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Observations of reproductive strategies for some dendrochirotid holothuroids (Echinodermata: Holothuroidea: Dendrochirotida)

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Abstract

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Some recently observed dendrochirotid holothuroid reproductive strategies are reported for the first time: fissiparity by *Cucuvitrum rowei* O'Loughlin and O'Hara; probable intra-coelomic brood fissiparity by *Staurothyone inconspicua* (Bell); intra-coelomic brood-protection by a species of *Parathyonidium* Heding; intra-coelomic brood auto-ingestion by *Neoamphicyclus materiae* O'Loughlin; brood-protection in anterior interradial marsupia by *Psolidiella mollis* (Ludwig and Heding). Some analysis is reported of marsupial brood-protection by Antarctic dendrochirotid holothuroids: the "*Cucumaria georgiana* group"; *Echinopsolus acanthocola* Gutt; *Echinopsolus parvipes* Massin; *Microchoerus splendidus* Gutt; *Psolidiella mollis* (Ludwig and Heding); *Psolus charcoti* Vaney. Confusion in the literature about brood-protection by the Subantarctic dendrochirotid *Cladodactyla crocea* (Lesson) is clarified.

Keywords Echinodermata, Holothuroidea, Dendrochirotida, auto-ingestion, brood-protection, fissiparity, intra-coelomic, marsupium.

Introduction

Large collections of holothuroids from coastal southern Australia and from Antarctica (Prydz Bay, the Bellingshausen Sea, the Antarctic Peninsula and the South Atlantic), most specimens held by Museum Victoria (NMV), have been studied by Mark O'Loughlin. This has resulted in many of the observations reported here. Fieldwork by John Eichler of the Marine Research Group (MRG) in Victoria has resulted in the recognition of fissiparity by a dendrochirotid species. Laboratory research on specimens by NMV volunteers Melanie Mackenzie and Emily Whitfield has contributed to observations reported in this work. John Eichler (MRG; JE), Leon Altoff and Audrey Falconer (MRG; LA), and Chris Rowley (NMV; CR) have provided photographs.

Fissiparity by *Cucuvitrum rowei* O'Loughlin and O'Hara

John Eichler collected a live specimen of *Cucuvitrum rowei* O'Loughlin and O'Hara, 1992 from Port Phillip Bay in SE Australia on 20 April 2008 (NMV F157401; variably 19 to 30 mm long live). During subsequent days peristaltic-like body contractions were observed and photographed (fig. 1a). Between April 22 and 25 the specimen divided transversely into two individuals (smaller 7 mm long). Peristaltic-like body contractions continued in both post-fissiparity individuals. Overnight on May 1 to 2 the larger individual divided transversely again (fig. 1b). Preservation and dissection of these individuals revealed that the larger post-fissiparity oral end individual had fully developed tentacles and calcareous ring, but lacked internal organs. Detached internal organ remnants were present in the smaller anal end individuals that lacked tentacles and ring. One apparent purpose of the peristaltic movements was to push the internal organs to the anal end of the coelom to provide a nutrient source for the subsequent regeneration of tentacles, ring and internal organs.

On 3 August 2008, seven smaller specimens were collected from Port Phillip Bay (NMV F161549; up to 12 mm long). After nine days none had undergone fissiparity. On 30 August 2008, five specimens were collected from Port Phillip Bay (NMV F161500; up to 16 mm long). Overnight on September

