

The genus *Herdmania* Lahille, 1888 (Tunicata, Ascidiacea) in Australian waters

PATRICIA KOTT FMLS

Queensland Museum, PO Box 3300, South Brisbane, Queensland, 4101, Australia

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Revision of material from Australian waters previously assigned to *Herdmania momus* (Savigny, 1816) has resulted in the recognition of five species (including two new indigenous species). A tropical Indo-West Pacific range is recorded for the type species (*H. momus*), although it is not recorded from Western Australia. A circum-continental range for the third and largest species, *H. grandis* (Heller, 1878) is confirmed. *Herdmania pallida* (Heller, 1878), with a wide range in the western Pacific and Indian Ocean including the north-eastern and north-western coasts of Australia, is a different species from the Atlantic Ocean species (formerly thought to be conspecific). *Herdmania fimbriae*, a new species with a geographical range from southern to north-eastern Australia, is distinct from *H. mentula*, also a new species, from the north-western coast. The structure of the gonads and their ducts and accessory membranes and the arrangement and number of body wall muscles distinguish the species. Species differences are supported by the maximum size of individuals, nature of their test, number of branchial folds, number of internal longitudinal vessels on the folds and between the dorsal lamina and dorsal fold, the size and form of the dorsal tubercle and dorsal lamina, and the shape of the ciliated opening of the neural duct, although these characters are affected to some extent by growth. A variety of accessory membranes associated with both male and female gonoducal apertures are found in the majority of species in this genus. © 2002 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 134, 359–374.

ADDITIONAL KEY WORDS: taxonomy – Indo-West Pacific – gonoducal membranes – calcareous spines.

INTRODUCTION

GENUS CHARACTERISTICS

Herdmania Lahille, 1888 is a genus of the Pyuridae distinguished from others by the needle-like, echinated, calcareous (vaterite: Lowenstam & Abbott, 1975) spines embedded in the test and body wall (including the pharyngeal wall between the stigmata), narrow dorsal lamina with marginal languets, a single gonad on each side of the body, left gonad enclosed in a simple horizontal gut loop, and compact liver embedded in the body wall over the pyloric part of the gut. Spicules are enclosed in slender membranous tubes in which they are aligned end-to-end (Lambert & Lambert, 1987). Spines, to at least 1.5 mm long in the posterior part of the body wall, decrease in length anteriorly and in the branchial vessels. They usually are arranged longitudinally in the siphons, but seem to be randomly orientated in the body wall except

when it contracts and, depending on the strength and number of muscles, the spines are drawn together, often parallel to one another, to form a dense calcareous felt-work. In large specimens spines may occur in tissues in which they are not present in juveniles (such as the oviducal hood: see *H. fimbriae* sp. nov., p. 359 and *H. momus*) There is no armature on the siphonal lining as there is in most pyurid genera. Individuals generally are large (to about 16 cm), with numerous (from seven to 13) branchial folds. Even though Kott (1985) drew attention to the unique characters that distinguish it from *Pyura*, *Herdmania* has not always been recognized as a separate genus (e.g. Monniot & Monniot, 1989; 1991; Monniot, 1989)

SPECIES CHARACTERISTICS

In discussing *Herdmania momus* (Savigny, 1816), Michaelsen (1918a,b) and Hartmeyer & Michaelsen (1928) referred to the close relationships of various *formae*, separated from one another largely on the basis of the numbers of branchial folds. They sug-

Corresponding author:
E-mail: patriciam@qm.qld.gov.au

gested that other characters such as the dorsal tubercle, the shape of the slit-like opening of the duct of the neural gland, and the numbers of internal longitudinal vessels on the branchial folds may correlate with the age (size) of the individual. Hartmeyer & Michaelsen (1928) thought the number of branchial folds was the one character that did not correlate directly with the size of the individual, and probably had some other (genetic?) significance. Their data support this hypothesis only very generally, larger specimens having 11–15 folds while smaller ones have 10–12 folds. Such age-determined variations (including the maximum size of the individuals) occur within certain limits, and those limits could be genetically determined. Nevertheless, despite their efforts to identify a consistent character that would divide a geographical/size-based grouping into distinct *formae*, Michaelsen (1918a,b) and Hartmeyer & Michaelsen (1928) consistently refer to *Pyura momus* (Savigny, 1816) sp. 'ampla' and emphasize the difficulties in recognizing genetically distinct taxa.

Kott (1952) acknowledged as valid var. *grandis* and var. *galei* and established *H. momus* var. *curvata* as a new variety (which subsequently was recognized as a junior synonym of *H. momus* f. *typica*: see Kott, 1957, 1966, 1972a). However, later Kott (1985) treated the differences between varieties of *H. momus* as the result of growth and maturity in the one species, as had Van Name (1945).

Since Kott's (1985) work, new taxonomically significant morphological characters have been determined allowing a reassessment of the genus, an important and conspicuous one in Australian waters.

GEOGRAPHIC RANGE

The genus is known mainly from shallow sub-littoral and continental shelf waters, the greatest depth recorded being for *H. pennata* (Monniot & Monniot, 1991) at 270 m off the Coral Sea Plateau. *Herdmania inflata* (Van Name, 1918) is known from the Philippines from 7 to 177 m. The most southerly records so far are from Tasmania (see below, *H. fimbriata* p. 361). The most northerly records are for *H. momus*: Rho (1975) from the Korea Strait and the possibly conspecific *H. momus*: Nishikawa (1991) from Sagami Bay, Japan. The genus is pan-tropical (known from the Atlantic, Pacific and Indian Oceans). It is recorded from Hawaii (Abbott *et al.*, 1997), but not from either the eastern Pacific Ocean or the Mediterranean.

Although individuals of each species are common, the genus is not diverse, only five species being known from Australia. The present revision is based on the examination of newly and previously recorded material. The species now known from Australian waters are *Herdmania momus* (Savigny, 1816), *H. grandis*

(Heller, 1878), *H. pallida* (Heller, 1878), and the new species *H. fimbriata* sp. nov. (p. 361) and *H. mentula* sp. nov. (p. 365).

Species of *Herdmania* not recorded from Australia are:

Herdmania columna (Monniot & Monniot, 1991), an unusual stalked species from New Caledonia at 100–160 m, has similar but more numerous gonads than *H. pennata* (see below).

Herdmania inflata (Van Name, 1918), from the Philippines at 7–177 m has one gonad on each side consisting of crowded testis follicles in an undulating line along the top of a straight ovarian tube (which is empty in the holotype) and the vas deferens irregularly interrupted, each separate section opening by one of many short openings scattered along the surface of the crowded testis follicles. Oviducal membranes are not present. Other characters are as reported by Van Name (1918). Although calcareous spines were not detected on re-examination of the holotype (USNM 6037), Van Name (1918, 75) refers to spines 'similar to those found in *Pyura pallida*'. The species resembles *H. momus* in its undulating testis with multiple openings of the vas deferens, but it differs in its straight ovary and lack of an oviducal membrane (see *H. momus*, Remarks). It appears to be the senior synonym of *H. polyducta* Monniot & Monniot, 1989, 2001.

Herdmania insolita Monniot & Monniot, 2001, from Indonesia, Philippines, Palau Is, and Yap, has gently undulating ovaries fringed by testis follicles, a common vas deferens and gonoducal membranes that resemble both *H. fimbriata* sp. nov. (p. 361) and *H. mentula* sp. nov. (p. 365). The anal border is not fringed as it is in *H. fimbriata* and the vas deferens does not project into the atrial cavity as it does in *H. mentula*.

Herdmania pennata (Monniot & Monniot, 1991) from New Caledonia and Chesterfield Reef at 230–270 m has, on each side, a tubular ovary fringed by branched testis follicles with several openings of a common vas deferens along the centre of the ovarian tube, including one at the base of the oviduct.

Herdmania momus: Nisikawa, 1991 from the Sea of Japan, has numerous, separate, short vas deferens openings along a convoluted band of testis follicles. It has an oviducal hood. The course of the ovary and the relationships of the various specimens reported to the nominal species are not known. Other specimens from Japan (*viz.* *H. momus*: Tokioka, 1949: 61; 1953: 277; 1967: 205) and *H. momus*: Rho, 1975 have similar characters although details of gonads and their gonoducal openings are not available.

Herdmania sp. from the Atlantic Ocean (see *Cynthia pallida*: Traustedt, 1883, 119; *Pyura momus*: Van Name, 1921, 498; *Herdmania momus*: Van Name,

1945, 341 and possibly *Rhabdocynthis pallida*: Sluiter, 1898b) has an undulating ovarian tube like *H. momus* but a common vas deferens with a single opening near the oviducal opening, and the latter is not protected by an oviducal membrane or hood as it is in *H. fimbriae* sp. nov. (p. 361).

Institutions housing the specimens examined in connection with this work are indicated as follows: AM, Australian Museum, Sydney; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth; USNM, United States National Museum of Natural History Washington DC, USA.

TAXONOMY

HERDMANIA FIMBRIAE SP.NOV. (FIG. 1)

Herdmania momus var. *galei* Kott, 1952: 281 (part, fig. 127 from Tasmania, and Bowen).

Herdmania momus: Kott, 1972a: 41 (part, intermediate-sized forms 3 km off Glenelg); 1972b: 189 (part, small upright specimens).

Distribution

Type Locality. South Australia (Point Turton jetty on piles and weed 3–4 m, coll. K. Gowlett Holmes 3.12.93 holotype SAM E2892; coll. K. Gowlett Holmes & W. Zeidler 20.4.94 paratypes SAM E2891).

