Fig. 4G), with elongate tines lying close together, extending just posterior to intercoxal sclerite of first legs.

Swimming legs 1 to 4 as in *D. excavatus* n. sp. in segmentation and in spine and seta formula. Leg 1 (Fig. 5A) ornamented with strong cuticular flanges on anterior surface of basis and first endopodal segment; ornamented with fine spinule rows along outer margin of second endopodal segment and first exopodal segment. Distal endopodal segment drawn into small, tooth-like distal process and with 1 small denticle subdistally on lateral margin. Three outer spines on distal exopodal segment increasing in length from proximal to distal; terminal spine shorter than adjacent spine, about equal in length to second spine on outer margin.

Fifth leg (Fig. 4H) represented by small exopodal lobe bearing 4 plumose setae. Leg 6 represented by unarmed genital operculum in female.



**Fig. 4** *Dissonus inaequalis* n. sp., adult female. A, habitus, dorsal view; B, genital complex and free abdomen, ventral view showing surface spinules; C, antennule, antero-ventral; D, antenna, ventral view *in situ*; E, maxillule *in situ*, ventral view; F, maxilliped (proximal segment not shown), posterior view; G, sternal furca; H, leg 5, enlarged from Fig. 4B. Scale-bars: A, 1 mm; B, 0.25 mm; C-F, 100  $\mu$ m; G, 50  $\mu$ m



**Fig. 5** *Dissonus inaequalis* n. sp., adult female. A, first leg, ventral. Adult male, B, habitus, dorsal; C, genital complex and free abdomen, ventral view showing surface spinules; D, antenna, ventral view *in situ*; E, maxillule drawn *in situ*; F, maxilliped (proximal segment omitted). Scale-bars: A,F, 100  $\mu$ m; B, 0.5 mm; C, 200  $\mu$ m; D-E, 50  $\mu$ m

### Male

Body form (Fig. 5B) and expressed segmentation similar to that of female. Body length 1.61 (1.48–1.82, based on 5 specimens). Genital complex (Fig. 5C) c.1.5 times longer than wide (L:W ratio 1:1.35–1.73), with length 0.45 (0.42–0.50) and width 0.30 (0.29–0.31); lateral margins evenly convex. Paired genital openings on ventral surface close to posterior margin. Ventral ornamentation of genital complex comprising 8 bifid anterior spinules arranged transversely in 4 pairs, plus 4 bifid spinules located laterally and positioned in oblique line between anterior spinules and leg 5. Abdomen (Fig. 5C) about as long as wide; length 0.15 (0.13–0.15, based on 5 specimens) and width 0.14 (0.14–0.15).

Most limbs as in female, except antenna, maxillule, and legs 5 and 6. Antenna (Fig. 5D) 3-segmented: proximal and middle segments unarmed; distal segment forming double-clawed subchela armed with 2 naked setae; accessory claw located about at mid-length and directed posteriorly. Postantennal process (Fig. 5D) represented by small raised process under subchela, bearing 3 setulate sensory papillae.

Maxillule (Fig. 5E) elongate, bearing 3 unequal naked setae anteriorly representing papillate palp, and with elongate posterior process carrying well developed, thin-walled spinous process subapically.

Maxilliped (Fig. 5F) similar to that of female but spine on subchela more robust and distal process on myxal margin slightly better developed.

Leg 5 (Fig. 5C) represented by row of 4 spiniform setal elements located laterally on genital segment about at mid-length. Leg 6 (Fig. 5C) represented by paired genital opercula, each carrying tiny spine.

### Remarks

The new species shares the possession of a sternal furca with slender, paired tines with four nominal congeners: *D. ruvetti* Nunes-Ruivo & Fourmanoir, 1956, *D. hoi* Tang & Kalman, 2005, *D. nudiventris* Kabata, 1965 and *D. pastinum* Deets & Dojiri, 1990. In *D. inaequalis* n. sp. the distal two of the outer spines on the terminal exopod segment of leg 1 differ markedly in size, whereas in all four listed congeners the distal two spines are of similar lengths. The new species can also readily be distinguished from *D. nudiventris* and *D. pastinum*, both of which also

utilise elasmobranchs as hosts, by the presence of an ornamentation of bifid spinules on the ventral surface of the genital complex in both sexes, since *D. nudiventris* and *D. pastinum* lack such ornamentation. It differs from *D. hoi* in the shape and ventral ornamentation pattern of the genital complex, and in the form of the maxillule: in *D. hoi* the papilla carrying the three anterior setae is elongate giving the limb a bifid appearance (Tang & Kalman, 2005), whereas in the new species this papilla is a small rounded knob as in all other species. Comparisons with *D. ruvetti* are more difficult as this species is incompletely described (Nunes-Ruivo & Fourmanoir, 1956). The body size of 4.0 mm given for both sexes of *D. ruvetti* is markedly larger than that of the new species (1.86 for females and 1.61 mm for males). The abdomen of *D. ruvetti* is described as 2-segmented and shown as 1.2 to 1.3 times longer than wide, whereas the one-segmented abdomen of the new species is about as long as wide in both sexes. The distal margin of the terminal endopod segment of leg 1 bears two small processes in the new species, whereas this margin is rounded and lacking processes in *D. ruvetti*.

The new species is the fourth in the genus to be described from an elasmobranch host and the first to be reported from a member of the family Hemiscylliidae (Table 4). The specimens from the Philippines are slightly larger than those from Sarawak, with a mean female body length of 2.1 mm (range 2.0–2.3, N = 3) and a male body length of 1.7 mm.

### *Dissonus heronensis* Kabata, 1966

*Host:* *Pseudobalistes fuscus* (Bloch & Schneider).

*Site:* Gills.

*Material examined:* Holotype male from collections of Natural History Museum, London: Reg. No. BMNH 1966.3.18.5; taken from gills of unspecified balistid host caught off Heron Island, Queensland, Australia.

*New Caledonian material:* 1♀, 1♂ from gills of *Pseudobalistes fuscus* (JNC928A), Récif To (22°29'30"S, 166°26'E) (NC), 14 Oct. 2003; 2♀♀ from gills of *P. fuscus* (JNC1281B), Passe de Dumbéa (22°21'S, 166°15'E) (NC), 22 Sept. 2004; 13♀♀, 1♂ from gills of *P. fuscus* (JNC1680), Récif



Toombo (22°32'S, 166°27'E) (NC), 13 Dec. 2006; 5♀, 9♂, 8 chalimus larvae from gills of *P. fuscus* (JNC1844), near Îlot Signal (22°17'S, 166°17'E) (NC), 30 May 2006. Prevalence off New Caledonia was 66% (4/6). The specimens of *P. fuscus* that were positive for *D. heronensis* were 350–550 mm in fork length and 804–4,700 g in weight.

*Voucher material*: 10 females and 5 males, MNHN-Cp2437–Cp2438; 11 females and 6 males, BMNH 2007.339–348.

## Description (Figs. 6–9)

### Adult female

Body (Fig. 6A) segmentation typical for genus. Body length 2.24 (2.07–2.35, based on 11 specimens). Genital complex (Fig. 6B) longer than wide, with length 0.66 (0.59–0.73, based on 11 specimens) and width 0.58 (0.52–0.63), with evenly rounded margins. Paired oviduct openings on ventral surface adjacent to posterior margin of complex. Some females carrying paired, crescent-like spermatophores ventrally, above genital complex; each spermatophore discharging via spermatophore tubule, which crosses to opposite side of body from where attached before entering copulatory pore (Fig. 8A,B). Ventral ornamentation of genital complex comprising 4 (rarely 5) bifid anterior spinules typically arranged transversely in 2 pairs, plus 4 bifid spinules located obliquely near lateral margin (Fig. 6B). Bifid spinules posteriorly-directed, tapering towards tips and *c.*19–20 µm in length (Fig. 9A). Abdomen (Fig. 6B) wider than long; length 0.19 (0.17–0.20, based on 11 specimens) and width 0.26 (0.24–0.38). Caudal rami (Fig. 6B) with 2 short and 4 long plumose setae. Egg-sacs uniseriate, *c.*1.56 in length, containing approx. 38 eggs (range 29–47).

Antennule as in *D. excavatus* n. sp.

Antenna uniramous (Fig. 6C), 3-segmented: proximal and middle segments unarmed; distal segment forming laterally-directed subchela armed with 2 naked setae. Postantennal process represented by small raised region under subchela, with 3 setulate sensory papillae located on adjacent surface.

Oral cone and mandible as in *D. excavatus* n. sp.