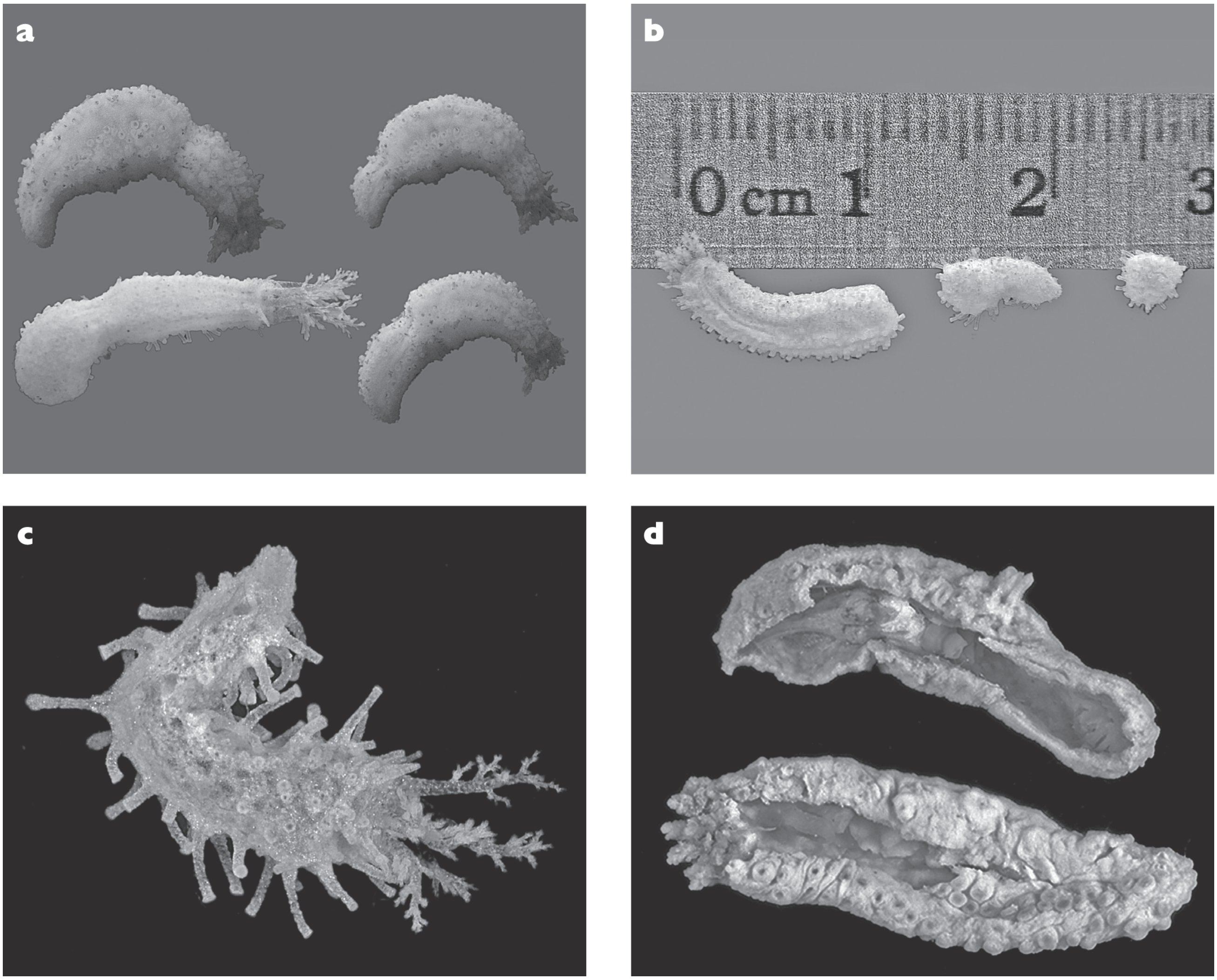

Figure 1. Fissiparity by *Cucuvitrum rowei* O'Loughlin and O'Hara. a, peristaltic contractions in live specimen (F157401; about 25 mm long; photo by JE). b, 3 live individuals resulting from fissiparity (F157401; JE). c, live specimen showing regenerating anal end (F157419; 4 mm long; LA). d, preserved specimens showing evidence of fissiparity, with fully developed tentacles and ring and lacking internal soft organs (upper), with developing tentacles and ring (lower) (F161501; LA).

