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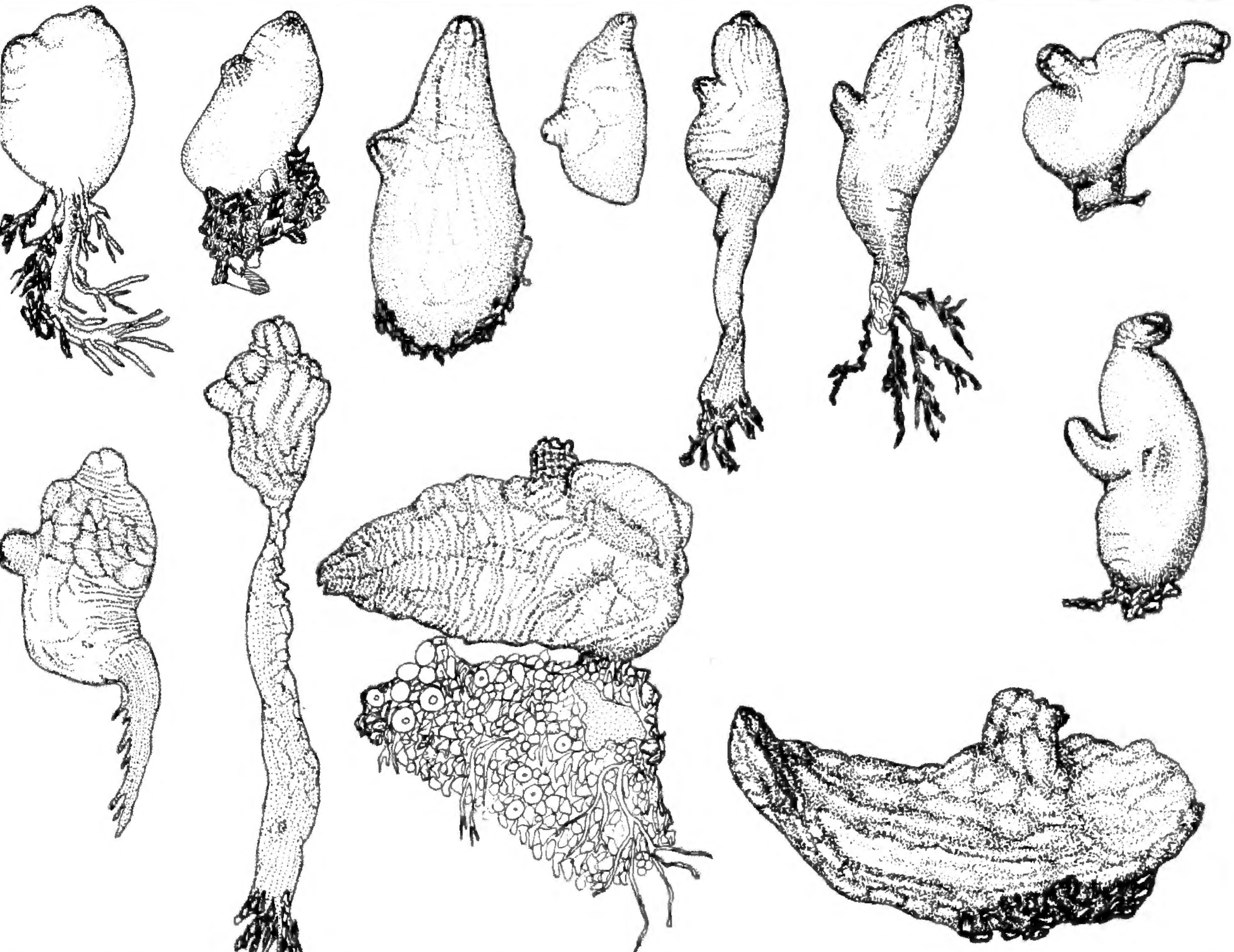

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THE AUSTRALIAN ASCIDIACEA
PART I, PHLEBOBRANCHIA AND STOLIDOBRANCHIA

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ABSTRACT

In the primarily solitary suborders of the Ascidiacea (Phlebobranchia and Stolidobranchia), 195 species in 37 genera and 8 families are now known to occur around the Australian continent. Included are 47 species new to science and 29 species not previously known to occur in these waters. Relatively few species of the known Indo-West Pacific fauna have not been recorded from Australian waters. Some of the less common and often monotypic genera known from the northern hemisphere are not represented; nor are some genera of the Polyzoinae from the Antarctic and Subantarctic, and abyssal and some interstitial genera.

Review and revision of familial and generic characters and relationships form the basis for dichotomous keys to all taxa. General intrageneric trends in morphology, including species groupings in the more diverse genera, are reflected in the keys and tables. In addition to newly recognized phylogenetically significant characters, adaptations (sometimes convergent) for particular habits and habitats are apparent. Adaptations observed in *Ascidia* spp. include internal ridges of the test that project into the body to hold it firmly in place. In *Polycarpa*, the tendency to a viviparous habit is reflected in a new species in which tailed larvae are incubated in the atrial cavity and another (like *P. tinctor*) in which direct developing embryos are brooded. Certain *Molgula* spp. are also viviparous. It is possible that viviparity in these genera and in the Polyzoinae contributes to their isolation in temperate waters to account for their relatively high numbers of indigenous species. A new solitary genus of the Plurellidae (Phlebobranchia) has family characteristics of an accessory branchial fold, secondary openings of the neural gland, gonads and heart embedded in the test, and separation of male and female components of the gonad and a reduction in their size (suggesting a primarily colonial habit for the family).

The biogeography of the fauna is affected by the Australian continent which appears to act as a bridge between tropical and temperate waters. The geographic position of Australia, in the centre of the Indo-West Pacific tropical region, appears to have influenced the fauna around the whole of the continent. Species of Indo-West Pacific range dominate the tropical fauna. Temperate fauna is relatively diverse, and includes tropical species in the southern part of their range, indigenous species (many probably isolated from tropical ancestors) and a relatively few species with temperate to subpolar affinities.

Keywords: Indo-West Pacific, Ascidiacea, Phlebobranchia, Stolidobranchia, viviparous, biogeography

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INTRODUCTION

The first collections of the class Ascidiacea from Australian waters were made principally across the southern coast at the beginning of the nineteenth century by the French expedition of l'Astrolabe. Quoy and Gaimard (1834) reported on these collections. The first large collections from the southern and eastern coasts of the continent were the Challenger collections, reported on by Herdman (1882, 1886). A small Australian Museum collection, mainly from Port Jackson, was reported on by Herdman (1899).

The first major collection from the tropical Western Pacific was made by the Siboga expedition at the turn of the century. The Siboga materials, which are from shallow reefal as well as from inter-reefal locations, are the basis for the study of the taxonomy of the Australian tropical Ascidiacea. As such, they emphasise that the northern coast of the continent is part of the Indo-West Pacific region. The Great Barrier Reef Expedition (1927–28) made a relatively small collection from Low Isles that was reported on by Hastings (1931).

The Swedish (Mortensen) expedition to north-western Australia (Hartmeyer 1919) and the German expedition to south-western Australia (Hartmeyer and Michaelsen 1928, 1930) made the first collections of any size from the western coast, substantially adding to the growing list of species known from Australia. Millar (1963) reported on a small collection of Australian material in the British Museum.

However, the status of taxonomic understanding of fauna is not always greatly advanced when it is assessed from necessarily limited samples, isolated from their populations and habitats. Further, with the sole exception of the Australian Museum collection (Herdman 1899), the type material of the Australian species taken by these visiting expeditions reposed in European museums, and easy reference to it was either impossible, or at best frustrating, for workers resident in Australia.

The collections from the south-western coast reported on by Hartmeyer and Michaelsen (1928, 1930) were the last to be made by visiting European expeditions. The maturing scientific institutions of Australia did not produce an indigenous expert on this group until the present author began her studies (Kott 1952–84). Her earlier works suffered from a lack of perspective resulting from inadequate collections, difficulty of access to type material, and the need to give identification priority over systematic taxonomic reviews.

The present volume, the first of a major review of the taxonomy of species of the Ascidiacea occurring in Australia, reports on the suborders Phlebobranchia and Stolidobranchia. There are 195 species now recorded from Australian waters, of which 47 are new to science and 29 are new records for these waters. All species are fully described and all records are summarised. In each case complete synonymy is given and relationships are discussed. Related species in each of the genera represented are grouped in summary tables which set out their principal characters and geographic range. In the text, the genera and higher taxa are arranged phylogenetically, while the species in each genus are arranged alphabetically. Dichotomous keys are given as aids to identification for all Australian species and all higher taxa. The phylogeny of each higher taxon is discussed, as is its biogeography. Species recorded from the Indo-West Pacific but not yet reported from Australian waters are summarised. With only four exceptions — *Cnemidocarpa posthuma* Michaelsen, *Polyandrocarpa abjornseni* (Michaelsen), *Chorizocarpa michaelseni* (Sluiter) and *Pyura pantex* (Savigny) — species descriptions are based on the material examined rather than on previously published accounts. Museum registration numbers are given for all the new and previously recorded material, including type specimens, that has been examined in connection with this work. The citation of a registration number indicates that the specimen has been examined.

The review is based on the examination of many thousands of specimens, including those in the collections of all Australian and some American and European museums. The author and her colleagues have added much new material from a wide range of habitats in the waters around the continent.

Abbreviations used to indicate the institutions in which specimens are lodged are as follows:

AM	Australian Museum, Sydney, New South Wales
BM	British Museum (Natural History), London, U.K.
MHN	Muséum Nationale d'Histoire Naturelle, Paris, France
OM	Otago Museum, Dunedin, New Zealand
QM	Queensland Museum, Brisbane, Queensland
SAM	South Australian Museum, Adelaide, South Australia
TM	Tasmanian Museum, Hobart, Tasmania
NMV	Museum of Victoria, Melbourne, Victoria
NTM	Northern Territory Museum, Darwin, Northern Territory
WAM	Western Australian Museum, Perth, Western Australia
USNM	U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.
ZMA	Zoological Museum of Amsterdam, Amsterdam, Netherlands
ZMC	Zoological Museum Copenhagen, Copenhagen, Denmark.

ACKNOWLEDGEMENTS

The author started working on the Ascidiacea in 1949. Since then, many people have helped her to continue her investigations.

The late Harold Thompson, the Chief of CSIRO Fisheries Division to 1955, gathered together the collection of Australian ascidians that now forms a large part of the collection of the Australian Museum, Sydney. The study of this collection under his guidance was my introduction to the group.