Maxillule (Fig. 6D) forming small lobe with finely striated surface bearing 3 unequal naked setae anteriorly on papilla representing palp, and with

tapering posterior process carrying tiny spinous process subdistally.

Maxilla (Fig. 9B) with curved distal processes ornamented with strips of serrated membrane orientated obliquely near tip.

Maxilliped (Fig. 6E) comprising robust protopod (corpus) and distal subchela incorporating endopodal segments and claw. Myxal margin of corpus with crescentic ridge proximally opposing tip of subchela; small sensory process present distal to ridge; rounded, sclerotised swelling present on posterior surface of corpus. Subchela with partial suture line marking plane of fusion between endopod and claw, bearing tiny seta at end of suture line; tip of subchela sclerotised.

Sternal furca absent.

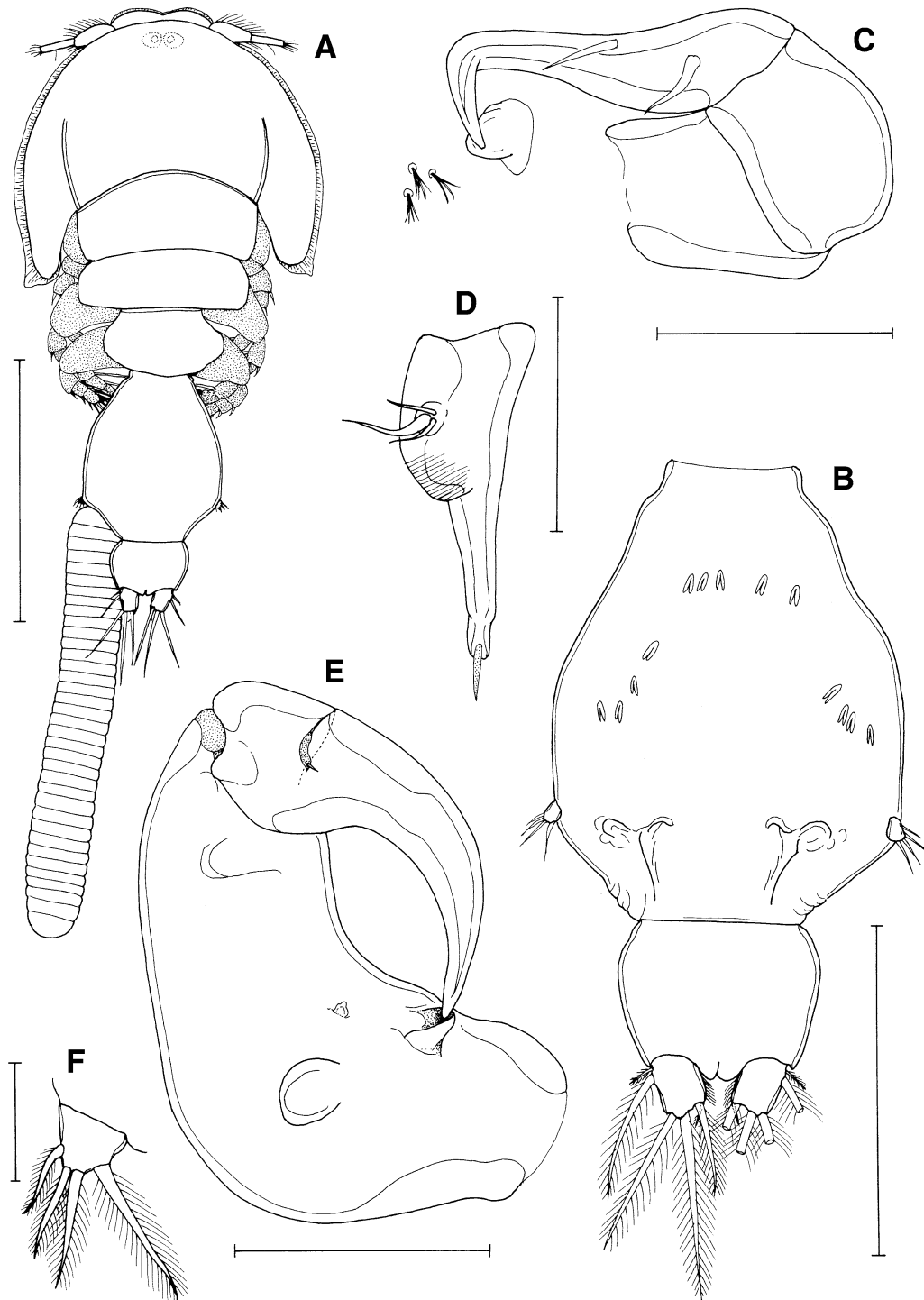
Swimming legs 1 to 4 as in *D. excavatus* n. sp. in segmentation and in spine and seta formula. Leg 1 (Fig. 7A) ornamented with sclerotised flanges on anterior surface of basis and first endopodal segment (arrowed in Fig. 9D); ornamented with fine spinule rows along outer margin of second endopodal and inner margin of first exopodal segments. Distal endopodal segment drawn into distal tooth-like process and with 2 smaller denticles subdistally on lateral margin (Fig. 9C). Leg 2 ornamented with strong sclerotised flange on anterior surface of coxa and with row of fine spinules along free posterior margin of basis. Legs 3 and 4 each with marginal membrane along free posterior margin of basis.

Fifth leg (Fig. 6F) represented by small lobe bearing 4 plumose setae. Leg 6 represented by unarmed genital operculum in female.