6 to 7 one of the larger individuals divided transversely. During his fieldwork John Eichler frequently noticed individuals in close proximity on the undersurface of rocks. This clustering may be a consequence of fissiparity.

Leon Altoff and Audrey Falconer photographed a live specimen in the field that showed regeneration of the anal end (fig. 1c; 4 mm long; NMV F157419). Dissection by Emily Whitfield of a large collection of NMV preserved specimens of *Cucuvitrum rowei* revealed rare individuals that showed evidence of fissiparity. Post-fissiparity oral ends lacked internal organs but had withdrawn fully developed tentacles and calcareous ring (fig. 1d; NMV F161501); and post-fissiparity anal ends showed a reduced developing calcareous ring and small tentacles (fig. 1d; NMV F161501), or lacked a calcareous ring and tentacles.

O'Loughlin (1991, 1994) reported fissiparity by similar mid-body transverse constriction and division in the dendrochirotid *Squamocnus aureoruber* O'Loughlin and O'Hara, 1992 from the rocky shallows of southern Australia. This is the first record of fissiparity by the dendrochirotid *Cucuvitrum rowei*, and the first record of peristaltic body movements in a dendrochirotid holothuroid.

Coelomic fissiparity by *Staurothyone inconspicua* (Bell)

Brood juveniles (45) removed from the coelom of a female *Staurothyone inconspicua* (Bell, 1887) from Opossum Bay in SE Tasmania are of different sizes and many show mid-body constrictions (fig. 2a; NMV F58613). One coelomic juvenile from another specimen from Opossum Bay shows a deep mid-body constriction (fig. 2b; NMV F58456). For this seasonally reproducing and coelomic brood-protecting species (see Materia et al. 1991), and with an assumption of a single fertilization event, these observations suggest intra-coelomic brood fissiparity and cloning. However, dissection of coelomic juveniles has to date failed to reveal confirming evidence of a coelomic juvenile that lacks a calcareous ring.

Balser (2004) reported on cloning by larvae of echinoderms, including holothuroids. The evidence here indicates probable intra-coelomic cloning by a holothuroid.

Coelomic brood-protection by a species of *Parathyonidium* Heding

A female specimen of an undescribed species of *Parathyonidum* Heding, 1954 from Eastern Antarctica (17 mm long, preserved; NMV F84983) has 39 differentiating coelomic juveniles of uniform size (2–3 mm long) (fig. 2c). Materia et al. (1991) reported coelomic brood-protection for *Neoamphicyclus materiae* O'Loughlin, 2007 (as *Neoamphicyclus lividus* Hickman, 1962) and *Staurothyone inconspicua* (Bell, 1887) from SE Australia. This is a third case of intra-coelomic brood-protection by a dendrochirotid holothuroid species.

Brood auto-ingestion by *Neoamphicyclus materiae* O'Loughlin

A 20 mm long female *Neoamphicyclus materiae* O'Loughlin, 2007 from Kitty Miller Bay on the coast of Victoria, collected on 25 October 1987, has 528 small coelomic brood juveniles (fig. 2d; NMV F58592). A 30 mm long female from Cape Otway on the coast of Victoria, collected on 29 December 1985, has one large coelomic brood juvenile (fig. 2d; NMV F76371). Typically this species has small coelomic brood juveniles in October (see Materia et al. 1991), and one or a few large coelomic juveniles are present in December or January (NMV F58606; F58720; fig. 2e). These observations indicate that intra-coelomic brood auto-ingestion occurs in *Neoamphicyclus materiae*.

Byrne (1996) reported intragonadal cannibalism in the small simultaneous hermaphrodite asterinids *Parvulastra vivipara* (Dartnall, 1969) and *Parvulastra parvivipara* (Keough and Dartnall, 1978) from southern Australia. This is the first report of intra-coelomic cannibalism in a holothuroid species.