The University of Queensland, and especially Professor W. Stephenson of the Zoology Department, gave me the support and facilities to continue the work during the years of family commitments which did not permit me to hold a permanent institutional appointment. Also during this period, the U.S. National Museum of Natural History (Smithsonian Institution), through the late Dr Waldo Schmitt, made its whole collection of Antarctic Ascidiacea available for examination and report. It thereby vastly increased my appreciation of the diversity of the class and gave me a perspective from which to study the fauna of the Indo-West Pacific (including Australia).

Professor C. Burdon Jones of James Cook University of North Queensland has given generous support to the continuing programme over many years, as have my colleagues Dr D.P. Abbott (formerly of Hopkins Marine Station, Stanford University, California), Dr R.H. Millar of the Scottish Marine Biological Association's Laboratory at Oban, and Professor T. Tokioka of Seto Marine Biological Laboratory, Japan. Dr Millar especially, with his experience of the Ascidiacea in the southern hemisphere and in the Indo-West Pacific, has helped to overcome much of the isolation in which I would otherwise have had to work.

Professor J. Ryland (formerly of the Department of Natural Resources) and Dr U. Raj (Director, Institute of Marine Sciences), both of the University of the South Pacific, provided opportunities to collect in Fiji and thus ensured that a large collection of material from another part of the western Pacific became available for comparison with that from Australian waters.

My own institution, the Queensland Museum, through its Board and Director (Dr A. Bartholomai) has long been committed to this project, and has provided funds for travel and collecting. Its support and encouragement are gratefully acknowledged here.

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Shirley Slacksmith, Dr B. Wilson (Western Australian Museum); Mr S. Shepherd (South Australian Fisheries Department); Ms Jeanette Watson (Museum of Victoria); Miss Alison Green and her colleagues (Tasmanian Museum); Mr P. Last (Tasmanian Fisheries); Dr R. Day and Miss Isobel Bennett (Sydney University); Mr Neville Coleman (Sydney); Professor W. Stephenson, Dr H. Choat, Dr D.R. Robertson and Mr D. Parry (University of Queensland); Dr P. Saenger (Brisbane); Dr P. Arnold, Mr A. Birtles, Dr L. Hammond, Dr J. Ottaway, Mr C. Roberts (James Cook University of North Queensland); Mr E. Lovell (Australian Institute of Marine Science); and Dr Carden Wallace, Mr A. Rozefelds, and Ms Lucille Crevola-Gillespie (Queensland Museum). Mr D. Heald added new material from Western Australia; Mr H. Duyverman from South Australia; Mr A.J. Blackman and Mr D. Cropp from Tasmania.

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COLLECTING METHODS

The collections of new material were made by various methods, depending on habitat type and programmes, as follows:

1. Grab or dredge surveys in which the whole fauna down to specimens of 1 mm diameter were taken: Bass Strait, Moreton Bay, Abbot Point (NW of Bowen) and Cleveland Bay (Townsville).
2. SCUBA diving: Houtman's Abrolhos, Shark Bay, Cockburn Sound, eastern end of the Great Australian Bight, Spencer and St. Vincent Gulfs, Investigator Strait, Western Port, Deal Island (Bass Strait) Bruny I. (SE Tasmania), Heron I., Lizard Island and the northern Great Barrier Reefs up to Torres Strait.
3. Intertidal shore collecting: Cockburn Sound, Hervey Bay, Heron I. and other locations in the Capricorn Group, Green I. and Lizard I.
4. Trawl and sometimes dredge surveys: the north-west and north-east shelfs from the Arafura Sea to the Abrolhos and from Torres Strait to Townsville. (Large solitary individuals from sea floor habitats only are taken in these surveys. Smaller species are taken only if they are epibionts on the test of large stolidobranch ascidians).
5. Storm debris tossed up on beaches has been a source of data for some of the more common species, especially from Tasmania.

The ascidian faunas of Houtman's Abrolhos, Cockburn Sound, Spencer and St Vincent Gulfs, Investigator Strait, Western Port, Bass Strait, Moreton Bay, Heron Island, Abbot Point, Cleveland Bay and Lizard Island have been well sampled for most habitats. Other locations have not been subjected to the same collecting effort for all habitats. The diversity of species recorded for the well sampled locations may seem to be greater than at others. This is unlikely to be the case; however it does reflect the fact that the ascidian fauna of Australian waters is not yet adequately sampled. This view is further reinforced by the number of species that require description as new in every collection that is made.

FIELD IDENTIFICATION OF ASCIDIACEA

Living ascidians bear little resemblance to the preserved material. With the exception of a few rigid gelatinous species (e.g. *Phallusia* spp.), contraction of the body dramatically alters its size, shape, the appearance of the siphons and the appearance of the surface test, wrinkles and creases appearing that are not characteristic of the living organism. Even narcotisation does not restore the body to the fully expanded condition of the living specimen. Further, colours change with oxidation of blood pigments and are subsequently lost in preservative. The brilliant and often characteristic colours of the body wall visible in the siphonal lining of the living specimens are invariably lost following fixation of the material.

In the present work, the appearance of living specimens is recorded wherever possible. However, for many species this information is not available and the descriptions are of the preserved material only. Colour notes and colour photographs accompanying preserved specimens are essential to the full documentation of species characteristics and will, in due course, ensure that field identification is possible for all species.

ANNOTATED GLOSSARY

The morphology of phlebobranch and stolidobranch ascidians is discussed below, together with the terms used and conventions followed in this volume. Diagrams of the internal structure of generalised phlebobranch and stolidobranch ascidians are given in Figs 1 and 2. Morphology of the Ascidiacea has been reviewed by Berrill (1950) and briefly by Kott (in press). Goodbody (1974) has reviewed the physiology and Millar (1971) the biology of the group.

apertures: openings of the body to the exterior. The branchial aperture is the incurrent opening (mouth) through which water is drawn into the pharynx. Having passed through the stigmata and into the atrial cavity, the water moves out of the body as the excurrent stream through the atrial aperture.

The ascidian's interaction with the environment takes places entirely through the apertures. Their orientation to enhance this interaction and the devices they have evolved for the protection of the apertures are of paramount importance.

(a) The commonest adaptation to enhance the interactions of the organism with its environment is the differential growth of one side of one or both siphons, which causes them to curve, thereby affecting the orientation of the apertures. The branchial siphon is usually turned horizontally or ventrally towards the substrate; the atrial siphon is usually oriented away from both the branchial siphon and the substrate. The apparent advantages are that the open incurrent aperture is thereby protected from falling sediments, the incurrent and excurrent streams are separated, and the excurrent stream is projected above and away from the animal. Differential growth of one or the other side of the siphons occurs, especially in species with a firm, gelatinous test (e.g. *Phallusia*) and in species of Pyuridae with tough, leathery tests and well-developed siphons. It is even more marked in the stalked species in which both apertures are on the dorsal surface (e.g., *pachydermatina* group of the genus *Pyura*, and *Polycarpa clavata*).

Orientation of the apertures is also achieved by thickening of the test in certain areas as in *Pyura ostreophila*, *P. crassacapitata* n.sp. and *Molgula ficus* in which the apertures are at opposite ends of a dorsal intersiphonal ridge of test. In *Adagnesia opaca*, the branchial aperture is forced to open downward (to the right) by a thickened ridge of test above and to the left of it. A corresponding ridge causes the atrial aperture to face upwards, away from the substrate.

(b) *Ascidia scaevola* has unique cylindrical, sandy false siphons (a cylinder of test that projects upwards around each sessile aperture). This may be an adaptation for a species that may lie partly buried in the substrate.

(c) Certain species have test processes that are especially long and thick around the apertures (*Hartmeyeria formosa*, *Halocynthia* spp.), which serve to modify the external environment immediately in their vicinity. They may also, by camouflaging the open apertures, be a protective device. Solid or hollow lobes of test around the apertures in *Pyura sacciformis* and *Molgula sabulosa* probably have a similar function.

(d) In certain species of Agnesiidae and Molgulidae found free on sandy substrates, short muscle-bands around the apertures and around the dorsal and ventral borders of the body are adapted to withdraw the apertures into the body and flatten it so that the test along each side of the antero-dorsal mid-line comes together over the withdrawn apertures. The test in these species is invariably thin, but rigid with embedded sand, which is absent only from a median strip around and between the apertures. In *Rhodosoma turcicum*, the muscle-bands are modified so that a large anterior extension of the body wall and test on the right side folds down as a lid over the apertures.

(e) In most species of Ascidiidae, circular muscles are absent from the immediate border of the apertures, where longitudinal bands alternate with the light-sensitive ocelli around the rim. When the muscles contract, the muscle-free parts of the border stand out in a frill so that the ocelli remain exposed to the light.

(f) Structures inside the siphons, such as siphonal armature, valves (in *Microcosmus* spp.) and vela (especially in the Molgulidae), also affect the incurrent feeding stream and protect both incurrent and excurrent apertures.