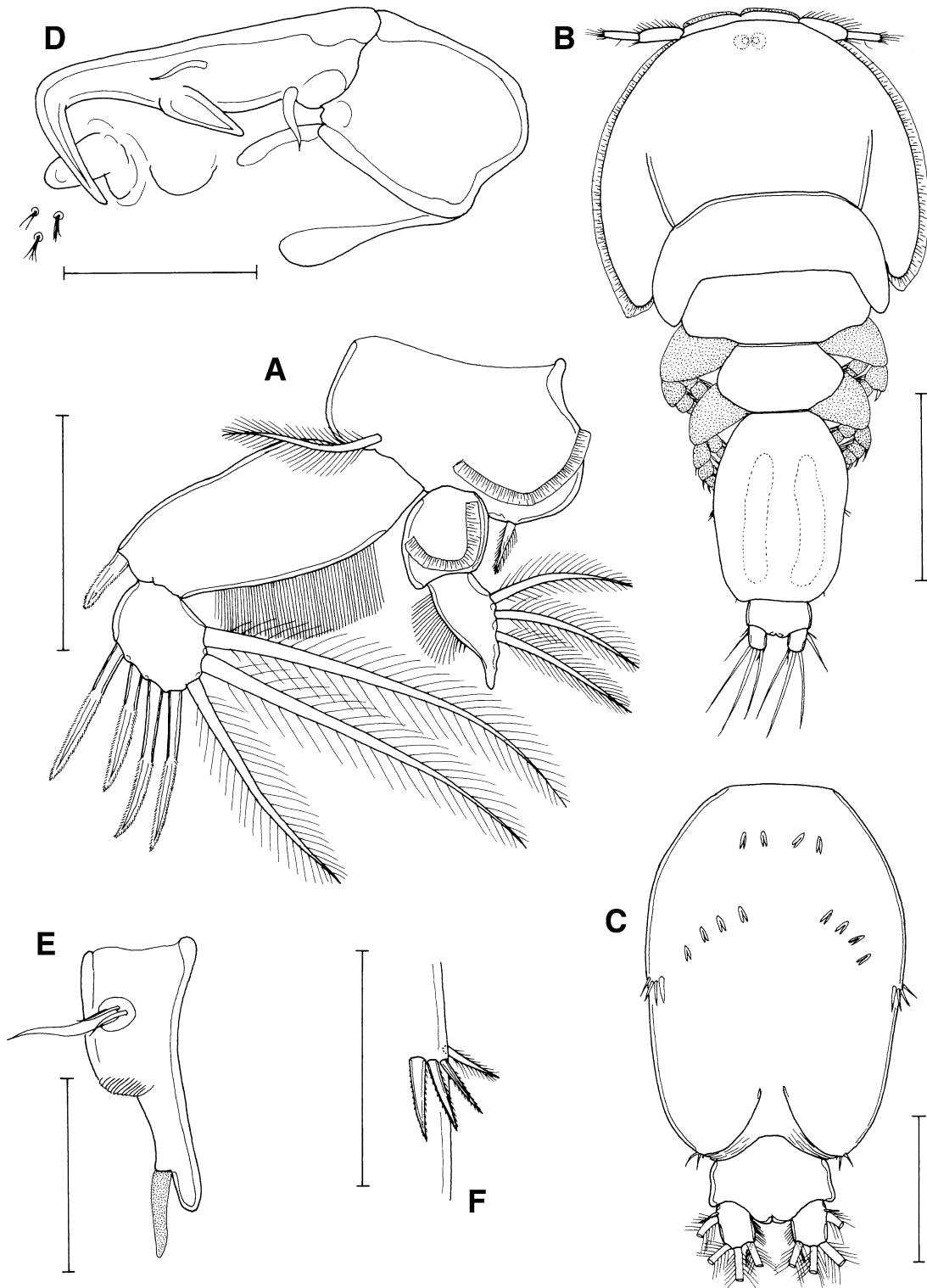
### Male

Body form (Fig. 7B) and expressed segmentation similar to that of female. Body length 1.71 (single specimen). Genital complex (Fig. 7C) longer than wide 0.50 × 0.35, with evenly convex lateral margins. Paired genital openings on ventral surface close to posterior margin. Spermatophores paired; each elongate, crescent-like in shape; tubule emerging from concave surface, in posterior third; convex surface sparsely hirsute; posterior tip bulbous (Fig. 8B). Ventral ornamentation of genital complex comprising 4 bifid anterior spinules arranged transversely in 2 pairs, plus 4 bifid spinules located laterally and positioned in an oblique line between anterior spinules and leg 5. Abdomen (Fig. 7C) 1.7 times wider than long, 0.10 × 0.17.

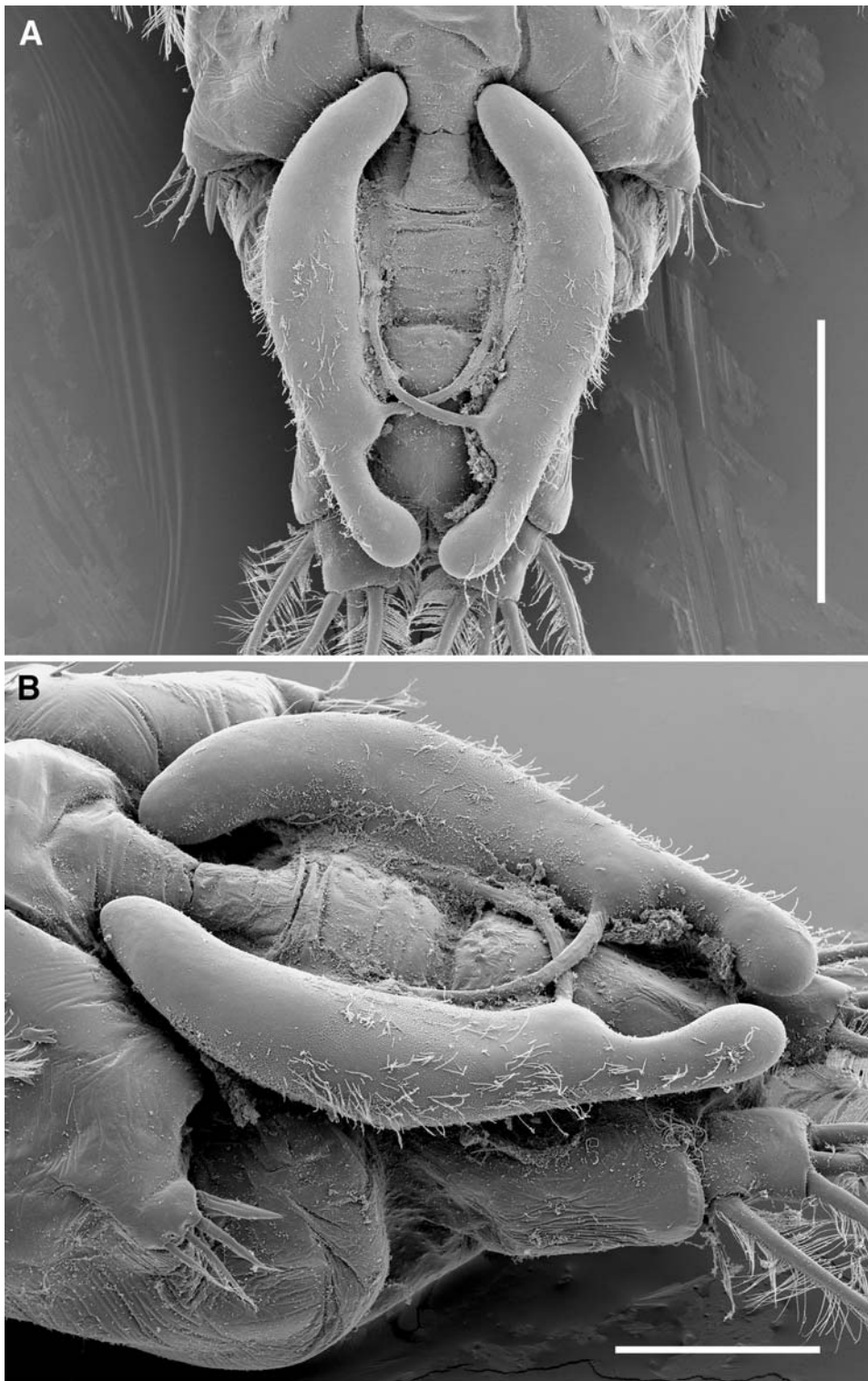




**Fig. 6** *Dissonus heronensis* Kabata, 1966, adult female. A, habitus, dorsal view; B, genital complex and free abdomen, ventral view showing surface spinules; C, antenna, ventral view *in situ*; D, maxillule drawn *in situ*, ventral view; E, maxilliped (proximal segment not shown), posterior view showing sensory process and crescentic ridge in myxal region; F, leg 5 ventral. Scale-bars: A, 1 mm; B, 0.5 mm; C-D, 100  $\mu$ m; E, 200  $\mu$ m; F, 50  $\mu$ m