Examined Material. South Australia (Investigator Group, QM GH933 GH2299; Gambier Group, QM GH4405). Tasmania (Nine Pin Point, QM G1999 GH2017). Queensland (Bowen, AM Y1827 Y1829). The species, also has been recorded from Tasmania (Kott, 1952) and South Australia (Glenelg, Kott, 1972a)

Description

Individuals sometimes upright, occasionally with short stalk. Up to 3 cm long. Upright individuals with atrial aperture terminal, branchial aperture directed laterally from halfway down the dorsum, both on short wart-like siphons. Other individuals sessile, fixed along their left sides. In preservative body laterally flattened, body wall closely adherent to gelatinous, thin white translucent test. Characteristic echinated needle-like spines in test, shorter and sparser than those crowded in body wall. Longest spines randomly orientated ones in posterior part of body wall, shorter ones anterior. Spines in siphonal walls orientated longitudinally.

Distinct circular muscle bands surround each siphon. On each side about 22 longitudinal branchial muscle bands extend almost parallel to one another and terminate in front of the horizontal gut loop on left and gonad on right. Twelve longitudinal atrial

muscles on each side, the three anterior bands cross the posterior ends of the five dorsal longitudinal branchial muscles and the posterior atrial ones extend a short distance across body behind branchial muscles terminating near anus and gonoducal openings. When contracted, longitudinal branchial muscles raise body wall and test in rounded ridge around siphons. Dorsal tubercle a small cushion in wide peritubercular 'V' with a simple U-shaped slit, its ends turned in.

Branchial sac with seven to nine broad folds on each side with up to 12 internal longitudinal vessels on folds and one or two in interspace. Between dorsal fold and dorsal lamina never more than three internal longitudinal vessels which sometimes are absent altogether. Gut a horizontal loop with usual compact liver of crowded tubules embedded in body wall over pyloric region. Anal border variable, bilabiate, each lip usually divided and variously subdivided into regular or irregular tongue-like to rounded lobes. Long ovarian tubes, one in gut loop on left and one in corresponding position on right, undulate regularly and have clumps of testis follicles around each outer curve. From each clump, a number of short vasa efferentia join into a short common duct extending across surface of ovary to join central vas deferens. Large circular to fan-shaped, sometimes frilled and occasionally fringed membranous hood projects from the body wall over upper mesial surface of distal end of the short oviduct. It usually folds around to form conical to cylindrical chamber in front of oviducal opening. In older specimens, oviducal hood becomes less membranous, and is vascularized, to form a firm and slightly concave circular lid over the usually large, circular or sometimes triangular opening. Proximal to the origin of the oviducal hood, the male duct opening is a transverse slit sometimes raised on a short papilla projecting from surface of oviduct or is sessile, on side of, or across surface of oviduct. Variable frilled or fringed membranes, and/or pointed or rounded and sometimes branched papillae usually project into atrial cavity from body wall over oviduct distal and/or proximal to male opening. In robust (to 3 cm) specimens from Bowen, gonoducal hoods and membranes contain spines.

Remarks

The species resembles the Atlantic *Herdmania momus*: Van Name, 1921, 1930 and 1945, *Cynthia pallida*: Traustedt, 1883 and *Rhabdocynthis pallida*: Sluiter, 1898b in having testis follicles clumped along the outsides of an undulating ovary and a common vas deferens opening at the base of the short oviduct. However, in the Atlantic species neither oviducal hood or chamber nor the fringed or frilled membranes and/or papillae around the male openings are present. The present species is similar in size and appearance

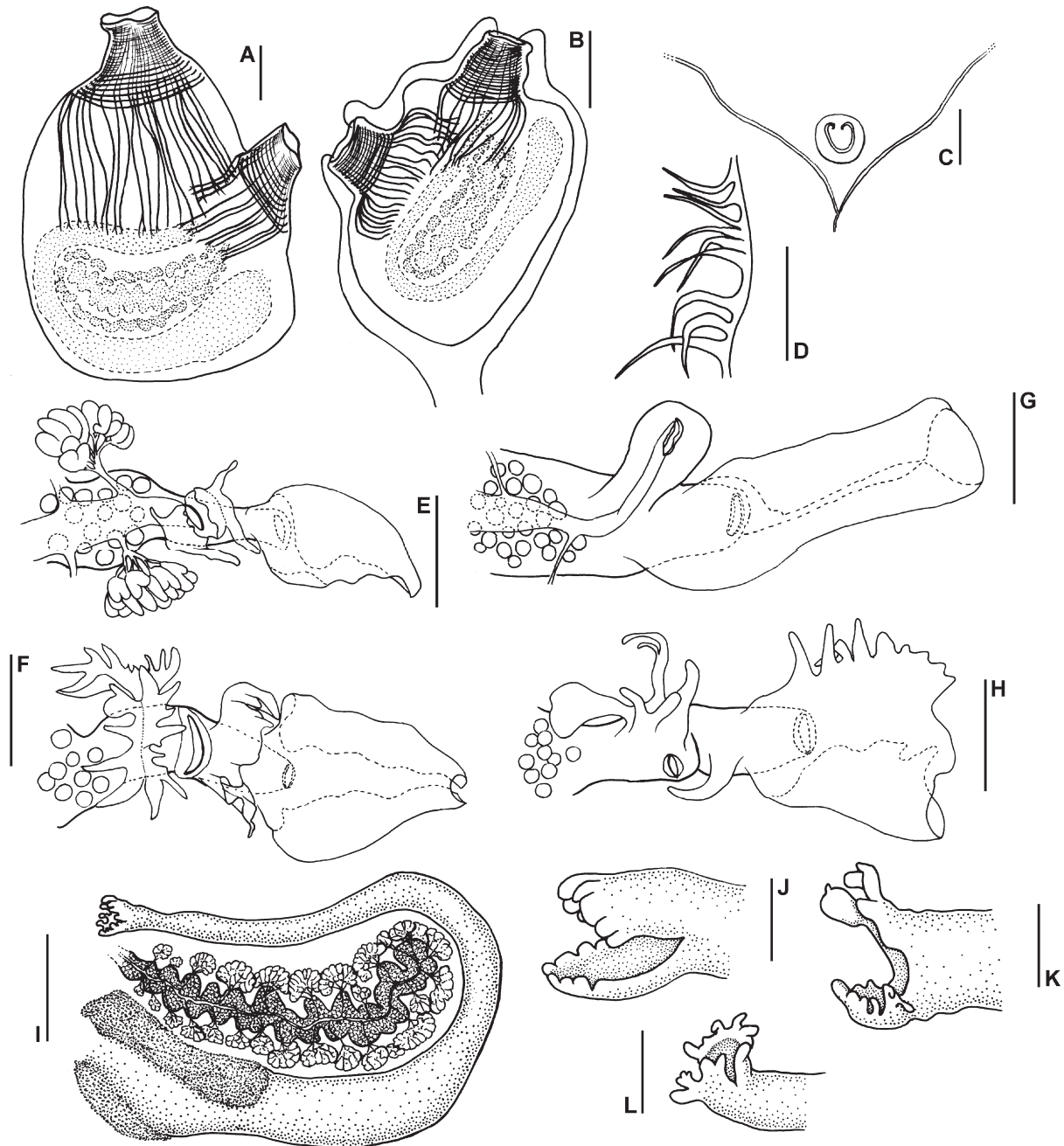


Figure 1. *Herdmania fimbriata* sp. nov. (A, C, D, I, SAM E2892; B, L, QM GH4405; E, K, QM GH 2299; F, G, J, SAM E2891; H, QM GH933). A, B, body wall from left side; C, dorsal tubercle; D, dorsal lamina; E–H, distal part of gonads showing gonoducal openings and membranes; I, gut loop and gonads; J–L, anal border. Scale bars: A, I = 5.0 mm; B = 2.0 mm; C–H, J–L = 1.0 mm.

and has an oviducal hood and lobed anus as in *Herdmania momus* (Savigny, 1816), but the undulations of its oviduct are not as pronounced, testis follicles do not form an undulating band along the top of the ovary, the vas deferens is not interrupted and it has only a single opening. *Herdmania momus*: Nishikawa, 1991 and possibly some *H. momus*: Tokioka, 1953 (pl. 69

fig. 3) also have an oviducal hood and differ from the present species in having an interrupted vas deferens, each section with a separate opening like *H. momus*. *Herdmania inflata* differs in its interrupted vas deferens as well as its lack of gonoducal membranes. *Herdmania mentula* sp. nov. (p. 365), similar to the presents species, is known only from the north-

western Australian coast and is distinguished by its freely projecting vas deferens and four shallow, smooth anal lobes (see below). The deeply scalloped anal border distinguishes the present species from *H. insolita* Monniot & Monniot, 2001 which has an even undivided anal margin.

HERDMANIA GRANDIS (HELLER, 1878) (FIG. 2)

Cynthia grandis Heller, 1878: 15. Herdman, 1891: 577.

Halocynthia grandis: Michaelsen, 1905: 85.

Pyura momus grandis: Hartmeyer & Michaelsen, 1928: 441. Hastings, 1931: 72.

Herdmania momus: Millar, 1960: 127; 1963: 70; 1966: 374. Kott, 1972b: 189; 1976: 84; 1985: 338 (part, see below).

Herdmania momus galei: Kott, 1952: 281 (part from Shell Harbour)

Herdmania momus grandis: Kott, 1952: 279; 1964: 142; 1966: 301. Tokioka, 1967: 206

Herdmania pallida grandis: Hartmeyer, 1909: 1340.

Cynthia complanata Herdman, 1882: 145.

Rhabdocynthia complanata: Herdman, 1891: 575.