ascending limb of gut loop: see **gut loop**

asexual reproduction: see **vegetative reproduction**

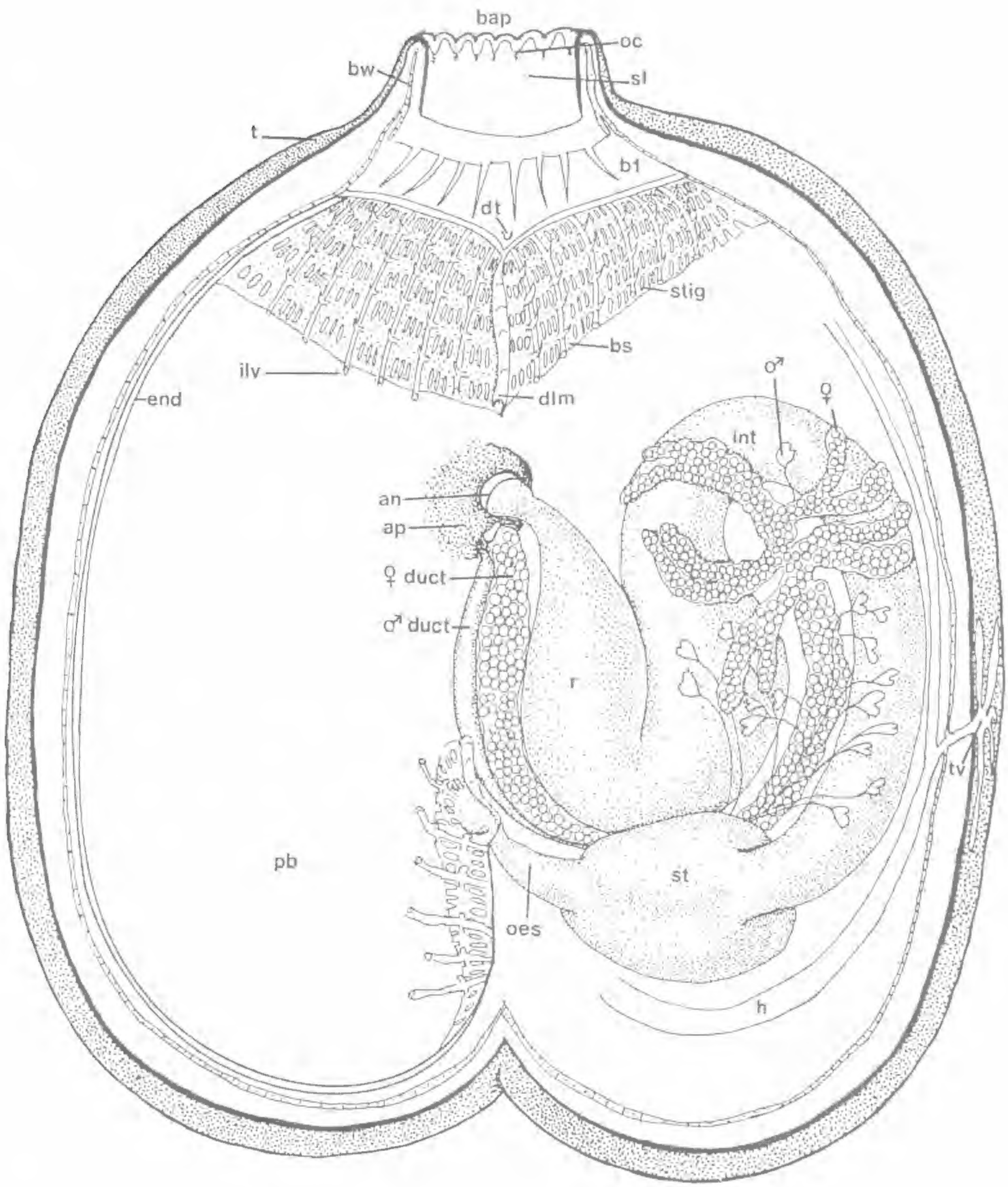


FIG. 1: Morphology of a phlebobranch ascidian (diagrammatic). The body is shown opened around the ventral mid-line (from the branchial aperture). The branchial sac has been largely removed to expose the peribranchial cavity and the organs embedded in the parietal body wall. (Symbols: **an**, anus; **ap**, atrial (excurrent) aperture; **b**, branchial tentacles (**b_1** simple; **b_2** branched); **bap**, branchial (incurrent) aperture; **bf**, branchial fold; **bs**, branchial sac; **bw**, body wall; **dct**, gonoduct; **dlm**, dorsal lamina; **dln**, dorsal languets; **dt**, dorsal tubercle (with opening of neural gland); **e**, endocarp (**e_1**, on gut; **e_2**, in gut loop); **end**, endostyle; **g**, gonad (♂ follicle, ♀ ovarian tube); **h**, heart; **ilv**, internal longitudinal branchial vessels; **int**, gut loop (**int_1** ascending limb; **int_2**, descending limb); **l**, liver diverticulum; **oc**, ocellus; **oes**, oesophagus; **pb**, peribranchial (atrial) cavity; **pg**, prebranchial (prepharyngeal) groove; **r**, rectum; **s**, siphonal spines; **sl**, siphonal lining; **st**, stomach; **stig**, stigmata (pharyngeal perforations); **t**, test; **tv**, test vessel; **vs**, ventral sinus).

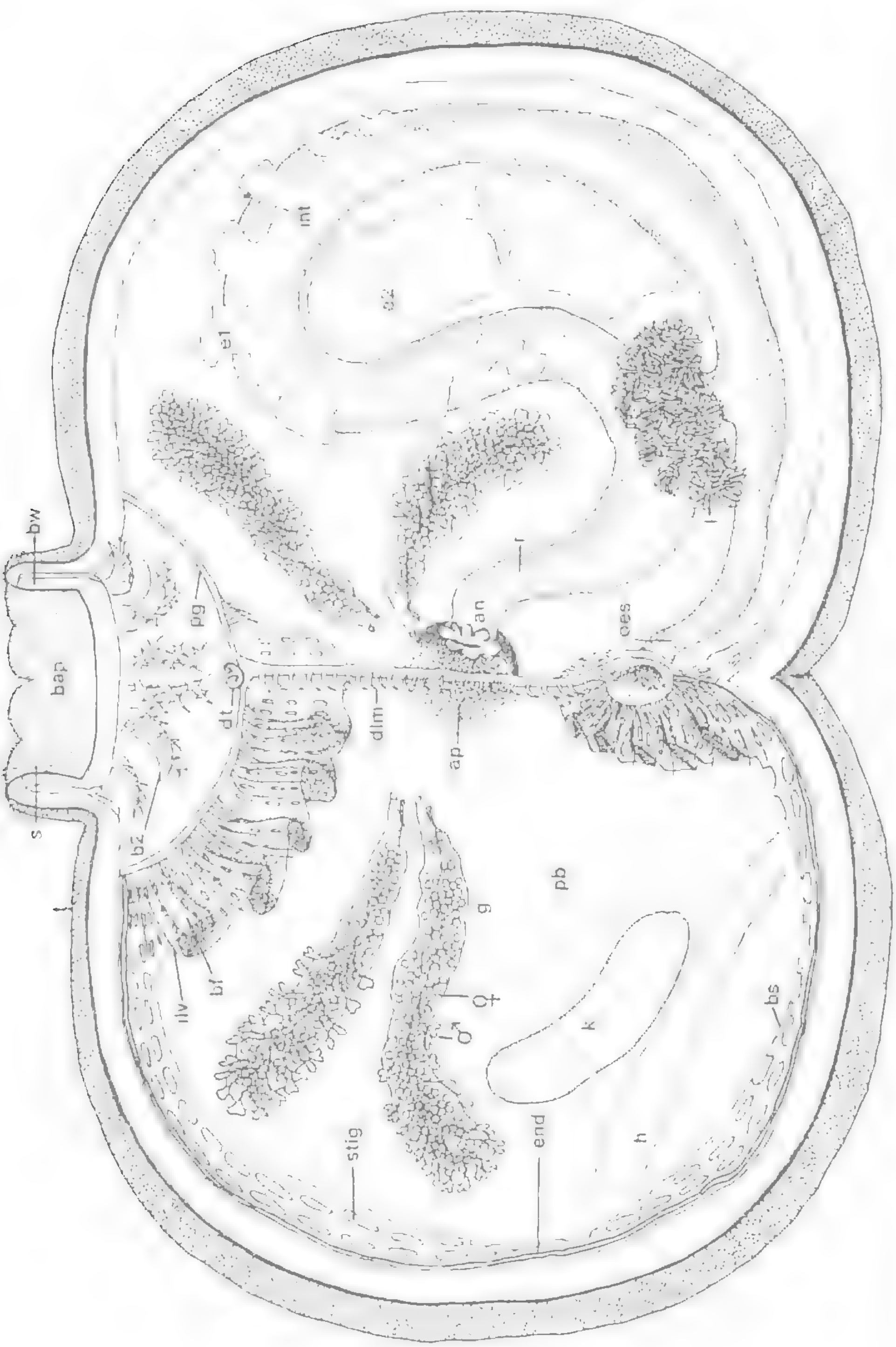


FIG. 2. Morphology of a composite stolidobranch ascidian, showing morphological characteristics of Styelidae, *Pyura* and Molgulidae (diagrammatic). The body is shown opened around the ventral mid-line (from the branchial aperture). The branchial sac has been largely removed to expose the peribranchial cavity and organs embedded in the parietal body wall. (For symbols used see Fig. 1)

atrial cavity: cavity around the dorsum and sides of the pharynx (into which the stigmata open), and which opens to the exterior by the dorsal atrial aperture. The cavity separates the pharynx from the parietal body wall. In the embryo, it develops from a pair of invaginations from the dorsal surface in the order Enterogona (Aplousobranchia and Phlebobranchia) and from a single median invagination in Pleurogona (Stolidobranchia).

branchial folds: longitudinal folds in the branchial wall that increase its filtration area. These are usually present in Stolidobranchia (Fig. 3). They are lost only in small vegetatively reproducing Polyzoinae and some small genera of the Molgulidae (e.g. *Eugyra, Pareugyrioides*). Branchial folds reach their greatest development in *Microcosmus*, where most of the branchial wall is thrown up into large, overlapping folds, up to 9 or 10 a side, with only a single internal longitudinal vessel present in the very narrow intervals between the folds.

In certain dorso-ventrally flattened, bottom-living phlebobranch species (*Ascidia scaevola* and family Plurellidae), which have a sandy, rigid test, the left side of the body is narrower than the right. However, the branchial sac remains at its primary diameter, the prepharyngeal groove curving across in front of the dorsal tubercle from the left to form a secondary branchial fold that accommodates the narrowed body wall (see Kott 1972c).

branchial formulae: conventional means of recording the numbers of internal longitudinal branchial vessels (in species with branchial folds); or the numbers of stigmata between the internal longitudinal branchial vessels (in species without branchial folds). In the former, the number of vessels on each fold is recorded in parentheses. In species without branchial folds, the numbers of stigmata between the longitudinal vessels are separated by a comma (representing the longitudinal vessel). Counts are made on the open branchial sac from the endostyle (E) to the dorsal lamina (DL) on the right side of the body and from the dorsal lamina to the endostyle on the left side of the body.

branchial papillae: papillae vertical to the plane of the branchial wall that support the internal longitudinal vessels at their junctions with the transverse vessels. They occur in the Phlebobranchia. These often project into the lumen, beyond the level of the internal longitudinal vessels, as spoon or sickle-shaped, free-standing papillae. Occasionally intermediate papillae are present on the internal longitudinal vessels between the transverse vessels (*Ascidia thompsoni, A. archaia*).

branchial sac: the pharynx of an ascidian (Fig. 3), perforated by rows of stigmata (see also **branchial formulae, branchial papillae, internal longitudinal vessels, infundibula**).

branchial tentacles: endodermal structures, either simple and tapering, or crescent-shaped with side branches. These are arranged on a ring muscle around the base of the branchial siphon.

budding: see **vegetative reproduction**

caecum: a hollow, blind-ended diverticulum (see **stomach caecum**).

descending limb of gut loop: see **gut loop**

distal: the end of an organ or structure toward which the contents or products move or which is farthest from the base or point of attachment. (See also **proximal**)

dorsal lamina: a fold of branchial wall along the mid-dorsal line of the pharynx. This is usually curved over to the right to guide the rod of food-enmeshed mucus posteriorly into the oesophagus, which is at the posterior end of the dorsal lamina. In species of the family Ascidiidae the dorsal lamina is often double anteriorly. (See also **dorsal languets**)

dorsal languets: small pointed projections usually in a single row along the dorsal mid-line. These take the place of the dorsal lamina in certain genera of the Pyuridae, Perophoridae and Agnesiidae.

dorsal tubercle: a small, flat cushion, protruding into the pharynx in the dorsal mid-line anterior to the prepharyngeal groove, onto which the duct of the neural gland opens. The opening is usually a narrow, ciliated slit which varies from simple to curved to convoluted, and sometimes interrupted to form many punctate openings or short slits (see also **neural gland**).

endocarps: thickenings or projections, usually richly supplied with blood vessels, from the parietal body wall into the atrial cavity. They are often found over the gut and gonads, and in the gut loop. They are present only in stolidobranch ascidians (Styelidae and Pyuridae) and may be involved in the excretory process (see Goodbody 1974).