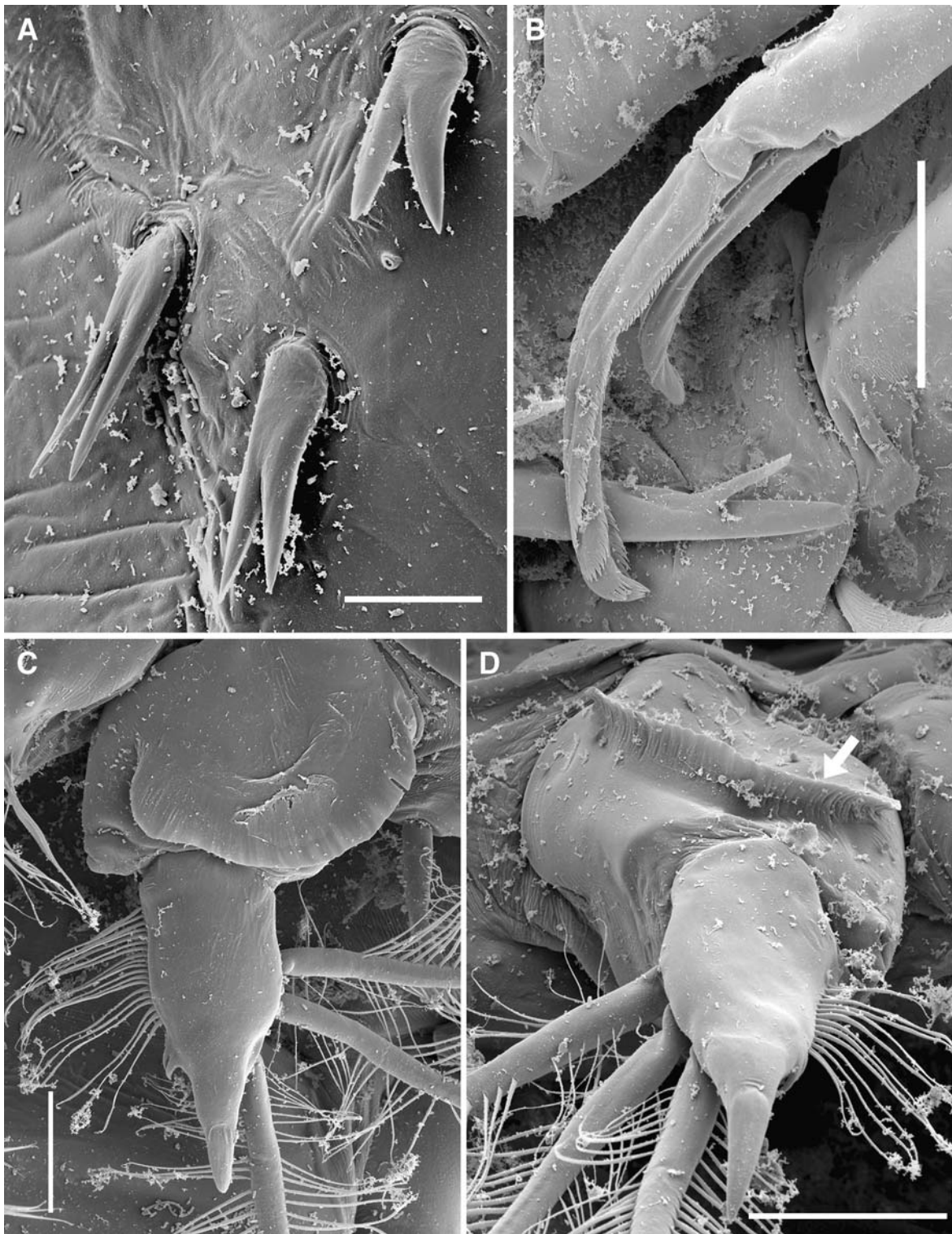


**Fig. 7** *Dissonus heronensis* Kabata, 1966, adult female, A, first leg, ventral. Adult male, B, habitus, dorsal; C, genital complex and free abdomen, ventral view showing surface spinules; D, antenna, ventral view *in situ*; E, maxillule drawn *in situ*; F, leg 5, ventral view. Scale-bars: A,D-F, 100  $\mu$ m; B, 0.5 mm; C, 200  $\mu$ m



**Fig. 8** *Dissonus heronensis* Kabata, 1966, SEM photographs. A, ventral view of genital region of adult female with pair of spermatophores attached; B, ventrolateral view of spermatophores *in situ* on female, showing fertilisation tubes each discharging into copulatory pore on opposite side of body. Scale-bars: A, 200  $\mu$ m; B, 100  $\mu$ m





**Fig. 9** *Dissonus heronensis* Kabata, 1966, SEM photographs. A, bifid spinules on ventral surface of genital complex; B, tip of maxilla showing serrated membranes ornamenting distal elements; C, endopod of leg. 1 ventral view; D, same, oblique view showing sclerotised flange (arrowed). Scale-bars: A, 10  $\mu$ m; B, 50  $\mu$ m; C-D, 20  $\mu$ m

Most limbs as in female, except antenna, maxillule, and legs 5 and 6. Antenna (Fig. 7D) 3-segmented: proximal and middle segments unarmed; distal segment forming double-clawed subchela armed with 2 naked setae; accessory claw located about at mid-length and directed postero-medially. Postantennal process (Fig. 7D) represented by small raised process under subchela, bearing 3 multisetulate sensory papillae.

Maxillule (Fig. 7E) with strongly striated surface bearing 3 unequal naked setae anteriorly on papilla representing palp, and with tapering posterior process rounded at apex and carrying subdistal process.

Leg 5 (Fig. 7F) represented by row of 4 spiniform setal elements located laterally on genital complex about at mid-length. Leg 6 (Fig. 7C) represented by paired genital opercula carrying 2 short setae and tiny spine.

#### Remarks

*Dissonus heronensis* was originally described from a single male specimen (Kabata, 1966) and the description was consequently incomplete. Lewis (1968) subsequently found both sexes and gave comprehensive descriptions, although his very detailed figures are difficult to interpret. The diagnostic characters that confirm the identity of the new material reported here are: the pattern of bifid spinules on the genital complex, the short, broad abdomen of the male, the form of the maxillule and the relative lengths of the outer spines on the terminal exopodal segment of leg 1. Both sexes of the Enewetak material are slightly smaller than the Australian and New Caledonian material (Table 2), but the host species are also different and, with such

small sample sizes, it is not possible to determine the significance of these differences.

*D. heronensis* is a widely distributed parasite, occurring on hosts belonging to the family Balistidae (Tables 2, 4). Two host species were already known, *Balistoides viridescens* (Bloch & Schneider) and *Abalistes stellaris* (Bloch & Schneider), to which we add a third, *Pseudobalistes fuscus*. Four other species of balistid from off New Caledonia were examined [*Abalistes stellatus* (Anonymous), *A. filamentosus* Matsuura & Yoshino (only recently recorded, see Randall & Justine (2007)), *Balistoides conspicillum* (Bloch & Schneider), *Sufflamen fraenatus* (Latreille)]. None of these harboured *D. heronensis*, although it is interesting to note that this copepod has been found in other species of balistids in other localities (Table 2), including *A. stellatus* (as *A. stellaris*).

#### *Dissonus manteri* Kabata, 1966

**Material examined:** Holotype, allotype and paratypes, BMNH 1966.3.18.2; taken from gills of *Epinephelus maculatus* (Bloch) (as *Plectropomus maculatus*) caught off Heron Island, Queensland, Australia.

**New Caledonian material:** 2♂♂ from gills of *Plectropomus leopardus* (JNC243G) Baie de Koutio (22°14'S, 166°24'E), New Caledonia (NC), 6 Mar. 2003; 4♀♀, 1♂ from gills of *P. leopardus* (JNC522B), Pointe Bovis, Baie de Dumbéa (NC), 27 May 2003; 2♀♀ from gills of *P. leopardus* (JNC523B), Pointe Bovis, Baie de Dumbéa (NC), 27 May 2003; 1♀ from gills of *P. leopardus* (JNC534C), near La Regnière Island (22°20'S, 166°18'E), off Noumea, (NC), 15 June 2003; 1♂ from gills of *P. leopardus* (JNC698A), Îlot Sainte Marie, off Noumea (NC), Oct. 2003; 1♀ from gills of *P. leopardus* (JNC1191B), Récif Le Sournois

**Table 2** Body lengths of *Dissonus heronensis* from different hosts and localities

Host species	Locality	Female BL (mm) mean (range)	Male BL (mm) mean	Data source
Balistidae gen. sp.	Australia (Heron Is.)	–	1.81 (N = 1)	Kabata, 1966
<i>Balistoides viridescens</i>	Enewetak	1.96 (1.82–2.03) (N = 5)	1.51 (N = 1)	Lewis, 1968
<i>Abalistes stellatus</i> (as <i>A. stellaris</i> )	Australia (Heron Is.)	2.19 (N = 1)	–	Ho & Dojiri, 1977
<i>Pseudobalistes fuscus</i>	New Caledonia	2.24 (2.07–2.35) (N = 11)	1.71 (N = 1)	Present account

BL, Body length

(22°31'S, 166°26'E) (NC), 08 July 2004; 2♀, 1♂ from gills of *P. leopardus* (JNC1392C), Ilôt Signal (22°17'S, 166°17'E), off Noumea (NC), 12 Oct. 2004; 1♀ from gills of *P. leopardus* (JNC1392D), Ilôt Signal, off Noumea (NC), 12 Oct. 2004; 1♀ from gills of *P. leopardus* (JNC1393D), Ilôt Signal, off Noumea (NC), 12 Oct. 2004. 1♀ from gills of *Epinephelus maculatus* (JNC399A), Récif To (22°29'S, 166°26'E) (NC), 15 Apr 2003; 2♀ from gills of *E. maculatus* (JNC1190B), Récif Le Sournois (NC), 08 July 2004. 9♀, 7♂ from gills of *E. cyanopodus* (JNC812A), off Noumea (NC), Aug. 2003; 5♀, 1♂ from gills of *E. cyanopodus* (JNC1267B), Passe de Dumbéa (22°21'S, 166°15'E) (NC), 19 Sept. 2004; 1♀, 1♂ from gills of *E. cyanopodus* (JNC1365A), Passe de Dumbéa (NC), 28 Sept. 2004; 11♀, 7♂ from gills of *E. cyanopodus* (JNC1395B), Passe de Dumbéa (NC), 15 Oct. 2004; 3♀ from gills of *E. cyanopodus* (JNC1625), Passe de Dumbéa (NC), 25 Oct. 2005; 1♀ from gills of *E. cyanopodus* (JNC1626), Passe de Dumbéa (NC), 25 Oct. 2005. 1♀ from gills of *Plectropomus laevis* (JNC1865), external slope, Fausse Passe de Uitoé (NC), 11 June 2006.