Microcosmus julinii von Drasche, 1884: 371. Herdman, 1891: 575.

Microcosmus draschii Herdman, 1891: 575; 1899: 20.

Herdmania armata Monniot & Monniot 2001: 337.

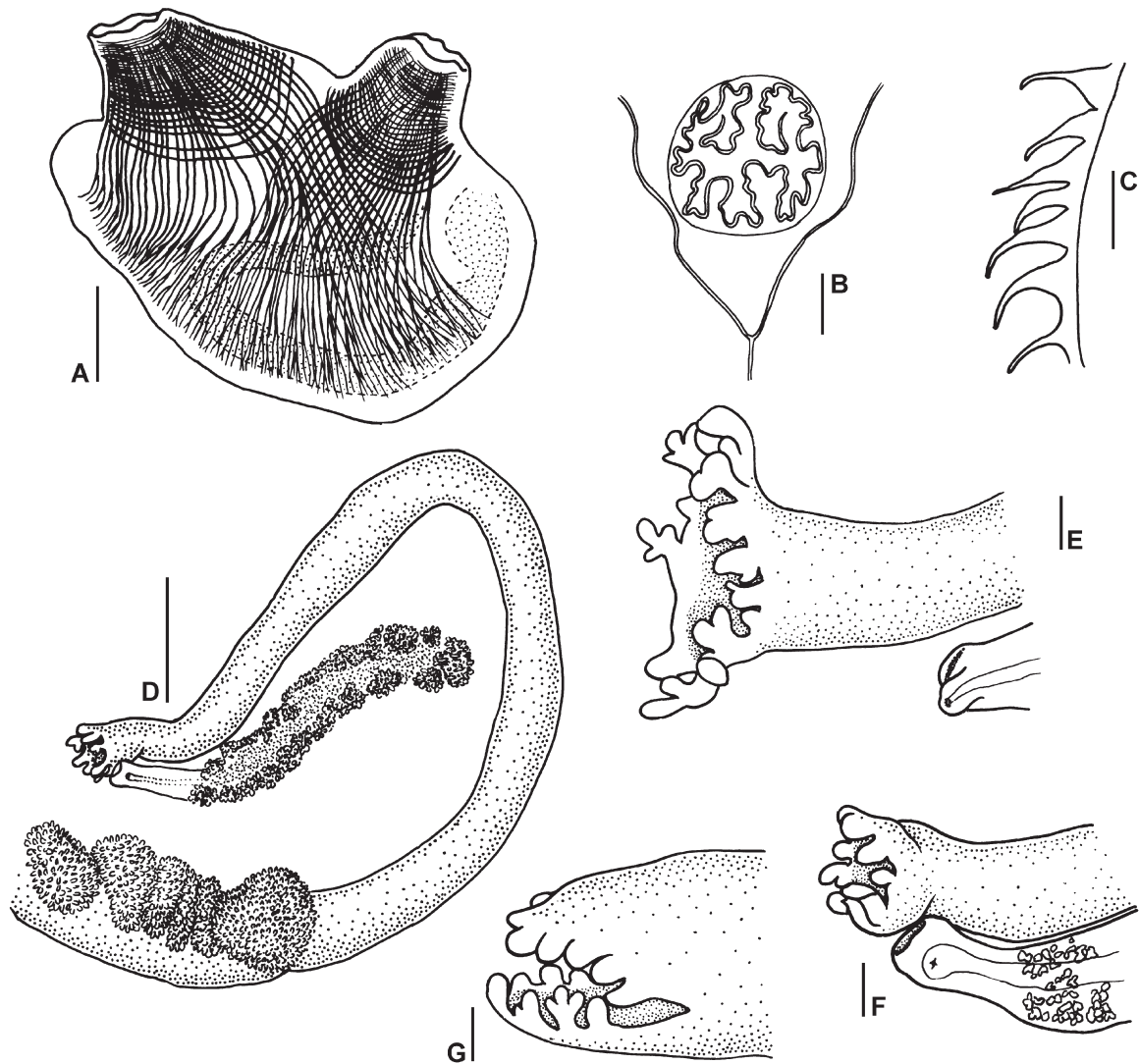


Figure 2. *Herdmania grandis* (A, C, D, F, QM GH377; B, E, QM GH2200; G, QM GH5759): A, body from left side showing muscles; B, dorsal tubercle showing early stage in development of convoluted slit; C, portion of dorsal lamina; D, gut loop; E, F, anus and gonoducal openings; G, anus. Scale bars: A, D = 5.0 mm; B, E-G = 1.0 mm; C = 0.5 mm.

Distribution

Previously Recorded. Western Australia (Geraldton to Albany, Hartmeyer & Michaelsen, 1928; Kott, 1952, 1972b, 1985). South Australia (Millar, 1960, 1963, 1966; Kott, 1976). New South Wales (Heller, 1878; Herdman, 1882, 1899; von Drasche, 1884; Kott, 1952, 1985). Queensland (Moreton Bay to Cairns, Hastings, 1931; Kott, 1952, 1966, 1964). Papua New Guinea (Monniot & Monniot 2001)

Examined Material. Western Australia (Port Hedland WAM Z11766/1179.83; Cockburn Sound QM G11896, WAM Z11772/1180.83 Z11774/1189.83 Z11775/115.72 Z11778/591.84 Z11780/1181.83 Z11781/756.82 Z11782/1182.83 Z11783/233.82 Z11784/232.82), South Australia (Port Naorlunga, QM G9318), Tasmania (Burnie, QM GH4691), Victoria (Bass Strait, QM GH2210), New South Wales (South Ulladulla QM G8578; Woolongong, QM GH5759; Shell Harbour AM Y1814; Arrawarra, QM GH2248; Byron Bay, QM G308514). Queensland (Tweed River, QM G308523; Moreton Bay, QM G4928 G5146 G5166 G8569 GH377; Mooloolaba, QM GH2349 GH2200; off Murdoch Point, QM GH769).

Hartmeyer & Michaelsen (1928) believed that the forms of *H. momus* occurring in Australia (ff. *grandis*, *galei*, *pallida*) owed their wide geographical range to transport by ships. For instance, f. *grandis*, previously known from Port Jackson could have been transported to the south-western Australian coast in that way. However, *H. grandis* is now known to occur around the whole Australian coast (see Kott, 1985 and new records, below) and most likely is part of the indigenous fauna.

Description

The largest known species of *Herdmania*, some specimens being up to 16 cm or more in maximum dimension. Test tough, leathery, wrinkled and opaque. Smaller individuals to 2 cm also have opaque test. Lower half of body, often less wrinkled than upper half, sometimes sandy and may be embedded in sediments. Epibionts including other ascidians, often on outside of test. One specimen (QM GH2210) has sand embedded in the test, making it hard and relatively brittle. Short cylindrical siphons originate close together in middle of upper surface and diverge from one another, or branchial siphon almost horizontal and atrial siphon vertical.

Characteristic *Herdmania* spines crowded in body wall, especially long in posterior end and shorter anteriorly. Crowded spines in siphons aligned longitudinally. In contracted body wall spines, crowded into calcareous felt-work, sometimes lie parallel to one another. Circular muscles are around each siphon and its base. About 30 (individuals 2 cm long) to 50 (individuals from 4 cm long) strong longitudinal muscle

bands on each side of the body radiate from atrial and branchial siphons and cross one another (the atrial muscles inside the branchial ones) on the sides of body, to create a meshwork of crowded muscles over whole body when contracted. In all specimens, muscles branch in lower half of body and form almost continuous layer over gut loop and gonads. Dorsal tubercle large, hemispherical cushion, usually filling anterior part of peritubercular area which has a narrow tongue-shaped extension projecting posteriorly in line with dorsal lamina. In smaller (2 cm: QM G308523) specimens opening of neural duct is a long slit undulating around circumference of dorsal tubercle with its ends turned in, the gap between them directed anteriorly. In larger specimens the slit is more convoluted, covering whole surface of tubercle. Dorsal lamina narrow, extending through centre of circular area delimited on each side by a deeply curved dorsal branchial fold. Rather fleshy and very pointed languets are on the edge of the dorsal lamina. From six (small specimens to 4 cm: QM G308523, GH2200; AM Y1814) to 12 (individuals to 10 cm or more) internal longitudinal vessels on flat area between dorsal fold on each side and short dorsal lamina converge at each end. From ten to 13 broad deeply curved, branchial folds on each side lie flat, folded up toward dorsum, ventral surface wider than dorsal surface of fold. Number of folds does not seem to be correlated with size, a specimen of 4 cm (QM GH769) having ten folds on each side, and one of 2 cm (QM G308523) having 11. Up to 23 internal longitudinal vessels on wider folds but only two or three in interspace.

Gut loop and gonads embedded deeply in body wall in most larger specimens, although often gonads were not detected, suggesting individuals might be senescent. Anal border has two or three regular pointed lobes with lobed or scalloped margins, or irregular branched lobes or is sometimes almost smooth (QM G8578 GH2248). Testis follicles either in patches over each side of, or all over, upper surface of long, tubular, straight to slightly sinuous ovary deeply embedded in body wall alongside distal limb of gut loop. Oviducal opening large, sometimes slightly indented. Common vas deferens extends along top of ovary, opening on short inconspicuous papilla near female opening. Specimen 2 cm long from Shell Harbour (AM Y1814), a juvenile without gonads, identifiable with present species by its slightly convoluted circular slit on dorsal tubercle, six internal longitudinal vessels between dorsal lamina and left dorsal fold, 11 branchial folds on each side and long body muscles extending down over gut and gonads.