The endocarps often appear to be localised thickenings of the body wall into which the gonads expand as they mature, and where they are afforded protection when they project into

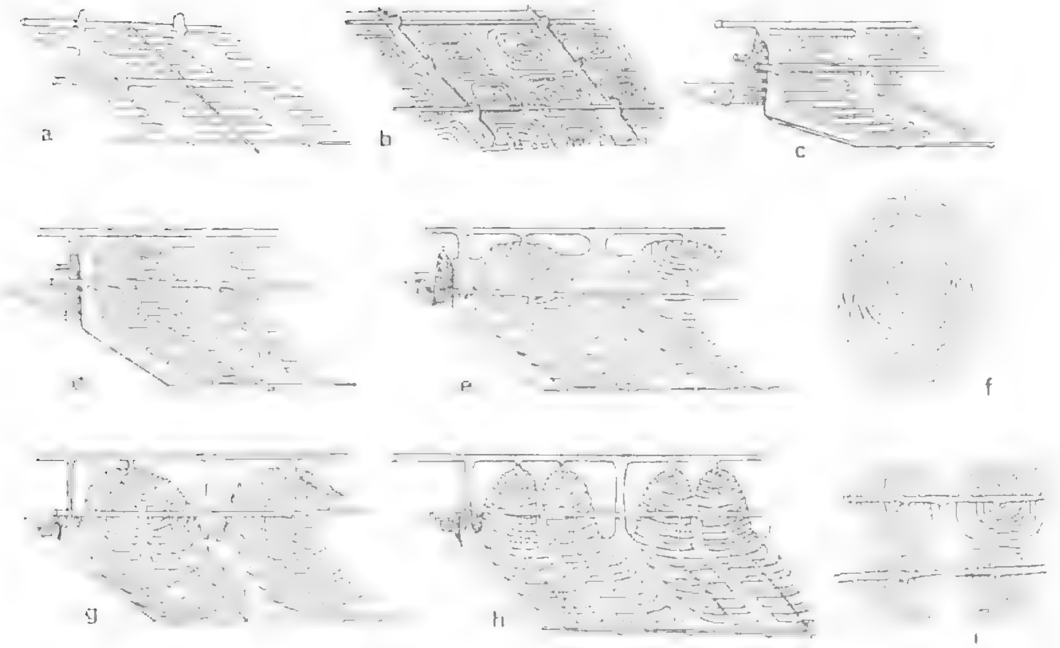


FIG. 3: Portions of branchial sacs of phlebobranch and stolidobranch ascidians (diagrammatic) — **a**, flat, without folds, internal longitudinal vessels supported by upright papillae, stigmata crossed by a parastigmatic vessel (Ascidiidae); **b**, flat sac, without folds, stigmata spiral (Corellidae, Agnesiidae); **c**, a branchial fold (Styelidae, Pyuridae), no parastigmatic vessels; **d**, stigmata curved (*Microcosmus* spp.), mesh crossed by a parastigmatic vessel; **e**, stigmata subdivided, curved at each end to form incipient infundibula, stigmata in the edge of the fold spiral (*Hartmeyeria, Ctenicella, Mogula* spp.); **f**, view of top of infundibula from (**e**); **g**, stigmata spiral around well developed infundibula (*Molgula* spp.), parastigmatic (radial) vessels present; **h**, infundibula subdivided (*Molgula* spp.); **i**, no branchial folds, 2 stigmata spiral together around conical infundibula with an internal longitudinal vessel along the top of the cones (*Eugyra* spp.).

the atrial cavity from the body wall (as in most Pyuridae for example). In Styelidae, the rather thin, leaf-like endocarps standing upright, projecting vertically into the atrial cavity from the body wall between and around the gonads may also have a protective function. They are present especially in those species of *Polycarpa* in which the gonads are only lightly attached and project into the atrial cavity (e.g. *Polycarpa papillata*). They are largely absent when the gonads are completely embedded (as in most species of the *pedunculata* group). These tall, crowded and projecting endocarps may also dissipate the course of the excurrent ciliary stream as it passes through the atrial cavity and thereby delay the release of gametes. The fact that they are especially tall and crowded around the internal opening of the atrial aperture in certain species (e.g. *Polycarpa chinensis*) supports this hypothesis, especially since the arrangement of gonads around the ventral border of the body suggests a tendency toward viviparity. Related members of the same species group (*P. tinctor, P. tinctorella* n.sp.) are viviparous (see *Polycarpa*).

Endocarps enclosed in the gut loop are either crowded and leaf-like or large and flat-topped (Styelinae generally). Their function appears to be to stabilise the gut loop, especially when it is not deeply embedded in the body wall.

endostyle: a deep groove along the ventral mid-line of the branchial sac lined with ciliated glandular epithelium which secretes the mucus that is moved up over the branchial wall (by ciliary action) to the dorsal lamina. This mucous sheet strains food particles from the water that passes through the stigmata. The endostyle has an iodine-binding capacity, which suggests its homology with the vertebrate thyroid gland (Goodbody 1974).

epicardium: paired sacs from each side of the posterior end of the dorsal mid-line of the pharynx that project back alongside the heart and internal organs in certain Aplousobranchia, in which they are involved in the vegetative process. In phlebobranch and stolidobranch ascidians, the sacs are embryonic, only vestiges of them remaining as excretory organs in the adult organism. (See Berrill 1950, also **excretory vesicles, kidney**).

excretory vesicles: vestiges of the embryonic epicardial sacs, present in phlebobranch and stolidobranch ascidians (with the exception of Perophoridae). (See Berrill 1950; also **epicardium, kidney**).

excurrent aperture, — stream: see **apertures**

gastric caecum: see **stomach caecum**

gastric reservoir: a spherical or oval expansion in the gastro-intestinal duct halfway between the stomach and the descending limb of the gut loop. It is present in *Rhodosoma* and the Perophoridae.

gastro-intestinal connective, — duct: the fine duct from the tubules of the pyloric gland that surround part of the descending limb of the gut loop. The duct opens into the ascending limb at the pyloric end of the stomach.

gonads: usually hermaphrodite with male and female ducts usually opening together. Male and female components are separated only in Plurellidae, one species each of *Polycarpa* (*P. tinctorella* n.sp.) and *Perophora* (*P. hutchisoni*), Botryllinae and in some genera of the Polyzoinae. There is usually only a single gonad, enclosed in the gut loop, in Phlebobranchia. In Pyuridae and Molgulidae there is a single gonad on each side of the body. In *Pyura* each gonad is subdivided into separate rounded or cuboid sacs on each side of common male and female ducts. *Styela* and *Cnemidocarpa* have several long sometimes branched gonads on each side. In *Polycarpa* and Polyzoinae there are usually numerous short gonads scattered over the body wall on each side.

The ovary is invariably sac like or tubular. Testis follicles are usually small, often branched, and very numerous. They spread out in the body wall over the gut loop in large solitary Phlebobranchia, but are clustered around the ovary in most other groups. In Styelidae the male follicles are around or beneath (lateral to), and sometimes partially surrounded by, the ovary. In Molgulidae they surround all or some part of the border of the ovary and in the Pyuridae they are most often on the mesial surface of the ovary.

The male follicles associated with each ovary are larger and less numerous in the genus *Polycarpa*, a trend that culminates in species with one or two male follicles with each ovary as in *Monandrocarpa* (Styelinae) and genera of the Polyzoinae. In most colonial species, the reduction in number of male follicles and increase in their relative size is marked, and occurs in colonial phlebobranchs (Perophoridae and *Plurella*) as well as stolidobranchs. It may be an economy that is compensated for by replication either of the gonads (*Polycarpa*) or of the zooids (colonial species). In *Microgastra* n.gen., a solitary genus of the Plurellidae, there is a single large male follicle as in *Plurella*, which suggests that the solitary condition in this family is a secondary rather than a primary characteristic.

The long gonads of most solitary Phlebobranchia, Pyuridae and some species of Molgulidae open by short ducts near the anus at the internal opening of the atrial aperture. The short gonads of *Polycarpa* and Polyzoinae also have short ducts, and their openings are usually distant from the atrial aperture, which reflects a tendency toward viviparity in that genus (see **endocarps** and *Polycarpa*). A similar tendency is apparent in certain *Molgula* spp. with short gonads, gonoducts opening distant from the atrial aperture and oviducts sometimes turned ventrally away from the atrial aperture, ensuring retention of eggs in the atrial cavity. In the viviparous Perophoridae, the ovary is small and sac-like. Long gonoducts extend dorsally before diverging, the oviduct turning over onto the right side of the atrial cavity (rather than towards the atrial aperture), where it acts as a brood-pouch for developing embryos. *Perophora hutchisoni* is an exception, the ovary being near the mid-dorsal line, separated from the testis follicles. The oviduct is accordingly much reduced in length. In Plurellidae, the sac-like ovaries are also present dorsally, around the postero-left side of the atrial opening and well separated from the testis. Their short oviducts open directly into the atrial opening together with the openings of the rather long vas deferens. Short oviducts opening near the atrial opening have a possible advantage in ensuring rapid release of the ova.

The male and female components of the gonads are separated from one another in many viviparous forms, possibly as a device to avoid self fertilisation. Certain genera of the Polyzoinae have ovaries present on one side only (either with or without associated male gonads), thereby ensuring that developing embryos are confined to one side of the peribranchial cavity. Ovaries are present only on the right side and are separate from the testis in the small, viviparous, direct developing *Polycarpa tinctorella* n.sp.