Brood-protection by *Psolidiella mollis* (Ludwig and Heding)

Psolidiella mollis (Ludwig & Heding, 1935) is an additional species of Antarctic dendrochirotid holothuroid that brood-protects in marsupia (see Table 1). Males have a long genital papilla (NMV F157414), and females have up to five anterior interradial internal marsupia (fig. 3a; NMV F104865). One female from Bouvet Island (fig. 3b; NMV F104882) has 46 and 60 differentiated embryos (3–4 mm long) in each of two marsupia, and 52, 53, and 60 undifferentiated eggs or embryos (1.3 mm long) in each of three marsupia, evidence of two fertilization events.

Table 1. Antarctic species with 5 anterior interradial marsupia.

"*Cucumaria georgiana* (Lampert, 1886) group"
Cucumaria acuta Massin, 1992
Cucumaria analis Vaney, 1908
Cucumaria aspera Vaney, 1908
Cucumaria attenuata Vaney, 1906
Cucumaria georgiana (Lampert, 1886)
Cucumaria joubini Vaney, 1914
Cucumaria lateralis Vaney, 1906
Cucumaria perfida Vaney, 1908
Cucumaria periprocta Vaney, 1908
Cucumaria secunda Vaney, 1908
Cucumaria vaneyi Cherbonnier, 1949
First reported: Vaney, 1925; Ekman, 1925
Echinopsolus acanthocola Gutt, 1990
First reported: De Ridder et al., 2005
Echinopsolus parvipes Massin 1992
First reported: Hétérier et al., 2004
Microchoerus splendidus Gutt, 1990
First reported: O'Loughlin, 1994
Psolidiella mollis (Ludwig and Heding, 1935)
First reported: this work
Psolus charcoti Vaney, 1914
First reported: O'Loughlin, 2001

Brood-protection in anterior interradial marsupia

A "*Cucumaria georgiana* (Lampert, 1886) group" was created by Gutt (1988) and adopted by Massin (1992) because of the systematic confusion resulting from many Antarctic cucumariid species having similar morphological characters. O'Loughlin (in O'Loughlin et al. 2009) included *Cucumaria aspera* Vaney in this group, but removed *Cucumaria armata* Vaney. A revised list is included within Table 1. All species within this "Group", and the five other species in Table 1, have the same brood-protecting habit that is unique to Antarctic holothuroids: males have a long genital papilla between the dorsal tentacle pair (fig. 3c), and do not have marsupia; females have a short genital papilla between the dorsal tentacle pair (fig. 3c), and have up to five anterior interradial marsupia with external pores (fig. 3d). Females in all the species in Table 1 have up to five marsupia, but all five may not be present in an individual.

A "*Cucumaria georgiana* group" female specimen from Casey Station in Eastern Antarctica, collected on 3 November 1997 (fig. 3e; NMV F85853), has 41 and 66 undifferentiated eggs or embryos (1.3 mm long) in each of two marsupia, and 25, 25 and 56 differentiated embryos (3–4 mm long) in each of three marsupia, evidence of two fertilization events.

A female specimen of *Psolus charcoti* Vaney, 1914 from Prydz Bay, collected on 21 February 1987 (fig. 3f; NMV F86009) has one and seven undifferentiated eggs or embryos (1.7 to 1.8 mm long) in each of two marsupia; seven differentiated embryos (3.5 mm long) in one marsupium; and one and four marsupial juveniles (4.0 mm long) in each of two marsupia. The data are evidence of three fertilization events.

Two female specimens from amongst many (up to 35 mm long, tentacles included) belonging to the "*Cucumaria*