Remarks

As well as becoming larger than those of other known species, individuals of this indigenous species, even

small specimens, are distinguished from others by their tough opaque test, large dorsal tubercle with convoluted slit, six or more internal longitudinal vessels between the short dorsal lamina and deeply curved dorsal fold, long and straight or almost straight ovarian tube with only occasional irregular, shallow undulations, testis follicles in clumps or crowded in an uninterrupted mass on the upper surface of the ovary (along each side or completely covering it), common vas deferens opening on a small papilla on top of the short oviduct, oviducal opening wide (without a hood) and long, strong radial muscles from each siphon crossing each other over the whole of each side of the body. This last character is unique, other species having radial muscles that terminate at the anterior limits of the gut loop (on the left) and the gonad (on the right). Possibly the contraction of these muscles in the present species cause the gonad on the left to be tightly associated with the distal limb of the gut loop. Further, the number, strength and length of the muscles in this species effects such strong contraction that spines are often drawn together in parallel to form a hard layer over the whole of the body wall.

HERDMANIA MENTULA SP.NOV. (FIG. 3)

Herdmania momus: Kott, 1985: 338 (part only).

Distribution

Type Locality. North-western Australia (Mary Anne Passage 21°15'S 115°50'E, 27 m, south of Barrow I., coll. R.J. Hannon 17.7.63, holotype WAM Z11771/WAM 1199.83; Mary Anne Reef buoy, paratypes WAM Z11759/WAM 212.82(1).

Examined Material. North-western Australia (Rowley Shoals, WAM Z11768/1197.83 Z11769/1198.83(1) Z11770/1188.83(1); Dampier Archipelago, WAM Z11765/761.82(1); Cape Preston, WAM Z11763/974.85; Monte Bello Is, WAM Z11762/918.93; North-west Cape, WAM Z11761/924.83; Learmonth, WAM Z11760/1188.83; Shark Bay, WAM Z11756/1193.83 Z11757/1196.83; Cervantes WAM Z11779/662.89.

Description

Specimens available from one to 6 cm (holotype) diameter, laterally flattened in preservative. Test thin, sometimes papery, white, slightly translucent, occasionally naked, but sometimes with sand completely encrusting it (WAM Z11762); or with Sea Grass (*Amphibolis*) fronds attached, forming a capsule around it (WAM Z11757 Z11779); or with a mixture of sand and other debris adhering (WAM Z11771).

Apertures on short divergent, naked siphons arising quite close together on the upper surface, atrial siphon

the longer one, curved horizontally, branchial siphon directed obliquely upwards. Body wall adheres closely to inside of test. Circular muscles surround each siphon and longitudinal muscles extend along their length, to about halfway down each side of body wall. Longitudinal siphonal muscles divert to respective sides of body from mid-dorsal line. About 20 longitudinal branchial and about 12 longitudinal atrial muscles on each side. Atrial muscles on right cross over and exchange fibres with posterior half of dorsal-most branchial muscles anterior to gonad. Similar number of atrial and branchial muscles cross one another on left, although all but anterior three cover distal (dorsal) extent of distal limb of gut loop and gonad. Large circular dorsal tubercle has deep U-shaped slit with both horns turned or coiled in.

Up to ten branchial folds per side. Branchial formula of holotype: E1(3)1(10)2(14)3(20)9(27)6(20)7(20)6(15)4(11)5DL. Dorsal lamina a narrow membrane with long pointed conical languets along its margin. Gut loop horizontal with usual compact liver in pyloric region enclosing left gonad. Anal border always divided into four shallow, smooth lips. Gonads, one per side, each a long, thick ovarian sac, only slightly undulating, with clumps of branched testis follicles around its margin, each clump connected to thick central common vas deferens by a vas efferens running at right angles to long axis of gonad. Oviducal opening large, shielded by circular to fan-shaped oviducal hood projecting from body wall over distal part of oviduct. Male opening on the tip of long cylindrical, distal part of vas deferens that projects free into atrial cavity. Occasionally body wall over this projection is produced into lobes or papillae around terminal aperture and in one specimen (WAM Z11761) a circle of pointed tentacle-like projections surrounds terminal aperture. Oviducal hood and projections around male aperture contain spines.

Remarks

The species is characterized by its smooth anal border with four shallow indentations and the projecting tip of the vas deferens. The tapering conical dorsal languets and narrow dorsal lamina, oviducal hood, projections around the male opening, central common vas deferens with a single aperture, clumps of male follicles and simple U-shaped slit on the dorsal tubercle with horns rolled in resemble *Herdmania fimbriae*, although the latter species has a regularly undulating ovary, fewer longitudinal branchial vessels, shorter longitudinal muscle bands and a deeply lobed anal border. Occasionally in *H. fimbriae* the tip of the vas deferens projects into the atrial cavity, but its free part is much shorter than in the present species. The species is distinguished from *H. pallida* by its oviducal hood, anal border and relatively few dorsal inter-

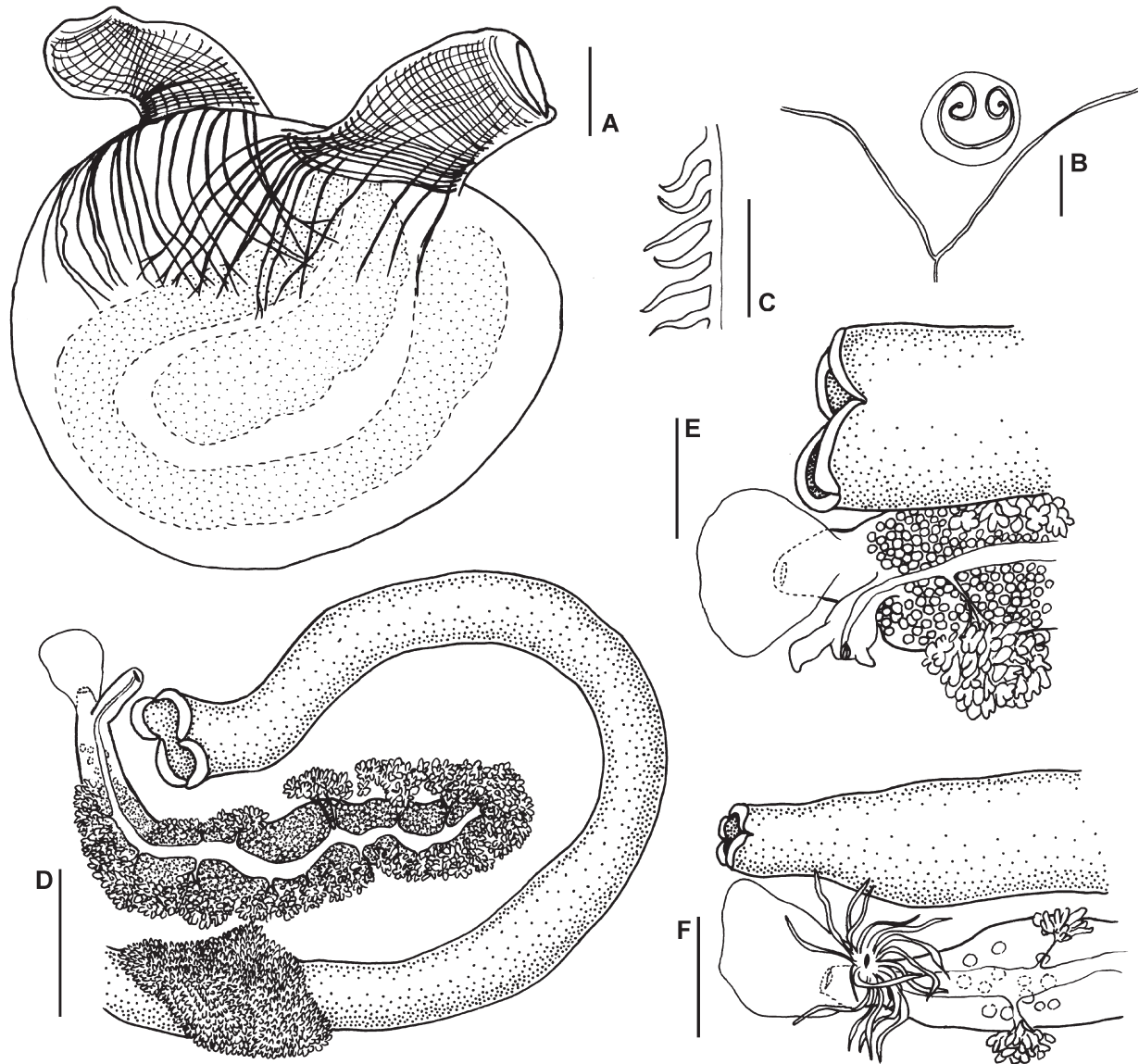


Figure 3. *Herdmania mentula* sp. nov. (A, E, WAM Z11756; B-D, WAM Z11771; F, WAM Z11761): A, body from left side showing muscles. B, dorsal tubercle; C, portion of dorsal lamina; D, gut and gonad; E, F, distal part of gut and gonads, showing gonoducal openings and membranes, and anal border. Scale bars: A, D = 5.0 mm; B, C, E, F = 1.0 mm.

nal longitudinal branchial vessels between the dorsal lamina and dorsal fold on each side. *Herdmania insolita* has shorter longitudinal muscles than the present species, fewer internal longitudinal branchial vessels on and between the folds and it lacks the freely projecting distal end of the vas deferens found in the present species.

The known range of the present species is between Cervantes and Rowley Shoals on the north-western Australian coast. *Herdmania fimbriata* is recorded from the western end of the Great Australian Bight to Bowen (Queensland). So far, neither of these species has been recorded from Torres Strait, the Arafura Sea,

south-western Australia, and north-eastern Australia north of Bowen.