Many *Molgula* spp. have vas deferens and oviducal openings far removed from one another or turned in opposite directions. This is also a likely device to avoid self-fertilisation. In certain species of *Molgula* (*M. calvata* and *M. manhattensis*), the male duct has numerous short openings along the length of the ovary. In *Pyura littoralis* (and no other known species), the female duct is subdivided into numerous short openings. The former adaptation can only be associated with a quick release of male gametes into the atrial cavity. The latter is very likely a device for retention of ova in the atrial cavity, as in *Polycarpa*.

gut loop: In phlebobranch and stolidobranch ascidians, the gut loop is embedded in the parietal body wall, usually to the left, but sometimes to the right (Corellidae), of the pharynx. It consists of an ascending (proximal) limb (the oesophagus, stomach and proximal part of the intestine) and a descending (distal) limb (distal part of the intestine) (Fig. 4). The rectum usually curves anteriorly from the descending limb of the loop, but is sometimes continuous with the descending limb, forming part of it. The ascending limb usually curves postero-ventrally and then anteriorly, from the oesophageal opening (at the posterior end of the dorsal lamina) to the point where the intestine bends dorsally, and usually posteriorly, to become the descending limb. The descending limb is anterior and dorsal to the ascending limb and often runs parallel to it. The two limbs of the gut loop are often close, forming a narrow loop, or may be wide apart to form an open loop. Gonads on the left side of the body are enclosed between the two limbs of the gut loop in most phlebobranch genera and in *Pyura*. Gonads are outside the gut loop in Styelidae and some genera of the Pyuridae and Molgulidae including *Molgula*.

The gut loop is variously curved, usually around the postero-ventral curve of the body, and it sometimes forms a deep secondary loop which is open anteriorly. The course of the gut and the shape of the gut loop are very much affected by the position of the atrial aperture in relation to the oesophageal opening. Occasionally the gut extends in a simple arc from posterior oesophageal opening to anterior atrial opening and does not form a loop. (See also **stomach**).

heart: a tubular organ that propels the blood through major vessels into open circulation by a wave of contraction that passes along it, changing direction from time to time (Berrill 1950, Goodbody 1974). It is inconspicuous in most preserved material. It extends more or less from the pole of the gut loop (where it is continuous with subendostylar and test vessels) to the pyloric region (where it is continuous with visceral vessels). It is close and parallel to the ascending limb of the gut loop in solitary Phlebobranchia and Plurellidae. In Perophoridae and the Stolidobranchia it forms an arc across the postero-ventral corner of the right side of the body, parallel to, rather than mirroring, the curve of the ascending limb of the gut loop.

incurrent aperture, — stream: see **apertures**

infundibula: funnel-like structures projecting into the lumen of the branchial sac, the open base of the funnel facing the atrial cavity (Fig. 3). Infundibula are sometimes formed in the branchial folds where the stigmata along each side of the fold curve at each end toward those of the opposite side (*Molgula* spp.). The apex of these infundibula is often formed by a conical projection from the edge of the fold around which stigmata spiral (*Molgula* spp., *Hartmeyeria* and *Ctenyura*). Projecting conical infundibula with long stigmata spiralling around them entirely replace the folds of the branchial wall in *Molgula* spp., *Eugyra* and *Pareugyrioides*. They also occur in Agnesiinae and Corellinae. It is possible that these infundibula, particularly the spiral stigmata, maximise filtering efficiency by creating vortices around the cone (Carlisle 1979).

internal longitudinal vessels: longitudinal blood vessels that extend down the inner surface of the branchial wall, crossing the transverse vessels (Fig. 3).

intestinal loop: the part of the gut loop distal to the stomach, consisting of ascending and descending limbs of intestine only.

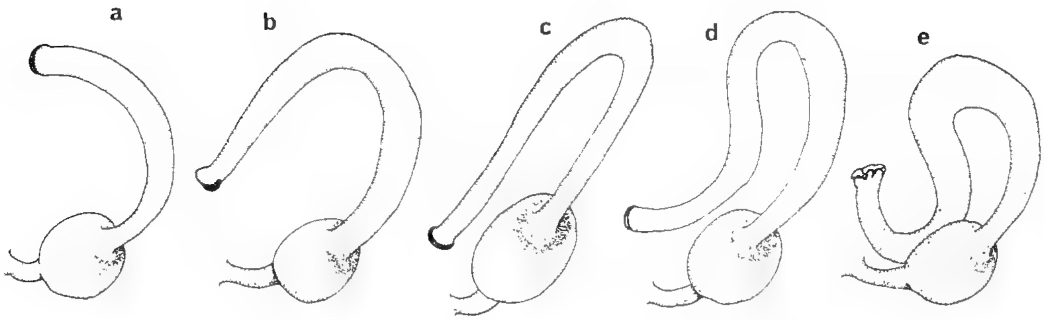


FIG. 4: Diagrams illustrating terms used in describing the gut loop — **a**, simple arc; **b**, simple open loop; **c**, narrow, straight loop: **d**, curved or J-shaped loop; **e**, deeply curved or U-shaped loop.

intestine: that part of the gut between the stomach and rectum.

kidney: a single, large excretory vesicle characteristic of the Molgulidae. Its origin is from the epicardium. (See also **excretory vesicles**).

languets: see **dorsal languets**

larvae: the relatively small (larval trunk less than 0.5 mm) tailed larvae of most solitary phlebobranch and stolidobranch ascidians hatch from externally fertilised ova. Most have a dorsal cerebral vesicle containing a light sensitive ocellus and a gravity sensitive otolith, and 3 triradially arranged cones of adhesive cells (adhesive organs) at the anterior end of the trunk (see Berrill 1929, 1931, 1935a, 1950, 1955; Millar 1971). Larvae are relatively unorganised and neither larval nor adult organs are well developed. Athough otherwise they resemble those of other solitary groups, larvae of *Polycarpa* have lost the ocellus and those of Molgulidae have neither ocellus nor adhesive organs and sometimes also lack an otolith. These groups appear to be adapted for habitats on the open sea-floor, where the absence of shadow removes the necessity for light sensitive larvae. This adaptation is enhanced in some of the species by a viviparous habit that reduces vulnerability of larvae to dispersal (Berrill 1931, 1955). Species of the subfamily Agnesiinae are also adapted for open sea floor habitats. Although one is known to be viviparous, and in several, fertilisation may be internal, nothing is known of their larvae.

Colonial phlebobranch and stolidobranch ascidians have relatively large viviparous larvae (larval trunk usually more than 0.5 mm) which hatch from internally fertilised ova. These larvae develop in a brood pouch (formed from the distal end of the oviduct) in the right peribranchial cavity in Perophoridae; free in the peribranchial cavity in Polyzoinae; and attached to the parietal body wall (either inside the atrium or externally) in Botryllinae. They are better organised than larvae of solitary forms (Berrill 1935a, 1950). Although both Botryllinae and Polyzoinae are probably derived from *Polycarpa* (in which the ocellus is lost), their larvae have a photolith (light sensitive cells added to the gravity sensitive otolith) (Grave 1932, Berrill 1950); and they have ectodermal ampullae (contributing to test development and attachment to the substrate). In Perophoridae adult organs (branchial sac and gut) are especially well developed. Their adhesive organs, in a median vertical line, have lost the primitive triradial arrangement and each is set in a cup of ectodermal cells (resembling the adhesive organs of Aplousobranchia).

All colonial ascidians (including the almost exclusively colonial Aplousobranchia) are alike in having large, well organised, fast swimming (Berrill 1931), usually light sensitive, and viviparous larvae. The larval characteristics are associated with a colonial habit rather than viviparity and, although in solitary forms viviparity is an adaptation for an open sea floor habitat, it is not in colonial ascidians. Selection for a colonial habit (Kott 1982) may be partly a result of the capacity of the colony to incubate the large larvae that have advantages for site selection in the turbulent habitats that Berrill (1955) has proposed are favoured by colonial species. (See also **viviparous**).

liver, — diverticula, — lamellae, — pouches: see **stomach**

neural gland: glandular tissue said to be dorsal to the neural ganglion in most Pleurogona and ventral to it in Enterogona (see Berrill 1950, Goodbody 1974). Variations in their relative position do occur with growth, however (see *Adagnesia opaca*). In the Phlebobranchia, the neural gland and ganglion are often displaced posteriorly, toward the base of the posteriorly positioned atrial aperture. They are lengthened in the stolidobranch species with the atrial aperture positioned posteriorly. The duct of the neural gland has a ciliated opening to the pharynx on the dorsal tubercle. This ciliated pit is thought to be sensory, and may have some secretary function. However, it is not yet known whether particles are swept into it or out of it (Goodbody 1974). In the family Plurellidae and genus *Phallusia* there are additional secondary ciliated openings from a long neural duct into the atrial cavity.

oesophageal opening: the opening from the pharynx into the oesophagus at the posterior end of the dorsal lamina.

oviparous: externally fertilised. (See also **viviparous**).

parastigmatic vessels: intermediate transverse vessels that cross the stigmata but do not interrupt them.

peribranchial cavity: see **atrial cavity**

peritubercular area: a V-shaped area at the anterior end of the dorsal lamina enclosed by the prepharyngeal groove where it slopes posteriorly at each side of the dorsal mid-line. The area usually contains the dorsal tubercle with the opening of the neural gland. (See also **neural gland**)

prebranchial area: the area between the prepharyngeal groove and the ring of branchial tentacles.

prepharyngeal groove: a groove around the anterior limits of the perforated part of the pharynx.

proximal: the end of an organ or structure away from which the contents or products move or which is closest to the base or point of attachment. (See also **distal**)

pyloric gland: see **gastro-intestinal connective**

rectum: the distal part of the gut, terminating in the anus, that bends toward the atrial aperture.

renal vesicles: see **excretory vesicles**

reservoir: see **gastric reservoir**

retropharyngeal groove: a groove in the posterior mid-line of the pharynx between the posterior end of the endostyle and the posterior border of the oesophageal opening. This is very variable in length and is sometimes absent altogether, the endostyle terminating near the oesophageal opening.

siphonal armature: minute (0.02 to 0.3 mm) hollow spines or scales in the cuticle of the test where it turns in to line the siphons. These occur in certain genera of the Styelidae and all genera of the Pyuridae. Siphonal scales are flattened, with a rounded anterior border. Spines are longer, pointed and often needle-like (Fig. 5).

Variations in the shape of the spines involve lengthening of the free terminal point and/or the open base, development of a flange that spreads out around the base and/or partial closure of the open base. A large spherical vesicle is present inside the spine or scale. Curved, flattened scales, with a rounded border, are present in the genus *Styela*, usually in *Cnemidocarpa* spp., in *Pyura* spp. of the *irregularis* group and in *Microcosmus squamiger*. Conical spines with an open base are present in *Polycarpa olitoria, Cnemidocarpa intestinata* n.sp., *Pyura ostreophila, P. spinifera, P. stolonifera, Microcosmus tuberculatus* n.sp. and *Microcosmus propinquus* (in which curved scales are also present). In *Pyura arenosa, P. australis, P. gibbosa* there is a long oval, open base. *Pyura sacciformis* has a wide flange developed around the wide-open base. The base is almost completely closed in *Pyura curvigona, P. obesa, P. tasmanensis* n.sp., *P. isobella* n.sp. and *Microcosmus pupa*. In *P. isobella* n.sp. the closed base is swollen and in *Pyura curvigona* a scale-like collar is present around the spine. In *Microcosmus australis, M. exasperatus, M. madagascariensis, M. planus* and *M. stoloniferus* the open base is long and oval and the free terminal spine is flattened.