*Taiwan Material*: 10 ♀♀ from *Plectropomus leopardus* caught off Dong-gang, Taiwan, 29 July 2003.

*Hosts*: *Plectropomus leopardus* (Lacépède), *Plectropomus laevis* (Lacépède), *Epinephelus cyanopodus* (Richardson) and *E. maculatus*.

*Site*: Gills.

*Localities*: New Caledonia, off Nouméa; off Taiwan (see Table 3).

*Voucher material*: 24 females and 10 males, MNHN Cp2427–Cp2431; 21 females and 11 males, BMNH

2007.349–358. The Taiwanese material of *D. manteri* is stored in the personal collection of C.-I. Lin.

## Remarks

*Dissonus manteri* is a distinctive species characterised by the possession of a sternal furca modified into a small tapering stylet. In the original description (Kabata, 1966), the hosts of this species were given as “unspecified serranid fish” and *Plectropomus maculatus* (Bloch) by Kabata (1966), but in the vial containing the holotype the label gives the latter host only. This is, therefore, the type-host which is now known as *Epinephelus maculatus*; the type-locality is off Heron Island. Ho & Dojiri (1977) recorded *P. leopardus* and *E. fario* (Thunberg) (the latter now known as *E. longispinis* (Kner)) as new hosts for *D. manteri* in Australian waters. The host *E. cyanopodus* is new for this copepod, as is *P. laevis*, both from New Caledonian waters. All these hosts are serranids belonging to the same subfamily, the Epinephelinae. *D. manteri* was not found in 11 other epinephelines examined from off New Caledonia, namely *Cephalopholis argus* Bloch & Schneider, *C. boenak* (Bloch), *C. sonnerati* (Valenciennes), *E. coioides* (Hamilton), *E. fasciatus* (Forsskål), *E. howlandi* (Günther), *E. malabaricus* (Bloch & Schneider), *E. merra* Bloch, *E. polyphkadion* (Bleeker), *Variola albimarginata* Baissac and *V. louti* (Forsskål).

In contrast to *D. heronensis*, body length varies little (Table 3) and, although sample sizes are small, it does not appear that there are any significant

**Table 3** Body lengths of *Dissonus manteri* from different hosts and localities

Host species	Locality	Female BL (mm) mean (range)	Male BL (mm) mean (range)	Data source
<i>Epinephelus maculatus</i>	Australia (Heron Is.)	? (1.72–2.07) (N = 6)	1.42 (N = 1)	Kabata, 1966
Unspecified serranid	New Caledonia	2.10 (2.09–2.11) (N = 2)	1.72 (N = 1)	Kabata, 1966
<i>Plectropomus leopardus</i> and <i>Epinephelus longispinis</i>	Australia	? (1.90–2.15) (N = ?)	? (1.55–1.87) (N = ?)	Ho & Dojiri, 1977
<i>Plectropomus laevis</i>	New Caledonia	2.07 (N = 1)	–	Present account
<i>Epinephelus cyanopodus</i>	New Caledonia	2.06 (1.80–2.25) (N = 22)	1.88 (1.82–2.03) (N = 8)	Present account
<i>Plectropomus leopardus</i>	New Caledonia	1.97 (1.85–2.23) (N = 7)	1.81 (1.65–1.96) (N = 2)	Present account
<i>Epinephelus maculatus</i>	New Caledonia	1.94 (1.83–2.07) (N = 3)	–	Present account
<i>Plectropomus leopardus</i>	Taiwan	1.97 (1.88–2.08) (N = 10)	–	Present account

BL, Body length



differences in body length with either host species or geographical locality. Females from the host *Plectropomus leopardus*, for example, have the same mean body length of 1.97 mm off New Caledonia and Taiwan, although the range of body lengths exhibited is greater off New Caledonia. Conversely the differences noted above in body length between females from four different hosts off New Caledonia (*P. leopardus*, *P. laevis*, *Epinephelus cyanopodus* and *E. maculatus*) are not significant.

### ***Dissonus nudiventris* Kabata, 1965**

Syn. *Dissonus pastinum* Deets & Dojiri, 1990 (new synonym)

*Material examined*: 6 adult males, 1 immature female and 10 chalimus stages, all collected from *Heterodontus portusjacksoni* at Port Willunga, South Australia, Australia in 1934, BMNH 1966.12.8.8.

#### Remarks

The original description of *Dissonus nudiventris* from *Heterodontus portusjacksoni* by Kabata (1965) contained errors, some of which were subsequently corrected by the author (Kabata, 1966). However, Kabata's statement that "there are no significant differences in the details of the appendages of the two sexes" was taken to indicate that the female antenna carried an accessory claw. Later, Tang & Kalman (2005) noted that the antenna of the female lacked the accessory claw present in males only in known *Dissonus* species. Unfortunately, before the publication of this correction, Deets & Dojiri (1990) used the lack of the accessory claw on the female antenna as a major distinguishing character justifying placement of their material in a new species, *D. pastinum*, which also occurred on a heterodontid shark. Kabata (1965) gave the body length of female *D. nudiventris* as 7.1 mm and the male as 7.60 (range 7.2–8.1) mm, considerably larger than *D. pastinum*. These dimensions would be by far the largest known for any species of *Dissonus*, but comparison with the scale-bars provided on the illustrations indicates that these lengths have been inadvertently doubled. The dimensions as indicated by the scale bars are in the order of 3.6 mm for both sexes, close to the 3.5 mm given for *D. pastinum*.

The other differences between *D. pastinum* and *D. nudiventris* given by Deets & Dojiri (1990) are: the absence of long spinules or setules of the cristae of the maxilla, the length of the sternal furca tines, and the ornamentation the terminal endopodal segment of leg 1. The ornamentation of the terminal endopodal segment of leg 1 does vary significantly between species of *Dissonus*, but this ornamentation is known to be particularly variable in *D. nudiventris* (cf. Deets & Dojiri, 1990, who figured differences between specimens), and the morphology described for *D. pastinum* can be encompassed within the range of *D. nudiventris*. Differences in the length of the tines of the sternal furca cannot be considered to be significant, given the variability already reported in the furca of *D. nudiventris* by Tang & Kalman (2005). The remaining difference, in the ornamentation of the maxilla, is not of sufficient magnitude to be significant at the specific level. It is therefore proposed here to consider *D. pastinum* Deets & Dojiri, 1990 as a junior subjective synonym of *D. nudiventris* Kabata, 1965. The species ranges from Japanese waters (Deets & Dojiri, 1990) to the waters off southern Australia (Kabata 1965, 1966; Tang & Kalman, 2005).