HERDMANIA MOMUS (SAVIGNY, 1816) (FIG. 4)

Cynthia momus Savigny, 1816: 143.

?*Halocynthia momus*: Sluiter, 1905a: 102; 1905b: 13.

Pyura momus: Hartmeyer, 1909: 1340.

Pyura momus f. *typica* Michaelsen, 1918a: 9; 1918b: 30.

Herdmania momus f. *curvata* Kott, 1952: 282; 1964: 143.

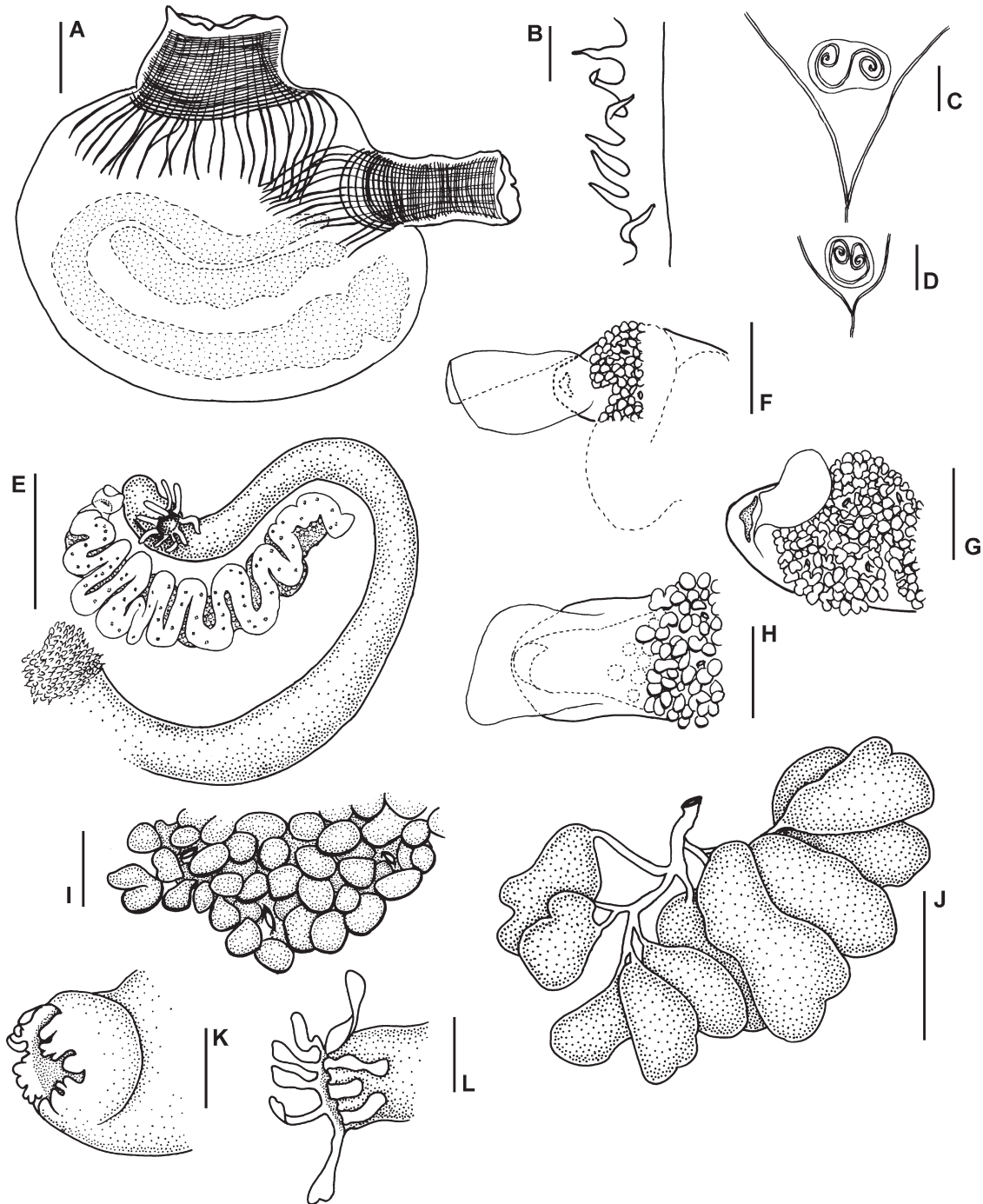


Figure 4. *Herdmania momus* (A, C, QM G10093; B, QM GH561; D, L, QM G308151; E-G, QM G9363; H, QM GH2554; I-K, QM GH771): A, body from left side showing muscles; B, portion of dorsal lamina; C, D, dorsal tubercles; E, gut loop and gonads; F-H, distal part of gonad showing oviducal hood and male openings surrounded by testis follicles; I, testis follicles with tips of vas deferens showing amongst them; J, clumps of testis follicles with vas deferens; K, L, anal borders. Scale bars: A, E = 5.0 mm; B-D, F = 1.0 mm; H, J = 0.5 mm; K, L = 2.0 mm.

Herdmania momus: Millar, 1975: 317?. Kott (1981): 208; 1985: 338 (part only).
Cynthia papietensis Herdman, 1882: 143; 1886: 406.
Herdmania contorta Monniot, 1992: 18.
Herdmania curvata: Kennett, 1997: 86. Kott (1998): 179.
Cynthia pallida: Herdman, 1886: 406.
Cynthia pallida billitonensis Sluiter, 1885: 183; 1890: 331.
Rhabdocynthia tenuis: Sluiter, 1895: 24.

Distribution

Previously Recorded. Queensland (SE Qld, Kott, 1964; Great Barrier Reef, Kott, 1952, 1964, 1985). Western Pacific (Fiji, Kott, 1981; French Polynesia, Herdman, 1882, 1886; Coral Sea Plateau, Monniot, 1992). Indonesia (Ambon, Billiton, Sluiter, 1885, 1890, 1895; Herdman, 1886). Indian Ocean (Sluiter, 1905a,b?). Red Sea (Savigny, 1816; Michaelsen, 1918a,b).
Examined Material. Queensland (Moreton Bay, QM G308580; Noosa, QM G4965; Capricorn Grp, AM Y1811 holotype *H. curvata* Kott, 1952; AM Y2334 paratypes *H. curvata* Kott, 1952; G9363 G10014 GH2554; Keppel I., G11999); Swain Reefs (QM GH4842.; Lizard I., GH771). Philippines (QM GH561-2).

Herdmania momus is tropical and in Australia has a recorded range in Queensland waters between Moreton Bay and Lizard I. where it is the common species in shallow water reefal and littoral habitats (Kott, 1964). It has not been recorded from the western coast of the continent although it is known from Indonesia and, in view of its presence in the Red Sea, is very likely to occur in the Indian Ocean. *Herdmania pallida* is recorded from the Arafura Sea (Tokioka, 1952) and Torres Strait (see below), but there are no records of the present species from the northern coast of the continent.

Description

Smaller specimens to 3 cm pink with translucent test; larger specimens (to 8 cm) test becomes tough, opaque or even leathery, especially anteriorly (QM G10014). Cylindrical siphons originate close to one another on upper surface, branchial siphon directed laterally and atrial siphon vertical. Minute spicules just under the surface layer of test, larger ones in internal layer. Largest spicules (to 1.5 mm long) in posterior end of body wall. They are shorter anteriorly and in blood vessels of branchial wall. Spines longitudinally arranged and parallel in siphons, but randomly orientated in body wall, in which they form a felt-work of calcareous spicules when it contracts. Circular muscles surround each siphon. On each side, about 20 longitudinal branchial muscles and 15 longitudinal

atrial muscles radiate over the anterior half of body terminating at the same level just anterior to horizontal gut loop on left and gonad on right. Anterior atrial muscles and posterior branchial ones cross each other. Dorsal tubercle, a small cushion in large open peritubercular 'V', usually has U-shaped slit with opening directed anteriorly in smaller specimens; larger specimens with both horns turned in or out, sometimes forming double spiral. One specimen (QM GH2554) has two separate U-shaped openings, the left one with the gap turned to the left. In one large specimen (8 cm) the dorsal tubercle is a circular cushion with a complex convoluted slit. Dorsal lamina a wide membrane with laterally flattened languets on the edge. In an 8 cm specimen the branchial sac has 8–12 wide, longitudinal folds on each side. Depending on size of individual, one to six internal longitudinal vessels are between dorsal lamina and dorsal fold. Gut in posterior half of body forms simple horizontal loop enclosing left gonad. Liver composed of several compact masses of small, vertical, crowded tubules tightly enclosed in body wall over pyloric region. Anal lobes variable, anus basically bilabiate with each lip subdivided into long, sometimes branched, ribbon-like lobes (QM G4965 G9363) or one or two triangular lobes with scalloped margins (QM G10014). Variations in anal border are not size dependent. Gonads, one on each side of the body, consist of a long ovarian tube in characteristic tight undulations obscured by an opaque band of testis follicles that undulates from side to side along the top of the ovary. Testis ducts numerous, short and vertical, with elliptical openings that appear to be sessile between crowded testis follicles. Oviduct short with fan-shaped to semicircular hood projecting from body wall just behind triangular oviducal opening close to anus. Oviducal hood large delicate, membranous, transparent in smaller specimens folding down over tip of oviduct to form conical chamber in front of opening. Smaller, firmer hood with vascular network in it forms slightly concave lid over oviducal opening in larger specimens. In large (about 6 cm) specimens from Philippines oviducal hood is a wide, fan-shaped flap, packed with spines symmetrically arranged across its width.