The spines and scales are usually evenly distributed and often overlap. They are directed upwards toward the aperture and may act as a protective device preventing entry of small organisms into the apertures. Siphonal armature often continues onto the external test around the apertures and sometimes over most of the surface of the test, especially on the anterior half of the body.

siphonal lining: invagination of the test into the siphons, terminating anterior to the branchial tentacles.

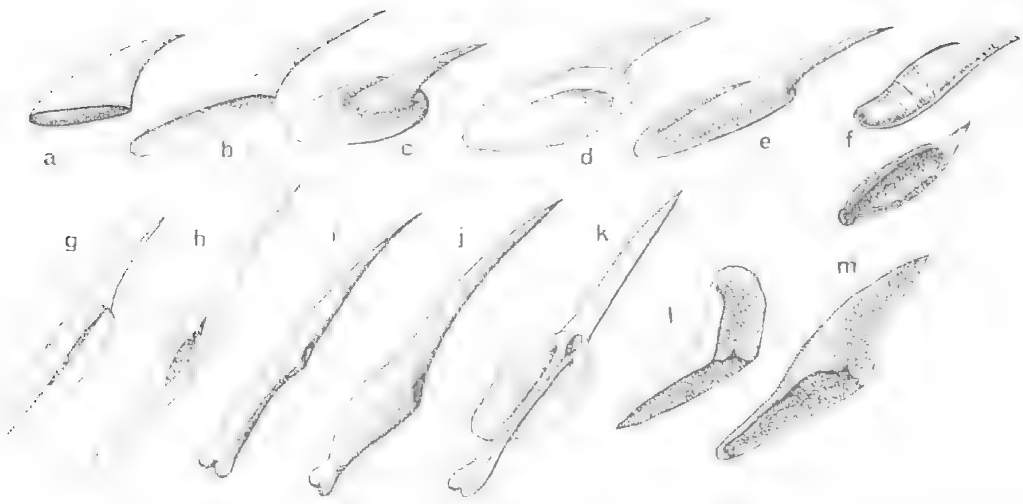


FIG. 5: Siphonal armature (diagrammatic) — **a**, curved, conical spine with basal flange (e.g. *Pyura sacciformis*); **b**, long curved spine with slight flange and partially closed base (e.g. *Pyura australis*); **c**, pointed scale or spine, hooked posteriorly (e.g. *Microcosmus exasperatus*, *M. australis*); **d**, rounded scale (e.g. *Cnemidocarpa* spp., *Microcosmus squamiger*, *Pyura irregularis* and related species); **e**, conical spine (e.g. *Polycarpa olitoria*, *Pyura stolonifera*, *P. ostreophila*, *P. spinifera*); **f**, pointed spine with base closed (*Pyura obesa*, *P. tasmanensis* n.sp.); **g**, pointed spine with closed base swollen (e.g. *Pyura isobella* n.sp.); **h**, pointed spine with scale (e.g. *Pyura curvigona*); **i**, flattened leaf-like spines (*Pyura arenosa*).

siphonal scales: see **siphonal armature**.

siphons: cylindrical extensions of the body by which the apertures are projected forwards, laterally or posteriorly. The siphonal lining often contains structures that complement those around the apertures, preventing entry of unwanted particles and predators into the branchial sac. The structures include the **siphonal armature** (see above); pocket valves in the siphonal lining of *Microcosmus australis*, *M. exasperatus* and *M. squamiger*; cartilaginous tongues in *M. helleri*; and muscular siphonal vela in most *Molgula* spp., certain *Pyura* (*P. molguloides*) and *Ascidia* (*A. prolata* n.sp.). The ring of branchial tentacles at the base of the branchial siphon also has a protective function, as does the membranous atrial velum often with a fringe of minute tentacles.

spicules: plate-like, spherical or stellate calcareous bodies found most often in the test of certain aplousobranch ascidians and several species of Pyuridae (*pachydermatina* group, *Ctenyura tetraplexa* n. sp.). They are not present in Phlebobranchia. *Herdmania momus* has barbed needle-like spicules in the body wall. *Pyura sacciformis* and *P. stolonifera* often have large branching spicules in the pharynx and body wall.

stigmata: ciliated perforations in the pharyngeal wall through which incurrent water passes into the atrial cavity (Fig. 3). These are oval, or long, narrow and rectangular. Usually the stigmata are longitudinal and arranged in regular transverse rows. Species in the genus *Boltenia*, characterised by transversely elongate stigmata, have not yet been recorded from Australian waters. In the Phlebobranchia, spiral stigmata are characteristic of the Agnesiinae and Corellinae. In the Stolidobranchia, curved or spiral stigmata are characteristic of the Molgulidae and certain genera of the Pyuridae (see **infundibula**).

In the counts of stigmata/mesh in the species descriptions that follow, the count is always from a mesh as close as possible to the centre of the branchial sac. A single branchial mesh is the rectangular area enclosed by internal longitudinal and transverse branchial vessels. It is sometimes crossed transversely by a parastigmatic vessel.

stolonic vessel: an epidermal vascular extension from the postero-ventral corner of the body wall of colonial zooids. It contains a continuation of the subendostylar sinus and is homologous with the test vessel of solitary forms (see **heart**). Many perophorid species have paired vascular projections joining the common basal stolonic vessel, from which there are sometimes branches returning blood to the zooid test, either in the primary or in accessory stolons. In Perophoridae the stolonic vessel has a mesenchymal septum that is involved in the vegetative process (Berrill 1935b, 1950). In Styelidae there is no mesenchymal septum, but there is a mesenchymal reticulum through which the haemocoele (open blood sinuses with mesenchymal cells) continues (Newberry 1965). In the Polyzoinae, and possibly the Botryllinae, buds formed from the pallial body wall are moved along the stolon by local changes in blood pressure and development of ectodermal ampullae from the tip of the growing stolonic vessel (Newberry 1965). (See also **vegetative reproduction**).

stomach: an expansion of the proximal part of the gut. It is lined with glandular epithelium. There are parallel longitudinal folds in the stomach wall in the family Styelidae and sometimes in the Phlebobranchia (Corellidae and occasionally in the Ascidiidae). In other Phlebobranchia the glandular epithelium lining the stomach is separated into 4 distinct longitudinal areas usually referred to as folds, but not forming true folds. The entire wall of the stomach is formed into irregular pockets or pouches or into tight groups of short or long parallel folds or lamellae often referred to as 'liver') in *Microcosmus*, *Hartmeyeria* and Molgulidae. In *Pyura*, and *Ctenyura*, there is little or no expansion of the gut to form a stomach, but single or multiple, branching outgrowths from the gut wall form arborescent liver diverticula protruding into the atrial cavity. In *Herdmania* and *Ctenicella* there are very extensive clumps of finger-like terminal lobules and branching tubules firmly embedded in the connective tissue of the parietal body wall over the gut. The prescence of an arborescent liver in the genera *Pyura*, *Ctenyura*, *Herdmania* and *Ctenicella*, supports the phylogenetic relationship of these genera suggested by the presence of dorsal languets.

stomach caecum: a blind diverticulum, sometimes curved, produced from the distal (pyloric) end of the stomach and protruding into the gut loop, usually present in the Botryllinae and Polyzoinae and sometimes in the Styelinae.

terminal ampullae: see **test vessels**.

test: the secretion of the ascidian ectoderm that encapsulates the body. It consists of a hyaline, proteinaceous, non-cellular matrix in which there are free blood cells (from the ectodermal test vessels) and cellulose-like fibres of tunicin (which has a similar structure to cellulose). There are no epithelial layers (Goodbody 1974) The test is attached to the body wall around the apertures and by test vessels from the body wall that penetrate it and divide into branches.

The test is usually firm, gelatinous and often translucent in most phlebobranch species. It becomes tough and leathery in Styelidae and Pyuridae. In the Molgulidae, it is more often thin, but very hard and brittle with embedded sand. However, species with sand-embedded test are not confined to the Molgulidae. They are known in all groups, especially bottom-living, sand-adapted forms (e.g. *Ascidia sceuevola*, *Microgastra granosa*, *Polycarpa chinensis*, *P. procera*, *P. rigida*, *P. tinctor*, *Pyura arenosa*, *Microcosmus planus*).

The leathery, fibrous test of Pyuridae and Styelinae has especially strong adhesive qualities. The surface is often irregular, extending into stalks and root-like processes, especially postero-ventrally, that enhance its firm attachment to hard substrates. In many species of all stolidobranch families, fine, hair-like extensions cover the surface. The sand that adheres to them creates a thick, protective layer around the body. This is an adaptation for a sandy habitat in *Cnemidocarpa floccosa*, *Pyura molguloides*, *Microcosmus helleri*, *Polycarpa molguloides*, *P. intonata* n.sp.). Commensal organisms, especially molluscs, are found in the test of species of both suborders.

In the family Plurellidae, not only is the whole body enclosed and protected by the sandy, rigid test, but also all the more imporant body organs (*viz*. the heart, neural ganglion, ovaries and testis) project from the external body wall and are embedded in it. In *Ascidia capillata* and *A. kreagra*, lamellae from the internal surface of the test project into the body wall around the gut, holding the body firmly in place.

test vessels: epidermal vessels from the body wall that enter and branch in the test. In many families these can be seen terminating in rounded ampullae near the surface of the test.

transverse branchial vessels: enlarged blood sinuses between the rows of stigmata. The lumen of these vessels is continuous with the dorsal and ventral sinus.

vanadocytes: morula cells of phlebobranch ascidians containing vanadium (Webb 1939, Goodbody 1974). In stolidobranch species, other elements, such as iron (Hawkins *et al.* 1983 b, c), are present in the morula cells. A previously held belief that vanadocytes had a very low pH has been shown to have resulted from the acid reaction that follows lysis of the cell wall (Hawkins *et al.* 1983a).

vascular stolon: narrow postero-ventral extension of the body and the common basal or axial stem that it joins, connecting the zooids of colonial phlebobranch and stolidobranch (non-embedded) species. It consists of a stolonic vessel with a covering of test. Accessory stolons, probably returning blood from the common vessel to the zooid test, occur in Perophoridae. (See also **stolonic vessel**).

vegetative reproduction: replication of zooids to form colonies. Two apparently unrelated vegetative processes occur in the Styelidae (Polyzoinae and Botryllinae) and in the Perophoridae. In the subfamilies of the Styelidae, buds develop from the body wall (pallial budding), although vascular budding (in the stolonic vessels) is also known to occur in the Botryllinae. In the Perophoridae, budding takes places in the stolons connecting the zooids (Berrill 1935b, 1938, 1948, 1950, 1961; Oka and Watanabe 1957; Newberry 1965; Sabbadin *et al.* 1975). The adaptive advantages of a colonial habit are discussed by Sabbadin (1979) and Kott (1982). (See also **vascular stolon, stolonic vessel**).

viviparous: species in which ova are internally fertilised, and embryos are brooded in the parental body, usually being released as swimming larvae. Vegetative colonial species are invariably viviparous (Kott 1982). Very occasionally, solitary species are viviparous (*Polycarpa tinctor, P. tinctorella* n.sp., *P. intonata* n.sp., *Molgula calvata, M. ellistoni, M. incidata* n.sp., *Eugyra pellucida*). Development is direct (Berrill 1931, 1955), the larval stage being suppressed in *Polycarpa tinctor, P. tinctorella* n.sp., *M. ellistoni* (See also **gonads, larvae**).