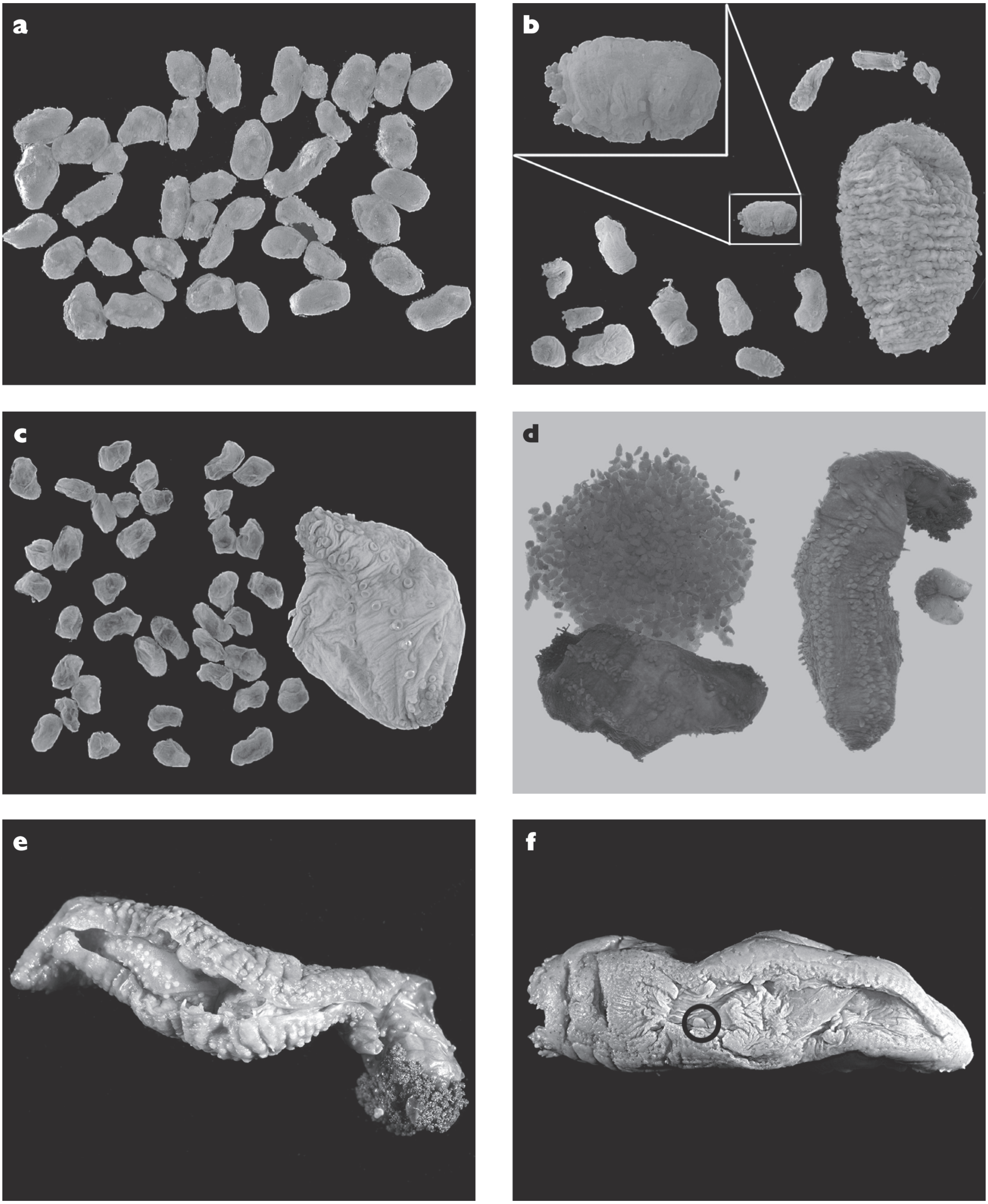

Figure 2. a, coelomic brood juveniles from a female *Staurothyone inconspicu*a (Bell) showing mid-body constrictions and variable sizes (F58613; photo by CR). b, coelomic juvenile of *S. inconspicua* showing a deep mid-body constriction (F58456; CR). c, coelomic juveniles from a female *Parathyonidium* Heding species (F84983; CR). d, many small (F58592, late October; CR) and one large (F76371, late December; CR) coelomic brood juveniles of *Neoamphicyclus materiae* O'Loughlin. e, single large coelomic juvenile of *N. materiae* (F58606; late December; LA). f, invaginated body wall marsupium of *Cladodactyla crocea* (Lesson) with single remaining egg/embryo (F106967; 27 mm long; LA).