Remarks

Michaelsen (1918a,b) reviewed and tabulated those taxa (as *formae*) known to contain the long echinated needle-like spines characteristic of this genus. In the group he assigned to f. *typica* (Michaelsen, 1918b: 40 no. 42) are specimens with the ovary a straight tube with small branches and testes around the edges. These and other specimens may not be accurately assigned. Nevertheless he interpreted the type speci-

mens of *H. momus* as having a continuously winding band of testis follicles along the top of the ovary. Although neither Savigny nor Michaelsen saw the separate male ducts, Savigny (1816) correctly identified the oviducal opening with a membranous 'cornet' around it. Kott (1957, 1966, 1972a) referred to *H. momus* var. *curvata* as a junior synonym of *H. momus* var. *typica*. Later (1985), she regarded all varieties of *Herdmania* as growth forms of the one taxon until Kennett (1997) observed the release of sperm from many points along the surface of the ovary. The multiplicity of separate short vasa deferentia from crowded clumps of lobed testis follicles were duly demonstrated, evenly spaced along the curved band of testis follicles on the surface of a tightly curved ovarian tube in specimens referable to *H. curvata* Kott, 1952 (a senior synonym of *H. contorta* Monniot, 1992: see Kott, 1998), now known to be a junior synonym of *H. momus*. Although Monniot (1992) shows a male duct opening at the base of the oviduct (Monniot, 1992, fig. 6b), he reports that he did not see either a vas deferens or its opening.

Cynthia pallida billitonensis Sluiter, 1885 from Indonesia has relatively few longitudinal muscles, the dorsal tubercle and dorsal lamina are like *H. momus* and the convoluted course of the testis follicles along the surface of the ovary can be seen in the figure (Sluiter, 1885; pl. IV figs 1–2). Also like the present species, *Rhabdocynthia tenuis*: Sluiter, 1895 from Ambon, with a translucent thin, gelatinous test, has seven folds per side, two internal longitudinal vessels in the interspace, a broad dorsal lamina with long thin languets and the slit on the dorsal tubercle with both horns spiralling in. It is taken from the same location as *Cynthia pallida*: Herdman, 1886, which also has a undulating ovary. *Cynthia papietensis* Herdman, 1882 and 1886, from Tahiti, with the same broad dorsal lamina as the present species and lacking internal longitudinal branchial vessels between the dorsal midline and the dorsal folds, is conspecific.

Herdmania momus: Millar, 1975 from Japan, Singapore and Indonesia cannot be accurately assigned owing to lack of information on gonads and gonoducts. Some specimens of the present species may be included, although others also may be present.

The species is distinguished by the tight undulations of its ovarian tube; the hood over and in front of the oviducal opening produced from the body wall over the oviduct; the undulating band of crowded clumps of testis follicles along the top of the ovary; a separate short, vertical duct from each clump of testis follicles; absence of a male opening at the base of the oviduct; relatively small dorsal tubercle with one or two U-shaped openings with the horns turned or spiralling in or out (except in one large specimen 8 cm, in which the slit is convoluted); and relatively few internal

longitudinal vessels between the dorsal lamina and dorsal fold.

Herdmania momus: Nishikawa, 1991 from the Sea of Japan has an oviducal hood and numerous vas deferens openings but the course of the ovary is not recorded. *Herdmania fimbriae* has a lobed anal border, an undulating ovarian tube and an oviducal hood, but it has a large, straight common vas deferens with a single opening surrounded by an elaborate membranous fringe. *Herdmania mentula* has a similar oviducal hood but a common vas deferens projecting into the atrial cavity at its distal end, a gently undulating ovary and the anal rim divided into four smooth, shallow lips.

Herdmania inflata (Van Name, 1918), from the Philippines (Fig. 5A), like the present species has many short vasa deferentia opening over the surface of the male follicles which are in a conspicuous undulating band. However, in *H. inflata* the ovary is straight, it lacks an oviducal hood, the vas deferens is less interrupted and the separate openings fewer than in *H. momus* and the terminal part of the vas deferens opens with the oviduct, on a cylindrical short projection into the atrial cavity.

HERDMANIA PALLIDA (HELLER, 1878) (FIG. 5B–E)

Cynthia pallida Heller, 1878: 14 (part, not specimens from Jamaica). Herdman, 1881: 60; 1882: 143; 1886: 405. Traustedt (1885): 35.

Rhabdocynthia pallida: Herdman, 1891: 575; 1906: 308. ?Sluiter, 1898a: 7; 1904 54; 1905a: 102; 1905b: 14.

Halocynthia pallida: Michaelsen, 1905: 83. Hartmeyer, 1906: 4.

Pyura pallida: Michaelsen, 1908: 269. Van Name, 1918: 76.

Pyura momus pallida: Michaelsen, 1918a: 10; 1918b: 30 (part, not Atlantic records); 1921: 1; ?1934: 133

Herdmania momus: Tokioka, 1952: 137; 1961: 132. Kott & Goodbody, 1982: 548. Abbott *et al.*, 1997: 51.

Pyura momus: Vasseur, 1967a: 119.

Pyura momus galei Michaelsen & Hartmeyer, 1927: 194. Hartmeyer & Michaelsen, 1928: 443

Herdmania momus galei: Kott, 1952: 281 (part, not AM Y1827 Y1829 and specimen from Tasmania, fig. 127; *H. fimbriae*; not specimen from Shell Harbour: *H. grandis*).

Rhabdocynthia ceylonica Herdman, 1906: 308. Monniot & Monniot, 1989: 239.

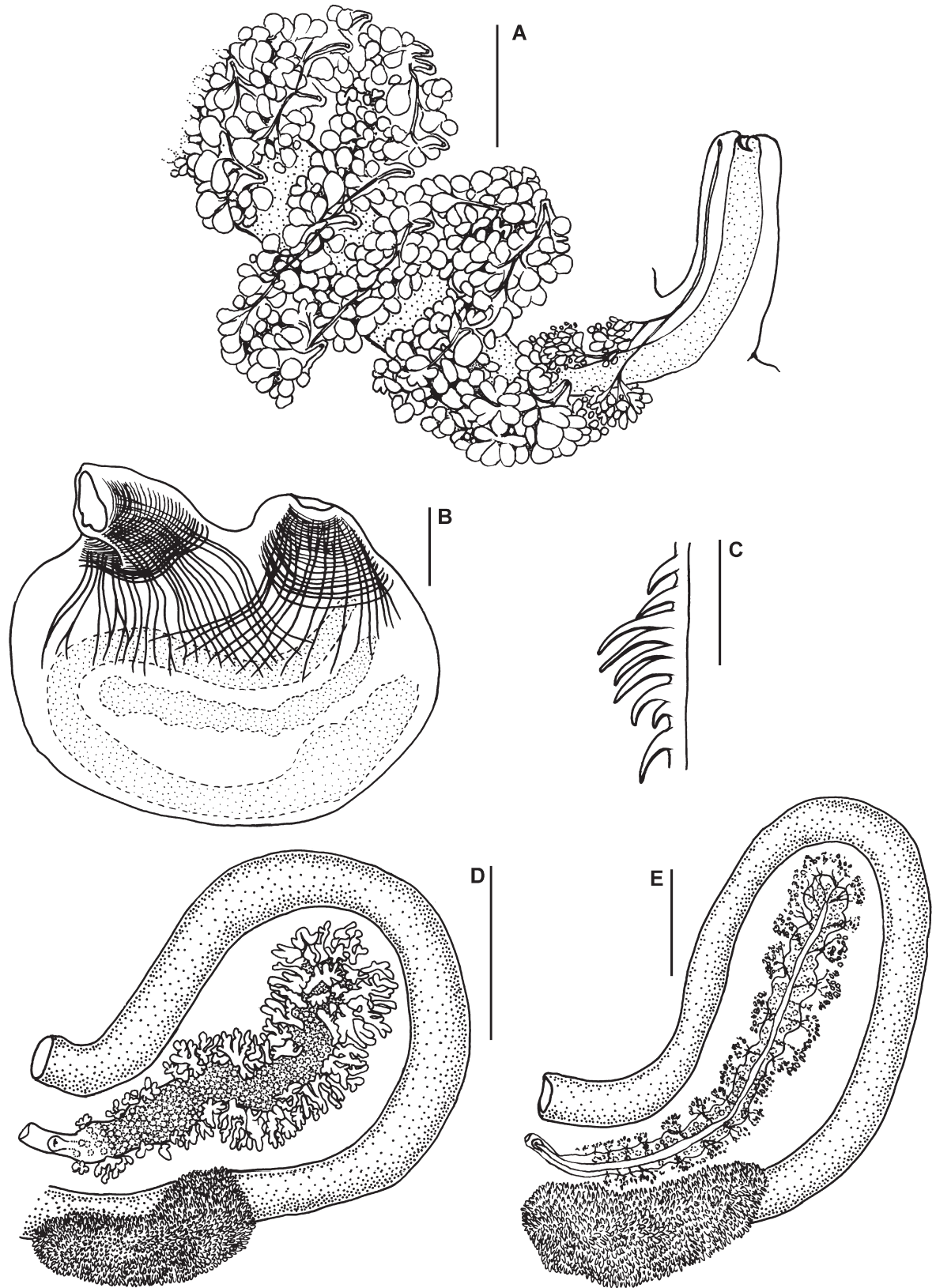
Not *Cynthia pallida*: Traustedt, 1883: 119, 133.

Not *Rhabdocynthia pallida*: Sluiter, 1898b: 25.

Not *Pyura momus pallida*: Michaelsen, 1918b: 30 (part from Atlantic locations).

Not *Pyura momus*: Van Name, 1921: 454; 1930: 498.