PHYLOGENY OF THE ASCIDIACEA

The Ascidiacea are a class of the subphylum Tunicata, phylum Chordata. Characteristics of the subphylum are a perforated pharynx; a dorsal neural ganglion; a hollow dorsal nerve chord and a tail with notochord-like supporting cells (present at some stage in the life history); an open blood system; no true coelom.

Characteristics of the class Ascidiacea are the external protective test secreted by the ectoderm; the peribranchial (atrial) cavity invaginated from the dorsal surface and lined with ectoderm; sessile (usually fixed) adult; and free-swimming larva. The larval tail, together with the dorsal nerve cord and notochord-like cells, are lost on metamorphosis, while the larval sensory vesicle becomes the neural gland and ganglion.

Speculations on the affinities of the Ascidiacea (which is believed to have included the ancestors of other classes of the Tunicata) are based on the presence of the larval dorsal neural vesicle and nerve cord, perforated pharynx and notochord-like cells.

The pharynx especially bears a close resemblance to that of Hemichordata but, as Berrill (1955) points out, both the pharynx and the antero-dorsal neural apparatus could be independent adaptations for similar habits in groups of filter-feeding organisms; they are not necessarily indicative of a common ancestry. Indeed, there is no real evidence of tunicate ancestry amongst known invertebrates.

It is most unlikely that the large, perforated pharynx that is characteristic of the Ascidiacea was a feature of an organism that was not fixed. The ancestor of the tunicates was probably a large, fixed, filter-feeding ascidian-like organism with free-swimming larvae that were subject to selective pressures for site selection and gene flow. The ascidian larval tail is an obvious adaptation for both functions. The notochord-like cells of the ascidian larval tail are not necessarily homologous with true chordate notochord cells, and the origin of the latter as an internal skeletal structure for the chordate body may well have been independent of the origin of similar cells as a skeletal structure in the ascidian larval tail.

Nevertheless, the most acceptable hypotheses of chordate evolution are those that propose an origin by neoteny from an ascidian-like ancestor, in which the larval tail is not lost and the free-swimming habit is prolonged (see Berrill 1955). The generally accepted chordate affinity of the Tunicata is supported by the presence of a larval neural vesicle, regarded as the homologue of the primitive vertebrate brain. Further compelling evidence for a phylogenetic relationship with

Cephalochordata and the chordates is the presence of an endostyle with an iodine-binding capacity, suggesting its homology with the vertebrate thyroid gland (Goodbody 1974). More recently (Hawkins *pers. comm.*), phosphocreatine has been found in the liver of *Pyura stolonifera*, suggesting a closer relationship to vertebrates than to invertebrates.

If the chordate ancestor did result from neoteny in an ascidian larva, the selective pressures must have been the opposite of those that appear to have effected the evolution of extant ascidians (Kott 1969a). Although larvae are retained in most extant forms (presumably for site selection and gene flow), they are free-swimming for only a very short time, many species are viviparous and in some, development is direct (Berrill 1955; Kott 1974, 1982). These strategies avoid dispersal and ensure population maintenance, which has obvious advantages for fixed organisms in which cross fertilisation can occur only by release into the external environment of either male, or both male and female gametes (internally or externally fertilised species, respectively).

Selection for long-lived larvae and subsequent neoteny would have been possible only in conditions where selective pressures affecting population maintainance were not stringent; where there was advantage associated with a longer free-swimming phase; and where the absence of readily available settlement sites delayed metamorphosis. These conditions would be satisfied in still waters where long-lived larvae would not be subjected to dispersal; in deep waters where long-lived larvae would derive advantages from plentiful food (micro-flora) supplies at the surface; and in waters where soft sediments concealed the hard substrata suitable for settlement sites.

CLASSIFICATION OF ASCIDIACEA

The two known orders of the Ascidiacea, Enterogona and Pleurogona, are characterised only by the origin of the atrial cavity: from a pair of dorsal invaginations (Enterogona) or a single dorsal invagination (Pleurogona). Since this is an embryonic character, the subordinal groupings are of most practical use. Further, the paired origin of the atrial cavity is a primitive condition and does not reflect the close phylogenetic relationship between Phlebobranchia (Enterogona) and Stolidobranchia (Pleurogona), both of which are separated from the Aplousobranchia (Enterogona) by primary characters associated with the function of the epicardum (Kott 1969a). In Aplousobranchia the epicardum is involved with the vegetative process and, with very few exceptions, members of the suborder are colonial.

In Phlebobranchia and Stolidobranchia the epicardium is involved with excretion and most families are primarily of solitary species. In Aplousobranchia there is progressive evolution of vegetative reproduction, colonial organisation and larval viviparity, while Phlebobranchia and Stolidobranchia are in a single, evolutionary line, characterised by the excretory function of the epicardium and adaptive advantages associated with a morphology that increases the efficiency of large, solitary individuals. Secondary changes that occur in certain phlebobranch and stolidobranch taxa as a result of vegetative processes independent of those in the Aplousobranchia are analagous, rather than homologous, with those in the latter suborder. This development of colonies, that parallels aplousobranch evolution, is probably a result of similar environmental pressures to maintain populations (Kott 1982).

Evolution in both lines is accompanied by loss of a capacity to accumulate vanadium. This capacity is a characteristic of the Ascidiacea and is most conspicuous in the more primitive members of the class. The vanadium chemistry of the Ascidiacea supports the phylogeny, discussed above, that is based on morphology and the nature of the vegetative processes. Aplousobranchia contain vanadium in oxidation state III, Phlebobranchia contain vanadium IV, and Stolidobranchia have lost the capacity to accumulate the element (Hawkins *et al.* 1983b).

Key to the Orders and Suborders of the Ascidiacea

1. Atrial cavity develops from paired dorsal invaginations. Gut, gonads and heart alongside or entirely posterior to branchial sac. Gonads single, unpaired (never present on side of body opposite to gut) and enclosed by or posterior to the primary gut loop; never anterior to it. Branchial sac not folded (Enterogona)........................ 2

   Atrial cavity develops from single, median-dorsal invagination. Gut, gonads and heart always alongside branchial sac (separated from it by atrial cavity) and never entirely posterior to it. Gonads paired or more numerous, usually present on both sides of body and on one side enclosed by or anterior to primary gut loop; never posterior to it. Branchial sac primarily folded (PLEUROGONA).......... STOLIDOBRANCHIA

2\. Gut loop, gonads and heart always entirely posterior to branchial sac.. APLOUSOBRANCHIA

Gut loop, gonads and heart never entirely posterior to branchial sac.. PHLEBOBRANCHIA

Order ENTEROGONA

Ascidians in which the atrial cavity develops from a pair of dorsal invaginations each side of the mid-line. These later fuse to form a single atrial opening in the mid-line. No trace of this developmental characteristic is present in the adult organism. Members of the order are readily recognised by their flat rather than folded branchial sac; their single, unpaired gonads either enclosed by or posterior to the gut loop; and by the characters of one or other of the two suborders, Aplousobranchia† and Phlebobranchia. Only in the family Plurellidae and in *Ascidia scaevola* (family Ascidiidae) does a secondary branchial fold form on the left side of the body.

Suborder PHLEBOBRANCHIA

This suborder primarily contains large solitary enterogonid ascidians characterised by their firm, gelatinous or cartilaginous, and usually translucent test. Sand is embedded in or adheres to the test in many species, but the surface is often naked and epibionts seldom occur. The pharynx occupies the full length of the body, and many internal longitudinal branchial vessels supported on vertical papillae are always present. The gut and gonads are embedded in the parietal body wall and the body is not separated into thorax and abdomen. There are simple branchial tentacles. With the sole exception of species of the family Plurellidae (in which the gonads project from the body wall to be embedded in the test and the ovarian tube is subdivided to form several separate female sacs), the single gonad is always enclosed in the gut loop. Except in species in which musculature has become specialised, muscle-bands are fine. They never form a thick layer in the body wall. With the exception of Perophoridae, fertilisation is usually external and larvae are primitive, with simple, unstalked, adhesive organs arranged in a triangle (Berrill 1950). Adult organs are not well developed until metamorphosis. Vegetative reproduction occurs only in the families Perophoridae and Plurellidae.

Colour in this group of ascidians usually results from pigmented blood cells present in vascular networks in the body wall, branchial sac and test vessels. It is seen through the otherwise translucent or transparent test. Generally, Phlebobranchia contain vanadium as yellow-coloured vanadium chromogen in vanadocytes and compartment cells (Webb 1939). The vanadium chromogen oxidizes to a red-brown colour on fixation. Red and orange pigment cells are also present in many species. Inter- and intra-specific variations in pigmentation result from variations in distribution of the blood cells (*Ascidia glabra*, *Ecteinascidia diaphanis*) and differences in the relative numbers of vanadium containing and other blood cells that are present (e.g. *Ascidia glabra*, *A. gemmata*, *A. kreagra* and *Ecteinascidia rubricollis*). More dramatic intra-specific colour variations that cause some individuals to be maroon purple, brown, or black are not understood (e.g. *Ascidia archaia*, *Ascidia liberata*).