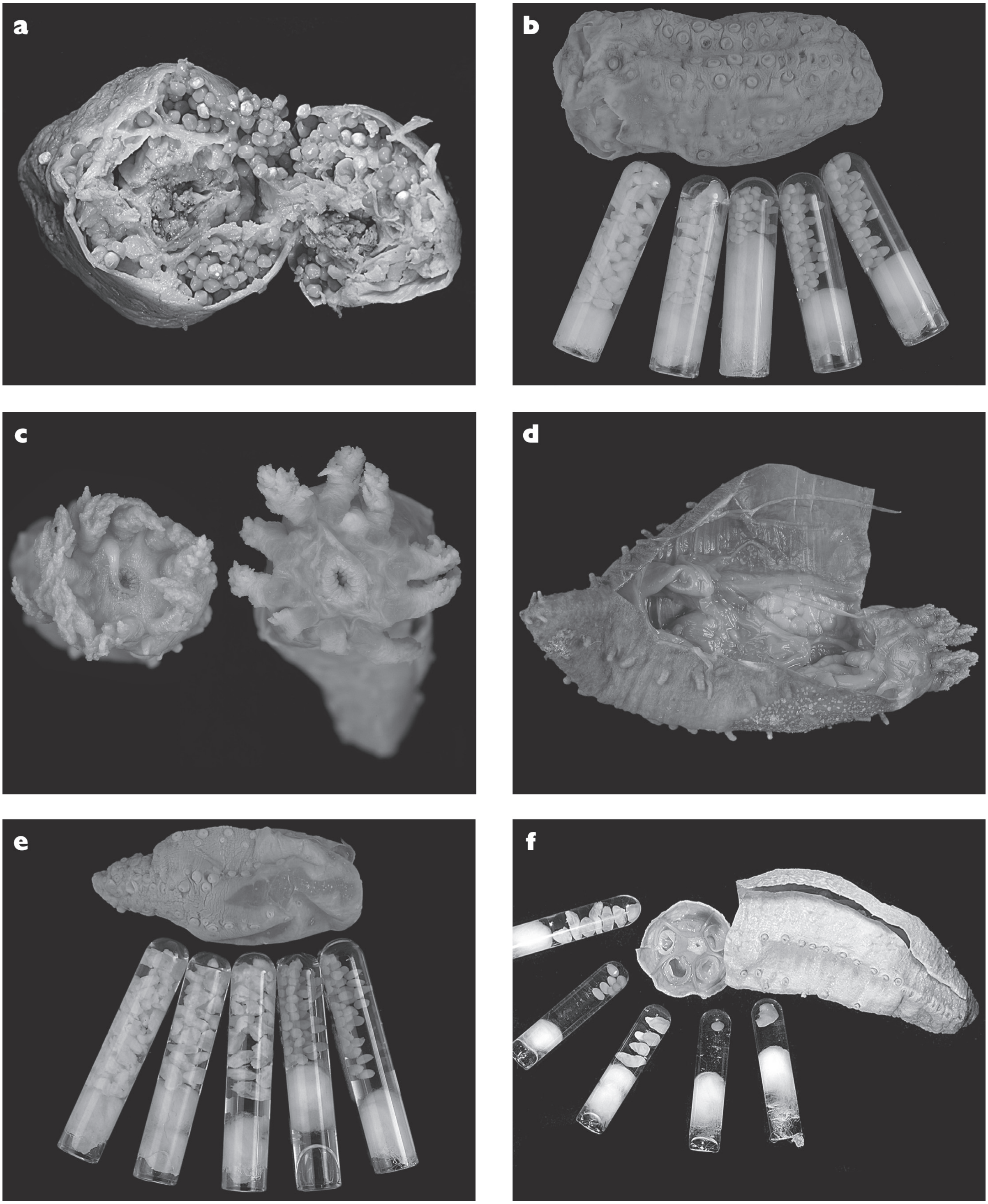

Figure 3. a, transverse section through anterior marsupia of *Psolidiella mollis* (Ludwig and Heding) (F104865; diameter about 15 mm; photo by LA). b, female *P. mollis* with differentiated embryos (3–4 mm long) from each of 2 marsupia (left), and undifferentiated eggs or embryos (1.3 mm long) from each of 3 marsupia (right) (F104882; specimen 45 mm long; CR). c, long male genital papilla of *Cucumaria acuta* Massin (F160042; left; CR); short female genital papilla of *C. acuta* (F160020; right; CR). d, internal marsupium of *C. acuta* (F160038; specimen 37 mm long; CR). e, *C. georgina* group species with differentiated embryos (3–4 mm long) from each of 3 marsupia (left), and undifferentiated eggs or embryos (1.3 mm long) from each of 2 marsupia (right) (F85853; 33 mm long; CR). f, *Psolus charcoti* Vaney with 1 and 7 undifferentiated eggs or embryos (1.7 to 1.8 mm long) from each of 2 marsupia; 7 differentiated embryos (3.5 mm long) from 1 marsupium (left); and 4 and 1 marsupial juveniles (4.0 mm long) from each of 2 marsupia (middle and right) (F86009; specimen 55 mm long; LA).

georgiana group", from Peter I Island in the Bellingshausen Sea taken at 124 m (Spanish BENTART 2003 collection; stn A5, 7–10 February), were examined. The gonad tubules had eggs 1.5 mm long. Marsupial juveniles were uniform in size (2–3 mm long). Numbers of juveniles in the marsupia were: 5, 0, 0, 0, 0 and 15, 13, 11, 0, 0. The data indicate two fertilization events.

Two female specimens from amongst many (up to 27 mm long, tentacles included) belonging to the "*Cucumaria georgiana* group", from Low Island near the Antarctic Peninsula taken at 86 m (Spanish BENTART 2006 collection; stn Low 45, 7–10 February), were examined. The gonad tubules lacked eggs. Marsupial juveniles were uniform in size (2–3 mm long). Numbers of juveniles in the marsupia were: 63, 39, 27, 0, 0 and 30, 27, 23, 17, 9. These data indicate one fertilization event.