### ***Dissonus similis* Kabata, 1966**

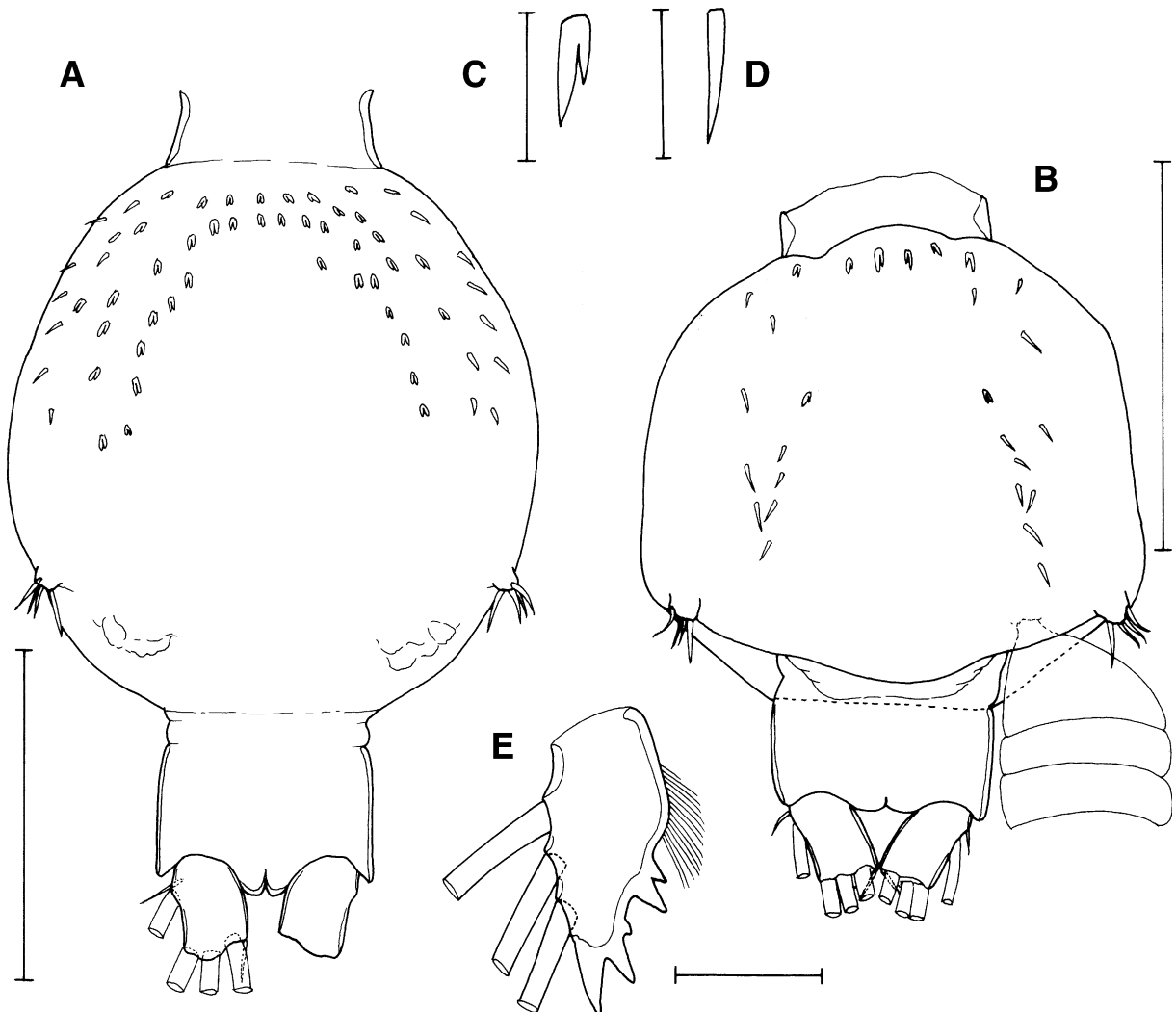
*Material examined*: Holotype female, taken from gills of *Tetractenos hamiltoni* (Richardson) (as *Spheroides hamiltoni*) caught off Green Island, Queensland, Australia on 11 November 1963, BMNH 1966.3.18.1.

#### Remarks

The original description (Kabata, 1966) of this species is accurate and provides sufficient detail for positive identification. The spinules on the ventral surface of the genital complex occupy a semicircular zone anteriorly (Fig. 10A) and extend more laterally than figured by Kabata (1966).

### ***Dissonus spinifer* Wilson, 1906**

*Material examined*: One female, stored in the collections of the United States National Museum of Natural History, Smithsonian Institution, Washington. The



**Fig. 10** *Dissonus* spp. A. *D. similis* Kabata, 1966, holotype female. Genital complex and free abdomen, ventral view showing bifid surface spinules. B–E. *D. spinifer*, adult female (USNM 52596). B, genital complex and free abdomen, ventral view showing surface spinules; C, detail of asymmetrical bifid spinule; D, detail of long simple spinule; E, distal endopodal segment of first leg. Scale-bars: A, B, 0.5 mm; C–E, 50  $\mu$ m

main label in the vial states “*Dissonus spinifer* n. gen. n. sp. Gills of *Tetrodon stellatus*. Ceylon, Pearl Fisheries”. An additional label provides the USNM registration number “56592”.

Description (Fig. 10B–E)

#### Adult female

Genital complex just wider than long,  $0.65 \times 0.60$ , with straight lateral margins tapering outwards to maximum width at level of fifth legs. Paired oviduct openings on

ventral surface adjacent to posterior margin of complex; paired copulatory pores located anterior to oviduct openings. Ventral ornamentation of genital complex comprising 6 bifid anterior spinules arranged more or less transversely in 3 pairs near anterior margin, plus pair of irregular, longitudinal rows of spinules located some distance from lateral margins (Fig. 10B). Anterior spinules bifid, but asymmetrical with inner branch smaller than outer branch (Fig. 10C). Spinules of lateral rows long and simple (Fig. 10D), except innermost spinule unequally bifid. First leg endopod with strong spinous projections along lateral and distal margins (Fig. 10E).

## Remarks

The female examined was from the same Pearl Fisheries (Ceylon) collection, made by William Herdman, as the type-material (USNM 32729). The host given on the label is now known as *Arothron stellatus* (Bloch & Schneider) and this host has already been recorded as a host of *Dissonus spinifer* by Pillai (1985) and of *D. similis* by Tang & Kalman (2005). This raises at least the possibility of confusion between *D. similis* and *D. spinifer*. Wilson (1906, 1907) stated that the entire ventral surface of the genital segment (=genital complex) of *D. spinifer* was sparsely covered with spines; however, re-examination shows a more restricted pattern with anterior and paired irregular longitudinal rows, at least in the female. The presence of long, simple spinules in *D. spinifer* (in posterior rows) and the presence of spinules back almost as far as the level of the fifth legs serve to differentiate between *D. spinifer* and *D. similis* (cf. Fig. 10A, B).

There is a marked similarity between the females of *D. spinifer* and *D. kapuri* in the size and shape of the genital complex and in the pattern and extent of the ventral spinulation. According to the original description of the latter (Ummerkutty, 1970), there is no sternal furca, but Pillai (1985) in his re-description noted the presence of a sternal stylet (in the male). The female examined on loan from the USNM had previously been dissected to remove the swimming legs and maxilliped, so the presence of a sternal stylet was not verifiable because of the damage to the mid-ventral region of the cephalothorax. Given the other similarities between these two species (in the maxilliped, endopod of leg 1 and even in the form of the maxillule), we consider it possible that *D. kapuri* is a synonym of *D. spinifer* and that this possibility warrants further investigation.

## Discussion

The presence of ridge-like surface ornamentation on the basis and first endopodal segment of the first leg has been noted as a distinctive feature of *Dissonus* species. It has variously been figured as or interpreted as a row of fine setules, a striated membrane (Kabata, 1966) and a sclerotised flange (Deets & Dojiri, 1990; Tang &

Kalman, 2005). SEM studies here confirm the robust nature of this ornamentation (Fig. 9C–D), and the term sclerotised flange seems most appropriate.

The genital spinules are typically bifid distally (Fig. 9A). Only Wilson (1906) reported simple spinules, in *D. spinifer*, and re-examination of this species confirms that some of the spinules are simple (although more anterior spinules are unequally bifid). Spinulation, when present, appears relatively constant in most species, although some intraspecific variation has been reported in *D. hoi* and some is noted here in *D. heronensis*. Five main spinulation patterns are found on the genital complex in the genus:

1. Two species, *D. similis* and *D. furcatus*, have numerous spinules distributed across the anterior third to half of the genital complex.
2. Four species, *D. excavatus* n. sp., *D. heronensis*, *D. hoi* (in the male) and *D. manteri*, typically share an anterior transverse row of four spinules (arranged in two pairs). The sexual dimorphism in spinule pattern of *D. hoi* is unusual, as the only other report of sexual dimorphism is that of Wilson (1906), who noted that the spines are larger and more numerous in the male than in the female of *D. spinifer*. In *D. hoi* the female has between five and eight anterior (typically seven) and two posterolateral spinules; the male has four anterior and three or four posterolateral spinules. No other species of *Dissonus* shows sexual dimorphism in the number and basic arrangement of genital spinules.
3. *D. inaequalis* n. sp. has a more or less transverse anterior row of eight spinules. It has two pairs of posterolateral spinules, as in *D. excavatus* n. sp. whereas *D. manteri* has only a single pair, *D. heronensis* has four pairs and *D. kapuri* has eight pairs.
4. *D. kapuri* and the female of *D. spinifer* appear to have a very similar pattern with a transverse row of bifid spinules plus paired, slightly diverging, irregular, posterior rows lying near the lateral margins. These are the only two species where the posterior rows extend well into the posterior third of the genital complex close to its posterior margin.
5. Three species, *D. glaber*, *D. ruveti* and *D. nudiventris*, lack ventral spinulation in both sexes.