Not *Herdmania momus*: Van Name, 1945: 341. Tokioka, 1949: 61; 1953: 277.



Distribution

Previously Recorded. Western Australia (Dirk Hartog, WAM Z11764/1195.83; Jurien Bay, WAM Z11776/242.87 Kott, 1985). The species is recorded from South Africa (Herdman, 1881, 1882; Sluiter, 1898a?; Michaelsen, 1934?). West Indian Ocean (Heller, 1878; Sluiter, 1905a,b?; Michaelsen, 1918a,b, 1921; Vasseur, 1967b). West Indian Ocean (Sluiter, 1898a,b?; Herdman, 1906; Michaelsen, 1908). Taiwan (Michaelsen, 1908). South China Sea (Kott & Goodbody, 1982). Japan (Hartmeyer, 1906; Tokioka, 1953). Tropical West Pacific (Heller, 1878; Tokioka, 1961; Vasseur, 1967a). Indonesia (Sluiter, 1904?). Arafura Sea (Tokioka, 1952). Fiji (Herdman, 1881, 1882). Tahiti (Heller, 1878): Philippines (Van Name, 1918). Hawaii (Abbott *et al.*, 1997). Australia (Broome, Hartmeyer & Michaelsen, 1928).

Examined Material. Hong Kong (QM G12781 G12792 G12803 GH217, Kott & Goodbody, 1982). Queensland (Bowen, AMY1813, Kott, 1952).

Description

Specimens to 9 cm (see Herdman, 1906) in maximum dimension with tough, opaque test. Apertures, on conspicuous diverging siphons on upper surface about one-third of body width apart. Individuals white, laterally flattened in preservative. Dorsal tubercle large, occupying upper half of V-shaped peritubercular area, conspicuous slit with both horns spiralling in. Dorsal lamina with tusk-shaped, pointed, tapering languets along edge of narrow membrane. Circular muscles surround each siphon. About nine of 16 radiating longitudinal atrial muscles and ten of about 21 branchial ones cross one another in upper half of each side terminating over distal limb of gut loop on left and anterior to gonad on right. Branchial folds about eight or nine per side. On each side two or three internal longitudinal vessels between dorsal fold and dorsal midline. Anal rim smooth, bilabiate or only slightly indented.

Branched testis follicles along each side of long, straight or slightly sinuous ovarian tube. Single duct from each clump of testis follicles crosses surface of ovary to join central vas deferens, which opens on small papilla near large opening of female duct. Sometimes clumps of testis follicles crowded together forming a continuous band around periphery of ovary; but often isolated from each other, or irregularly distributed.

Remarks

Sluiter's (1904) material from Indonesia (especially the specimens with transparent test) and from the West Indian Ocean and South Africa (Sluiter, 1898a, 1905a,b) could be either the present species or *H. momus* (known from the same geographical range). *Herdmania momus* is known only from tropical locations, however, while the present species has been recorded further north to Japan and Taiwan. From South Africa, Herdman (1881, 1882) has reported specimens like the present species with similar gonads, dorsal lamina, dorsal tubercle and smooth anal border; and it is probable that Michaelsen's (1934) specimen is conspecific, this being the only species known from South Africa. Tokioka (1961) has reported specimens with similar features from Noumea. Specimens 2.5 cm and 4.5 cm long from the Arafura Sea (Tokioka, 1949) have eight or more internal longitudinal vessels between the mid-dorsal line and the dorsal fold on each side as in *H. grandis*. Although this is a high number for *H. pallida*, gonads, dorsal tubercle and anal border are similar, suggesting that variations in the number of dorsal internal longitudinal vessels are greater than previously known.

Tokioka (1949, 1953, 1967) assigned specimens from Japan to *H. momus*, and though one (Tokioka, 1953; pl. 68 fig. 6, specimen 110) has a similar gonad, they all are said to have about 12 anal lobes which distinguishes them from the present species. From Sri Lanka, the large specimens of *Rhabdocynthis pallida*: Herdman (1906) appear to be correctly assigned to the present species. The holotype of *R. ceylonica* Herdman, 1906 from the same location, re-examined by Monniot & Monniot (1989), also has gonads, and a simple dorsal tubercle like the present species.

The present species most resembles *H. grandis*, having similar gonads, with a common vas deferens opening on the oviduct near the large female opening and lacking oviducal hood or membranes associated with the gonoducal openings. It has a smooth anal opening (which is rare in *H. grandis*), its dorsal tubercle has a double spiral opening (not convoluted as in *H. grandis*), dorsal languets are tusk-like rather than laterally flattened (as in *H. grandis*), longitudinal body muscles are confined to the body wall anterior to the gonads (rather than occupying the whole side of the body as in *H. grandis*) and testis follicles are around the periphery of the ovary, sometimes in clumps (rather than on top of the ovary as in *H.*

Figure 5. *Herdmania inflata* (A, USNM 6037): A, distal portion of right gonad. *Herdmania pallida* (B, E, QM G12803; C, QM 12792; D, AM Y1813): B, body from left side showing muscles; C, portion of dorsal lamina; D, E, gut loops and gonads. Scale bars: B, D, E = 5.0 mm; A, C = 1.0 mm.

grandis). On rare occasions (see Tokioka, 1952) there are as many as eight internal longitudinal vessels between the dorsal mid-line and the dorsal fold as in *H. grandis*, although this is exceptional.

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REFERENCES

- Abbott DP, Newberry AT, Morris KM. 1997.** 6B, Ascidians (Urochordata). In: Lambert G, ed. *Reef and shore fauna of Hawaii i-viii*, pp. 1–64. Honolulu: Bishop Museum Press.
- von Drasche R. 1884.** Ueber einiger neue und weniger Gekannte aussereuropaische einfach ascidien. *Denkschriften Akademie Wissenschaftlichen Wien* **48**: 369–387.
- Hartmeyer R. 1906.** Ein Beitrag zur Kenntnis der japanischen Ascidiensfauna. *Zoologischer Anzeiger* **31**: 1–30.
- Hartmeyer R. 1909–11.** Ascidien (continuation of work by Seeliger). In: Bronn HG, ed. *Klassen und Ordnungen des Tierreichs*, Vol. 3. suppl. part 89–98. Leipzig: Winter CF, pp. 1281–1772 (Abstract, repeating lists of species, by Schepotieff, A 1911. *Archives für Naturgeschichte* **6**, 3–27.)
- Hartmeyer R, Michaelsen W. 1928.** Ascidae Diktyobranchiae und Ptychobranchiae. *Fauna Südwest-Australien* **5**: 251–460.
- Hastings AB. 1931.** Tunicata. *Scientific Reports of the Great Barrier Reef Expedition 1928–29*. **4** (3): 69–109.
- Heller C. 1878.** Beiträge zur nahern Kenntnis der Tunicaten. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften Wien* **77** (1): 2–28.
- Herdman WA. 1881.** Preliminary report on the Tunicata of the Challenger Expedition. Cynthiidae; Molgulidae. *Proceedings of the Royal Society of Edinburgh* **11** (3): 52–88. **11** (4): 233–240.
- Herdman WA. 1882.** Report on the Tunicata collected during the voyage of H.M.S. *Challenger* during the years 1873–76. Part I, Ascidae simplices. *Report on the Scientific Results of the Exploring voyage of H. M. S. 'Challenger' during the years 1875–1876, Zoology* **6**: 296pp., 37 plates.
- Herdman WA. 1886.** Report on the Tunicata collected during the voyage of H.M.S. *Challenger* during the years 1873–76. Part II, Ascidae compositae. *Report on the Scientific Results of the Exploring voyage of H. M. S. 'Challenger' during the years 1875–1876, Zoology* **14** (38): 1–425.
- Herdman WA. 1891.** A revised classification of the Tunicata, with definitions of the orders, sub-orders, families, sub-families and genera, and analytical keys to the species. *Journal of Linnean Society London Zoology* **23**: 558–652.
- Herdman WA. 1899.** Descriptive catalogue of Tunicata in the Australian Museum. *Australian Museum Catalogue* **17**: 1–139.
- Herdman WA. 1906.** Report on the Tunicata. *Ceylon Pearl Oyster Fisheries suppl. rept.* **39**: 295–348.
- Kennett CVD. 1997.** Isolation and characterisation of genes expressed during embryogenesis of the ascidian *Herdmania Curvata*. PhD Thesis, University of Queensland. Brisbane, Australia.
- Kott P. 1952.** Ascidians of Australia 1. Stolidobranchiata and Phlebobranchiata. *Australian Journal of Marine and Freshwater Research* **3** (3): 206–333.
- Kott P. 1957.** The sessile Tunicata. *Scientific Report John Murray Expedition* **10** (4): 129–150.
- Kott P. 1964.** Stolidobranch and phlebobranch ascidians from the Queensland coast. *Papers from the Department of Zoology, University of Queensland* **2** (17): 127–152.
- Kott P. 1966.** Ascidians of northern Australia. *Papers from the Department of Zoology, University of Queensland* **2** (15): 279–304.
- Kott P. 1972a.** The ascidians of South Australia I. Spencer Gulf, St Vincent Gulf and Encounter Bay. *Transactions of the Royal Society of South Australia* **96** (1): 1–52.
- Kott P. 1972b.** The ascidians of South Australia II. Eastern Sector of the Great Australian Bight and Investigator Strait. *Transactions of the Royal Society of South Australia* **96** (4): 165–196.
- Kott P. 1976.** Ascidian fauna of Western Port Bay, Victoria and a comparison with that of Port Phillip Bay. *Memoirs of the National Museum of Victoria* **37**: 53–96.
- Kott P. 1981.** The ascidians of the reef flats of Fiji. *Proceedings of the Linnean Society of New South Wales* **105** (3): 147–212.
- Kott P. 1985.** The Australian Ascidiacea Part 1, Phlebobranchia and Stolidobranchia. *Memoirs of the Queensland Museum* **23**: 1–440.
- Kott P. 1998.** Tunicata. In: Wells A, Houston W.W.K, eds *Zoological Catalogue of Australia, Hemichordata, Tunicata, Cephalochordata, Vol. 34*. pp. 51–252, 259–261 (App. I-III), 265–292 (Index). Melbourne: CSIRO Publishing.
- Kott P, Goodbody I. 1982.** The ascidians of Hong Kong. In: Morton BS, Tseng CK, eds *Proceedings of the First International Marine Biological Workshop: the flora and fauna of Hong Kong and Southern China, Hong Kong, Vol. 1*. pp. 503–554. Hong Kong: University Press.
- Lahille F. 1888.** Etude systématique des tuniciers. *Comptes Rendus Hebdomadaires des sciences de l'Académie des Sciences* **1887** (2): 667–677.
- Lambert G, Lambert CC. 1987.** Spicule formation in the solitary ascidian *Herdmania momus*. *Journal of Morphology* **192**: 145–159.
- Lowenstam HA, Abbott DP. 1975.** Vaterite: a mineralisation