The differing gonad and marsupial data for the same time of the year, and the significantly different sizes of the specimens from very large samples, are evidence of two different species within the specimens of the "*Cucumaria georgiana* group" from Peter I Island and Low Island.

Hétérier et al. (2004) reported that preliminary observations indicated that *Echinopsolus acanthocola* Gutt, 1990 and *Echinopsolus parvipes* Massin, 1992 "could brood". De Ridder et al. (2005) confirmed internal brood-protection for *Echinopsolus acanthocola*. Brood-protection in anterior interradial marsupia is confirmed here for both species of *Echinopsolus*.

Marsupium in *Cladodactyla crocea* (Lesson)

For the subantarctic dendrochirotid species *Cladodactyla crocea* (Lesson, 1830), Wyville-Thomson (1878) reported "no special marsupium"; Bell (1908) reported "brood pouches"; Vaney (1925) reported "two brood pouches"; and Ekman (1925) reported "sexual maturity comes late" and "no brood pouches". Museum Victoria specimens of *Cladodactyla crocea* from the Burdwood Bank (NMV F160031) and Falkland Islands (NMV F106967) that were studied in this work have a single dorsal longitudinal invaginated body wall marsupium (fig. 2f). A small and presumably young specimen from the Burdwood Bank, collected on 25 January 2004 (NMV F160031), is 8 mm long, has eggs in gonad tubules, and a dorsal invaginated marsupium with eggs/embryos. Presumably the authors referred to above were observing specimens that were not *Cladodactyla crocea*.

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