The utilisation of both elasmobranch and actinopterygian hosts within a single genus is relatively unusual in parasitic copepods. Morphological

**Table 4** Known hosts of *Dissonus* species

Copepod	Host – Family: Species*	Record
<b>Elasmobranch fishes</b>		
<i>D. furcatus</i>	Orectolobidae: not specified	Kirtisinghe, 1950
<i>D. inaequalis</i> n. sp.	Hemiscylliidae: <i>Chiloscyllium punctatum</i> Müller & Henle	Present account
<i>D. nudiventris</i>	Heterodontidae: <i>Heterodontus portusjacksoni</i> (Meyer) as <i>H. philippi</i> Blainville	Kabata, 1965
<i>D. nudiventris</i>	Heterodontidae: <i>Heterodontus portusjacksoni</i> (Meyer)	Kabata, 1966; Tang & Kalman 2005
<i>D. nudiventris</i>	Unspecified elasmobranch	Kabata, 1966
<i>D. nudiventris</i>	Rhinobatidae: <i>Trygonorrhina fasciata</i> Müller & Henle as <i>Trygonorhina fasciata guaneries</i> Whitley	Kabata, 1966
<i>D. nudiventris</i>	Triakiidae: <i>Mustelus antarcticus</i> Günther as <i>Emissola antarctica</i> (Günther)	Kabata, 1966
<i>D. nudiventris</i> (as <i>D. pastinum</i> )	Heterodontidae: <i>Heterodontus japonicus</i> (Dumeril)	Deets & Dojiri, 1990
<b>Actinopterygian fishes</b>		
<i>D. excavatus</i> n. sp.	Labridae: <i>Bodianus perditio</i> (Quoy & Gaimard)	Present account
<i>D. excavatus</i> n. sp.	Lutjanidae: <i>Macolor niger</i> (Forskål)	Present account
<i>D. glaber</i>	Pentacerotidae: <i>Evistias acutirostris</i> (Temnick & Schlegel) as <i>Histiopertus acutirostris</i>	Kurtz, 1924
<i>D. heronensis</i>	Balistidae: unspecified	Kabata, 1966
<i>D. heronensis</i>	Balistidae: <i>Balistoides viridescens</i> (Bloch & Schneider)	Lewis, 1968
<i>D. heronensis</i>	Balistidae: <i>Abalistes stellatus</i> (Anonymous) as <i>A. stellaris</i> (Bloch & Schneider)**	Ho & Dojiri, 1977
<i>D. heronensis</i>	Balistidae: <i>Pseudobalistes fuscus</i> (Bloch & Schneider)	Present account
<i>D. hoi</i>	Carangidae: <i>Seriola hippos</i> Günther	Tang & Kalman, 2005
<i>D. kapuri</i>	Unknown	Ummerkuty, 1970
<i>D. manteri</i>	Serranidae: unspecified	Kabata, 1966
<i>D. manteri</i>	Serranidae: <i>Epinephelus maculatus</i> (Bloch) as <i>Plectropomus maculatus</i>	Kabata, 1966
<i>D. manteri</i>	Serranidae: <i>Plectropomus leopardus</i> (Lacépède)	Ho & Dojiri, 1977
<i>D. manteri</i>	Serranidae: <i>Epinephelus longispinis</i> (Kner, 1864) as <i>Epinephelus fario</i>	Ho & Dojiri, 1977
<i>D. manteri</i>	Serranidae: <i>Plectropomus laevis</i> (Lacépède)	Present account
<i>D. manteri</i>	Serranidae: <i>Epinephelus cyanopodus</i> (Richardson)	Present account
<i>D. ruveti</i>	Gempylidae: <i>Ruvettus pretiosus</i> Cocco	Nunes-Ruivo & Fourmanoir, 1956
<i>D. similis</i>	Tetraodontidae: <i>Tetractenos hamiltoni</i> (Richardson) as <i>Spheroides hamiltoni</i> (Gray & Richardson)	Kabata, 1966
<i>D. similis</i>	Tetraodontidae: <i>Arothron meleagris</i> (Lacépède) as <i>A. meleagris</i> (Block & Schneider)	Lewis, 1968
<i>D. similis</i>	Tetraodontidae: <i>Arothron meleagris</i> (Lacépède)	Tang & Kalman, 2005
<i>D. similis</i>	Tetraodontidae: <i>Arothron hispidus</i> (Linnaeus)	Tang & Kalman, 2005
<i>D. similis</i>	Tetraodontidae: <i>Arothron stellatus</i> (Bloch & Schneider)	Tang & Kalman, 2005
<i>D. similis</i>	Tetraodontidae: <i>Arothron nigropunctatus</i> (Bloch & Schneider)	Tang & Kalman, 2005
<i>D. spinifer</i>	Unknown	Wilson, 1906
<i>D. spinifer</i>	Tetraodontidae: <i>Arothron stellatus</i> (Bloch & Schneider) as <i>Tetraodon stellatus</i>	Pillai, 1985

\* All host names were checked against <http://www.FishBase.com> on 24 November, 2006

\*\* For the valid name of *A. stellatus*, see the discussion in Matsuura & Yoshino (2004)

comparisons between species utilising elasmobranch hosts and those using actinopterygian hosts do not reveal any characters that would support a subdivision of the genus according to host preference. The distributions of major character states, such as the presence or absence of a sternal furca and the presence or absence of genital spinulation, are not congruent with the pattern of host utilisation.

Similar patterns of host utilisation are found within the family Taeniacanthidae, which includes three genera, *Taeniacanthus* Sumpf, 1871, *Taeniacanthodes* Wilson, 1935 and *Irodes* Wilson, 1911, exhibiting similar host-specificity, each with some species occurring on elasmobranchs and others on actinopterygian hosts (Dojiri & Cressey, 1987). Other examples of such broad host specificity at the generic level are more isolated, such as the large genus *Ergasilus* von Nordmann, 1832, which primarily uses actinopterygian fishes as hosts but contains a single species, *E. ogawai* Kabata, 1992, reported parasitising a sawfish (Ogawa, 1991). At the level of the individual parasite species, there are several examples of similarly broad host utilisation, such as the dichelesthid *Anthosoma crassum* (Abildgaard, 1794) and the caligid *Caligus elongatus* von Nordmann, 1832.

*Dissonus* species exhibit variable levels of host-specificity (Table 4). Two species have been recorded from five different hosts, but in both cases the hosts come from related genera within a single family. *D. manteri* has been reported from five host species belonging to two genera within the serranid subfamily Epinephelinae, and *D. similis* has been reported from five hosts in two genera of the Tetraodontidae. Lower host-specificity is reported from *D. nudiventris*, which utilises hosts from three different elasmobranch families, the Heterodontidae, Rhinobatidae and Triakiidae. At the other end of the scale, five species are currently specific to a single host species.

### Key to species of *Dissonus*

1. Ventral spinulation on genital complex extending, in form of paired longitudinal rows, well into posterior third of complex, almost reaching posterior margin ..... 2
  - Ventral spinulation on genital complex present or absent; if present then restricted to anterior half of genital complex ..... 3
2. Genital spinulation comprising 8 anterior spinules arranged in more or less transverse row, and paired longitudinal rows of 8 bifid spinules ..... *D. kapuri*
  - Genital spinulation comprising 6 anterior spinules arranged in more or less transverse row, and paired longitudinal rows of mostly long, simple spinules ..... *D. spinifer*
3. Simple sternal stylet or bifid sternal furca present in mid ventral surface anterior to first swimming legs ..... 4
  - Sternal furca or sternal stylet lacking ..... 8
4. Simple sternal stylet tapering anteriorly; genital spinulation comprising 2 more or less transverse anterior pairs and 1 posterolateral pair ..... *D. manteri*
  - Bifid sternal furca present ..... 5
5. Proximal 2 spines on outer margin of second exopod segment of leg 1 short, less than half width of segment; distal endopodal segment of leg 1 lacking denticles; free abdomen apparently 2-segmented ..... *D. ruveti*
  - Proximal 2 spines on outer margin of second exopod segment of leg 1 usually longer than width of segment (if shorter then distal endopod segment of leg 1 with marginal denticles); free abdomen 1-segmented ..... 6
6. Genital spinulation present ..... 7
  - Genital spinulation absent ..... *D. nudiventris*
7. Maxillule with elongate, rigid anterior papilla carrying 3 setae, longest of which extends beyond tip of posterior process; genital spinulation sexually dimorphic; female genital complex wider than long ..... *D. hoi*
  - Maxillule with small anterior papilla carrying 3 setae, longest of which does not extend beyond tip of posterior process; genital spinulation comprising 8 anterior spinules and 2 pairs of posterolateral spinules in both sexes; female genital complex longer than wide ..... *D. inaequalis*
8. Genital spinulation absent ..... *D. glaber*
  - Genital spinulation present ..... 9
9. Genital spinulation extends over most of anterior ventral surface; numerous spinules present ... 10
  - Genital spinulation reduced, typically with transverse row of about 4 spinules located anteriorly and paired lateral rows lying slightly obliquely to longitudinal axis ..... 11