- product of the hard tissues of a marine organism (Ascidacea). *Science N.Y.* **188**: 363–365.
- Michaelsen W. 1905.** Revision von Heller's Asciden-Typen aus dem Museum Godeffroy. *Zoologische Jahrbücher (suppl.)* **8**: 71–120.
- Michaelsen W. 1908.** Die Pyuriden (Halocynthiiden) des Naturhistorischen Museums zu Hamburger. *Mitteilungen Zoologische Museum Hamburger.* **25** (2): 227–287.
- Michaelsen W. 1918a.** Die Ptychobranchen und Diktyobranchen Asciden des westlichen Indischen Ozeans. *Jahrbuch der Hamburgischen. Wissenschaftlichen Anstalten* **35** (2): 1–71.
- Michaelsen W. 1918b.** Expedition S.M. Schiff 'Pola' in das Rote Meer nördliche und südliche halfte 1895–96–1897/98 zoologische Ergebnisse, xxxii Ascidia Ptychobranchia und Dictyobranchia des Rote Meeres. *Denkschriften Akademie Wissenschaftlichen Wien* **95**: 1–120.
- Michaelsen W. 1921.** Asciden vom westlichen Indischen Ozean aus dem Reichsmuseum zu Stockholm. *Arkiv för Zoology* **13** (23): 1–18.
- Michaelsen W. 1934.** The ascidians of the Cape Province of South Africa. *Transactions of the Royal Society of South Africa* **22** (2): 129–163.
- Michaelsen W, Hartmeyer R. 1927.** Zur Kenntnis phlebobranchiata und diktyobranchiata Asciden. *Mitteilungen Zoologische Museum Berlin* **13**: 159–196.
- Millar R.H. 1960.** Ascidiacea. *Discovery Reports* **30**: 1–160.
- Millar R.H. 1963.** Australian ascidians in the British Museum (Natural History). *Proceedings of the Zoological Society London* **141** (4): 689–746.
- Millar R.H. 1966.** Ascidiacea, Port Phillip Survey. *Memoirs of the National Museum of Victoria* **27**: 357–375.
- Millar R.H. 1975.** Ascidians from the Indo-West Pacific region in the Zoological Museum, Copenhagen (Tunicata, Ascidiacea). *Steenstrupia* **3** (20): 205–336.
- Monniot C. 1989.** Ascidies de Nouvelle-Calédonie VI. Pyuridae et Mogulidae. *Bulletin du Muséum National d'Histoire Naturelle, Paris Série 4.* **11A** (3): 475–507.
- Monniot C. 1992.** Ascidies de Nouvelle-Caledonia XI. Phlébobranches et Stolidobranches Du Plateau Chesterfield. *Bulletin du Muséum National d'Histoire Naturelle, Paris Série 4.* **14A** (1): 1–22.
- Monniot C, Monniot F. 1989.** Ascidies (*Musorstom* 1 & 2). In: Forest J, ed. *Resultats Des Campagnes Musorstom, Vol. 4. Mémoires du Muséum National d'Histoire Naturelle, Paris* **143** (A): 229–245.
- Monniot C, Monniot F. 1991.** Tunicata: peuplement d'ascidies profondes en Nouvelle-Calédonie, diversité des stratégies adaptatives. In: Crosnier A, ed. *Resultats Des Campagnes Musorstom, Vol. 8. Mémoires du Muséum National d'Histoire Naturelle* (1) **151** (A): 357–448.
- Monniot F, Monniot C. 2001.** Ascidians from the tropical western Pacific. *Zoosystema* **23** (2): 201–388.
- Nishikawa T. 1991.** The ascidians of the Japan Sea II. *Publications of the Seto Marine Biology Laboratory* **35** (1–3): 25–170.
- Rho Boon Jo. 1975.** Study on the classification and the distribution of the marine benthic animals in Korea 3, ascidians. *Journal of the Korean Research Institute for Better Living* **15**: 121–169.
- Savigny J.C. 1816.** *Mémoires sur les Animaux sans Vertèbres. Part 2.* Paris 1–239.
- Sluiter C.P. 1885.** Ueber einige einfachen Asciden von der Insel Billiton. *Natuurkundig Tijdschrift voor Nederlandsch Indië* **45**: 160–232.
- Sluiter C.P. 1890.** Die Evertebraten aus der Sammlung des königlichen Naturwissenschaftlichen Vereins in niederländisch Indien in Batavia. *Natuurkundig Tijdschrift voor Nederlandsch Indië* **50**: 329–348.
- Sluiter C.P. 1895.** Tunicaten. In Semon R. *Zoologische Forschungsreisen in Australien und den Malagischen Archipel. Denkschriften der Medizinisch-Naturwissenschaftlichen Gesellschaft zu Jena* **8**: 163–186; Nachtrag zu den tunicaten, 325–326.
- Sluiter C.P. 1898a.** Beiträge zur Kenntnis der Fauna von Sudafrica II. Tunicaten. *Zoologische Jahrbücher Abtheilung für Systematik, Geographie, und Biologie der Thiere* **11**: 1–64.
- Sluiter C.P. 1898b.** Tuniciers réunis en 1896 par la Chazalie dans la Mer des Antilles. *Mémoires de la Société Zoologique de France* **11**: 5–34.
- Sluiter C.P. 1904.** Die Tunicaten der Siboga-Expedition. Part I, Die sozialen und holosomen Asciden. *Siboga Expeditie* **56A**: 1–126.
- Sluiter C.P. 1905a.** Tuniciers réunis en 1904 par M. Ch. Gravier dans la Golfe de Tadjourah (Somalie Française). *Bulletin du Muséum d'Histoire Naturelle, Paris* **11**: 100–103.
- Sluiter C.P. 1905b.** Tuniciers réunis en 1904 par M. Ch. Gravier dans le Golfe de Tadjourah (Somalie Française). *Mémoires de la Société Zoologique de France* **18**: 5–21.
- Tokioka T. 1949.** Contributions to the Japanese ascidian fauna II. Notes on some ascidians collected chiefly along the coast of Kii Peninsula. *Publications of the Seto Marine Biological Laboratory* **1** (2): 39–64.
- Tokioka T. 1952.** Ascidians collected by Messrs Renzi Wada and Seizi Wada from the Pearl Oyster bed in the Arafura Sea in 1940. *Publications of the Seto Marine Biological Laboratory* **2** (2): 91–142.
- Tokioka T. 1953.** *Ascidians of Sagami Bay.* Tokyo: Iwanami Shoten.
- Tokioka T. 1961.** Ascidians collected during the Melanesia Expedition 1, Ascidians presented by Dr R.L.A. Catala of the Aquarium of Noumea. *Publications of the Seto Marine Biological Laboratory* **9** (1): 104–138.
- Tokioka T. 1967.** Pacific Tunicata of the United States National Museum. *Bulletin of the United States National Museum* **251**: 1–242.
- Traustedt M.P.A. 1883.** Vestindiske Ascidae Simplices. Anden Afdeling. Mogulidae og Cynthiadae. *Videnskabelige Meddelelser fra den naturhistorisk Forening i Kjöbenhavn* **1882**: 108–136.
- Traustedt M.P.A. 1885.** Ascidae simplices far det Stille Ocean. *Videnskabelige Meddelelser fra den naturhistorisk Forening i Kjöbenhavn* **1884**: 1–160.
- Van Name W.G. 1918.** Ascidians from the Philippines and

- adjacent waters. *Bulletin of the United States National Museum* **100** (1): 49–174.
- Van Name WG. 1921.** Ascidians of the West Indian region and south eastern United States. *Bulletin American Museum Natural History* **44**: 283–494.
- Van Name WG. 1930.** The ascidians of Porto Rico and the Virgin Islands. *Scientific Survey of Puerto Rico* **10** (4): 403–512.
- Van Name WG. 1945.** The North and South American ascidians. *Bulletin American Museum Natural History* **84**: 1–476.
- Vasseur P. 1967a.** Contribution a l'étude des ascidies de l'Île Maurice (Archipel des Mascareignes, Océan Indien). *Recueil des Travaux Station marine d'Endoume Fasc. hors ser. suppl.* **6**: 101–139.
- Vasseur P. 1967b.** *Ascidies de Nouvelle Calédonie*. Paris: Édition de la Fondation Singer-Polignac.