10. Genital spinules extend over anterior half to two thirds of ventral surface of genital complex ..... *D. similis*  
 – Genital spinules extend over anterior third of ventral surface of genital complex ... *D. furcatus*  
 11. Paired lateral rows of genital spinules each with 4 spinules; outer margin of distal exopodal segment of leg 1 with 4 spines of similar length ..... *D. heronensis*  
 – Paired lateral rows of genital spinules each with 2 spinules; outer margin of distal exopodal segment of leg 1 strongly indented, with 1 short spine proximal to indentation and 1 short plus 2 long spines distal to it ..... *D. excavatus*

**Acknowledgements** The type-material of *Dissonus inaequalis* n. sp. was collected by Janine Cairn under collecting permit No. UPE:40/2001/19SJ.924 from the Economic Planning Unit in Kuala Lumpur, and under research agreement No. SBC-RA-0050-JNC from the Sarawak Biodiversity Centre in Kuching. This work was supported in part with funds from US National Science Foundation (NSF) grants Nos DEB 0103640 and DEB 0542846. Field collections in Taiwan were supported in part by a grant from the Paramitas Foundation to JSH. CLL acknowledges support from projects NSC 91-2313-B-415-010 and NSC 94-2311-B-415-004 from the National Science of Council of Taiwan. The collaboration between GAB and SO was supported by a short term invitation fellowship from the Japan Society for the Promotion of Science. We are grateful to T Chad Walter for arranging the loan of the *D. spinifer* material from the USNM. We would like to thank Danny Tang for his careful review and for his suggested improvements to the manuscript. Prof. C. Chauvet (University of New Caledonia) kindly provided several of the groupers examined. Identification of all *Bodianus* specimens mentioned in this paper was kindly confirmed (from photographs) by Martin Gomon (Museum Victoria, Melbourne, Australia), who also provided comments and literature; identification of most other labrids was kindly confirmed (from photographs) by Ronald Fricke (Staatliches Museum für Naturkunde, Stuttgart, Germany). In New Caledonia, Julie Mounier, volunteer technician, and Charles Beaufrière, Audrey Guérin, Anaïs Guillou, Amandine Marie, Chloé Journo, Violette Justine, Eric Bureau, Maya Robert, Damien Hinsinger, Géraldine Colli, Lenaïg Hemery and Aude Sigura, all students, participated in the fishing operations and parasitological survey. Sam Tereua, Miguel Clarque and Napoléon Colombani, captains of the RV 'Coris' provided safe navigation. Angelo di Matteo (IRD) provided technical help. This paper is a contribution to the EU funded network of Excellence, EDIT.

## References

- Boxshall, G. A. (1990). The skeletomusculature of siphonostomatoid copepods, with an analysis of adaptive radiation in structure of the oral cone. *Philosophical Transactions of the Royal Society of London, Series B*, 328, 167–212.
- Boxshall, G. A., & Halsey, S. H. (2004). *An Introduction to copepod diversity* (966 pp). London: The Ray Society.
- Boxshall, G. A., & Justine, J.-L. (2005). A new genus of parasitic copepod (Siphonostomatoida: Caligidae) from a Razorback Scabbardfish, *Assurger anzac* Alexander (Trichiuridae) off New Caledonia. *Folia Parasitologica*, 52, 349–358.
- Deets, G. B., & Dojiri, M. (1990). *Dissonus pastinum* n. sp. (Siphonostomatoida: Dissonidae), a copepod parasitic on a horn shark from Japan. *Beaufortia*, 41, 49–54.
- Dojiri, M., & Cressey, R. F. (1987). Revision of the Taeni-acanthidae (Copepoda: Poecilostomatoida) parasitic on fishes and sea urchins. *Smithsonian Contributions to Zoology*, 447, 1–250.
- Ho, J.-S., & Dojiri, M. (1977). Parasitic copepods on the fishes of the Great Barrier Reef, Australia Part II. Caligoida: *Dissonus*, *Lepeophtheirus* and *Dentigryps*. *Publications of the Seto Marine Biological Laboratory*, 24, 77–97.
- Huys, R., & Boxshall, G. A. (1991). *Copepod evolution* (468 pp). London: The Ray Society.
- Kabata, Z. (1965). Parasitic Copepoda of fishes. *Report B.A.N.Z. Antarctic Research Expedition (B)*, 8(6), 1–16, 1–7.
- Kabata, Z. (1966). Copepoda parasitic on Australian fishes, V. Genus *Dissonus* (Dissonidae). *Annals and Magazine of Natural History, (series 13)*, 9, 211–226.
- Kabata, Z. (1979). *Parasitic Copepoda of British fishes* (468 pp). London: The Ray Society.
- Kirtisinghe, P. (1950). Parasitic copepods of fish from Ceylon. III. *Parasitology*, 40, 77–86.
- Kurtz, H. (1924). Parasitische Copepoden aus der Sammlung des Naturhistorischen Museums in Wien. I. *Pholidopus (Acht-heinus) intermedius* und *Dissonus glaber*, zwei neue Arten aus der Familie der Caligidae. *Sitzungsberichte Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe. Wien, Abt. I*, 133, 613–624.
- Lewis, A. G. (1968). Copepod crustaceans parasitic on the fishes of Enewetok Atoll. *Proceedings of the US National Museum*, 125, 1–78.
- Lim, L. H. S., & Justine, J.-L. (2007). *Haliotrema banana* sp. n. (Monogenea, Ancyrocephalidae) from *Bodianus perditio* (Perciformes: Labridae) off New Caledonia. *Folia Parasitologica*, 54, 203–207.
- Matsuura, K., & Yoshino, T. (2004). A New Triggerfish of the Genus *Abalistes* (Tetraodontiformes: Balistidae) from the Western Pacific. *Records of the Australian Museum*, 56, 189–194.
- Nunes-Ruivo, L., & Fourmanoir, P. (1956). Copepodes parasites de poissons de Madagascar I. *Memoires de l'Institut Scientifique de Madagascar, Series A*, 10, 69–80.
- Ogawa, K. (1991). Ectoparasites of sawfish, *Pristis microdon*, caught in fresh waters of Australia and Papua New Guinea. *University Museum, University of Tokyo, Nature and Culture*, 3, 91–101.
- Pillai, N. K. (1968). Additions to the copepod parasites of South Indian fishes. *Parasitology*, 58, 9–36.
- Pillai, N. K. (1985). *Fauna of India. Parasitic copepods of marine fishes* (900 pp). Calcutta: Zoological Survey of India.
- Randall, J. E., & Justine, J.-L. (2007). The triggerfish *Abalistes filamentosus* from New Caledonia, a first record for the South Pacific. *Cybiurn*, in press.
- Skoracki, M. (1999). New genus and species of Syringophilidae from Eurasian Reed-Warbler, *Acrocephalus scirpaceus*



- (Sylviidae: Passeriformes) (Acari: Prostigmata). *Genus (Wroclaw)*, 10, 155–162.
- Skoracki, M. (2004). A new name for *Dissonus* Skoracki, 1999 not Wilson, 1906 (Acari: Prostigmata: Syringophilidae). *Genus (Wroclaw)*, 15, 445–446.
- Tang, D., & Kalman, J. E. (2005). A new caligiform copepod (Siphonostomatoida: Dissonidae) parasitic on *Seriola hippos* from western Australian waters, with new records and morphological variation for *Dissonus nudiventris* and *Dissonus similis* and an updated key to the species of *Dissonus*. *Journal of Parasitology*, 91, 427–437.
- Ummerkuty, A. N. P. (1970). Studies on the crustacean fauna of Mysore coast – 3. Description of *Caligotrogus kapuri* n. gen. and n. sp. with remarks on its affinities. *Journal of the Kerala Academy of Biology*, 2, 3–14.
- Wilson, C. B. (1906). Report on some parasitic Copepoda collected by Professor Herdman, at Ceylon, in 1902. In W. A. Herdman (Ed.), *Report to Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar*, 5, 189–210, 1–5.
- Wilson, C. B. (1907). North American parasitic copepods belonging to the family Caligidae. Part 2. The Trebinae and Euryphorinae. *Proceedings of the United States National Museum*, 31(1504), 669–720, 15–20.
- Yamaguti, S. (1963). *Parasitic Copepoda and Branchiura of fishes* (1104 pp). New York: Interscience Publishers.