The families Ascidiidae, Plurellidae and Perophoridae are all well represented in shallow waters of the Australian continental shelf. The families Agnesiidae and Corellidae are represented here by very few species and are more diverse in abyssal or colder waters of the northern hemisphere. Octacnemidae (containing the genera *Hypobythius*, *Benthascidia*, *Dicopia*, *Megalodicopia* and *Octacnemus*) is an exclusively abyssal family not represented in Australia (see Monniot and Monniot 1972)

KEY TO THE FAMILIES OF PHLEBOBRANCHIA
(* not recorded from Australia)

1\. Stigmata absent or reduced .... OCTACNEMIDAE*

Stigmata present and regular 2

2\. Gonads enclosed in primary gut loop......... 3

Gonads not enclosed in primary gut loop ....PLURELLIDAE

3\. Solitary 4

Colonial .... PEROPHORIDAE

4\. Gut on left of branchial sac........................ 5

Gut not on left of branchial sac (CORELLIDAE) 7

5\. Internal longitudinal branchial vessels not interrupted .... ASCIDIIDAE

Internal longitudinal branchial vessels interrupted or absent (AGNESIIDAE)........ 6

6\. Stigmata straight .... CIALLUSIINAE*

Stigmata spiral .... AGNESIINAE

7\. Stigmata straight .... RHODOSOMATINAE

Stigmata spiral .... CORELLINAE

† Aplousobranch Ascidians will be discussed in Part II of the present work.

Family ASCIDIIDAE Adams, 1858

Phlebobranch ascidians with numerous rows of straight stigmata, and internal longitudinal vessels with papillae at their junctions with the transverse vessels. There are usually no branchial folds, although the branchial wall is often finely pleated between the internal longitudinal vessels. The gut loop is on the left side of the branchial sac.

Generally the test is firm, translucent, gelatinous and naked, although there are a few species with thin, brittle, sand-embedded test. Gonads are always enclosed in the gut loop. They consist of a tubular, usually branched, ovary and small, branching male follicles that spread over the mesial side of the gut loop. The heart is to the left of the mid-line, ventral and more or less parallel to the postero-ventral curve of the gut loop, its anterior end continuous with the sub-endostylar vessel. The main test vessel branches off the sub-endostylar vessel just distal to its junction with the heart.

There are three genera (*Ascidiella*, *Ascidia* and *Phallusia*) recorded from Australia. Of these, the genus *Ascidia* is especially diverse. Both *Ascidia* and *Phallusia*, however, are conspicuous components of the Australian ascidian fauna. The affinities of the species are most often with the fauna of the Indo-West Pacific rather than that of the sub-antarctic. There are some temperate indigenous species around the southern half of the continent.

Only a single genus (the monotypic interstitial *Psammascidia* Monniot, 1962a) from the English Channel has not been recorded from Australia. The abyssal *Bathyascidia* Hartmeyer, 1901 is probably a synonym of *Ascidia*.

Key to Genera of Ascidiidae
(* not recorded from Australia)

1. Neural gland with openings into peribranchial cavity .... *Phallusia*
   Neural gland without openings into peribranchial cavity 2
2. Individuals less than 2 mm long .... *Psammascidia* *
   Individuals not less than 2 mm long 3
3. Branchial papillae project above internal longitudinal vessels..................... *Ascidia*
   Branchial papillae do not project above internal longitudinal vessels....... *Ascidiella*

Genus Ascidiella Roule, 1884

Type species: *Ascidia aspersa* Mueller, 1776

The genus is distinguished from *Ascidia* by the absence of secondary branchial papillae projecting into the lumen of the pharynx at the junction of the internal longitudinal and transverse vessels.

There are also differences in the blood cells and blood chemistry of *Ascidiella* and *Ascidia* that justify the separation of these two morphologically similar genera. *Ascidiella* has vanadium-containing blood cells different from the characteristic vandadocytes of the genus *Ascidia*. Further, there is some evidence that the vanadium in the former genus is not bound in the same chromogen molecule that is found in *Ascidia* (Webb 1939).

The few species in the genus appear to be closely related (see Berrill 1950). The only species recorded from the southern hemisphere (from New Zealand, south-western Australia, Victoria and Tasmania) does not appear to be distinct from *Ascidiella aspersa*, which is known from the Mediterranean Sea, the English Channel, the Irish Sea and the west coast of Ireland and Scotland.

Ascidiella aspersa (Mueller, 1776)
(Fig. 6)

Ascidia aspersa Mueller, 1776, p.225. Herdman, 1881b, p.281. Harant, 1829, p.56; 1931, p.303. Lindsay and Thompson, 1930, p.3. Thompson, 1933, p.25. Brewin, 1946, p.107; 1950b, p.344. Kott, 1952, p.307.
Phallusia aspersa: Traustedt, 1883b, p.467.
Ascidiella aspersa: Kiaer, 1893, p.23. Hartmeyer, 1912b, p.291; 1915a, p.306; 1924, p.81; (not: 1920a, p.210, < *Ascidia glabra*). Berrill, 1928, p.159; 1950, p.154. Arnback, 1934, *typica* p.28. Azéma 1937, p.49. Millar, 1963, p.722.
Phallusia cristata Risso, 1826, p.276.
Ascidiella cristata: Roule, 1884, p.220.
Ascidia pustulosa Alder, 1863, p.154. Alder and Hancock, 1905, p.138.
Ascidia affinis Hancock, 1870, p.361. Alder and Hancock, 1905, p.138.

Distribution

New Records: Western Australia (Swan River, WAM 1.75; Bunbury, WAM 17.75). Victoria (Port Phillip Bay, QM G9406). Tasmania (Spring Bay, QM GH2483; Bruny I., QM GH2571; Dickson's Beach, TM D1811).

Previously Recorded: Western Australia (Swan River — Millar 1962; Albany — Kott 1952). South Australia (St Vincent Gulf — Kott 1952). Tasmania (d'Entrecasteaux Channel — Kott 1952). New Zealand (Otago Harbour — Brewin 1946 1950b).

The Australian records are all from protected or semi-enclosed waterways. In particular Western Australian records include specimens from Pt Walter, a considerable distance up the Swan River estuary, where there is a deep marine habitat overlaid by brackish water. The record from Albany is in Oyster Harbour. These populations appear to be isolated, both from one another and from the European populations. European populations, however, occupy similar habitats to the southern

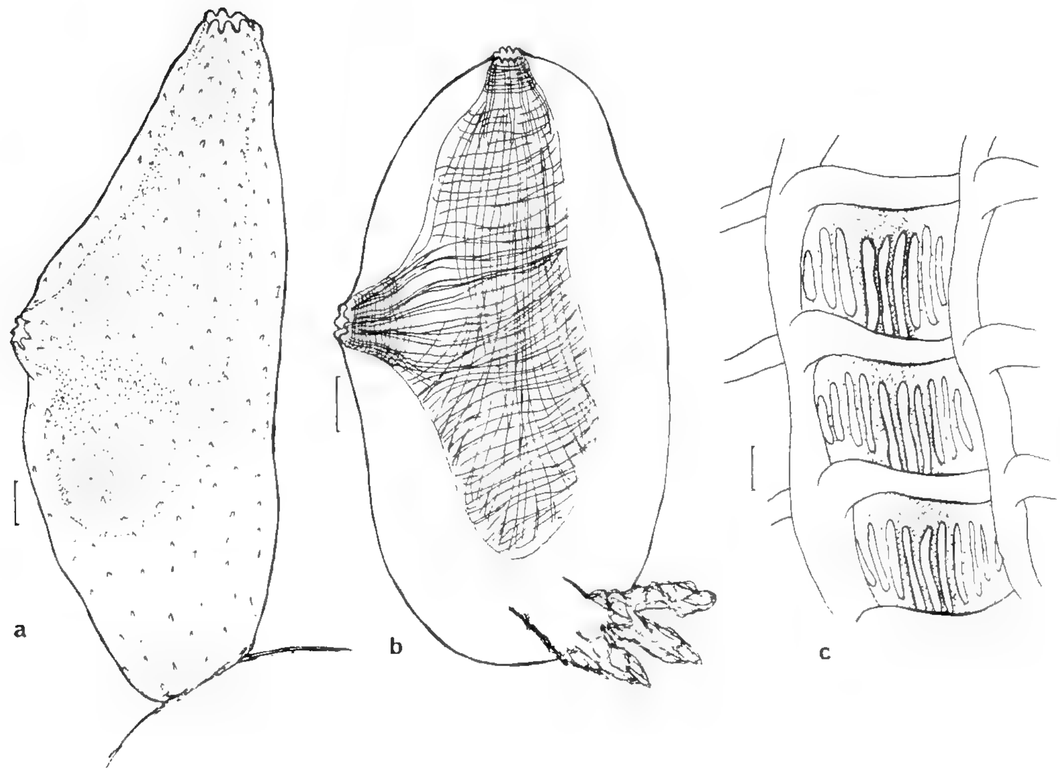


FIG. 6: *Ascidiella aspersa* — **a**, external appearance (QM GH2483); **b**, right side of body wall showing musculature (QM GH9406); **c**, portion of branchial sac. (Scales: **a**, 2.0 mm; **b**, 5.0 mm; **c**, 0.1 mm)

hemisphere ones, being 'particularly abundant in the inner-reaches of salt estuaries and harbours' (Berrill 1950, p. 155). The species is taken from shallow sub-tidal waters, seldom at depths in excess of 50 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are long, and more or less egg-shaped, up to 6 cm in length; the anterior end tapers to a short, conical, terminal branchial siphon. A similar short atrial siphon is present one-third to halfway down the dorsal surface. Both siphons are ridged. Posteriorly the body is rounded. There are 8 to 10 branchial lobes and 6 atrial lobes. Papillae, with single or multiple terminal points, are scattered on the surface, especially on the right side of the test and around the apertures. These are often present on rounded swellings of the test. The test is firm but thin and transparent, sometimes almost glassy.

The body is usually attached by the whole of the left side.

INTERNAL STRUCTURE: There are longitudinal muscles radiating from the siphons. On the right side these form an irregular open mesh with internal circular muscles. The muscles terminate parallel to one another around the ventral margin of the body. There are streaks and patches of orange pigment embedded in the body wall of preserved specimens around and between the apertures. The branchial tentacles are not numerous: about 15 larger tentacles alternating with rudimentary ones. The round dorsal tubercle is present in a V-shaped peritubercular area and has a U-shaped slit with both horns turned in or out. The neural ganglion is present just posterior to the tubercle. The dorsal lamina is double for only a very short part of its anterior extent. It is ribbed on both sides, although the ribs on the right do not reach the edge of the plain-edged membrane.

The branchial wall has single, minute pleats between the longitudinal vessels, with up to 10 stigmata in each pleat. There are no secondary branchial papillae.

The gut forms a tight double loop. The stomach is lined with parallel longitudinal folds. The anal border is smooth. The gonads are crowded in the primary gut loop. Small, branched male follicles spread between and over both sides of the gut loop. The ovary is tubular. Eggs are 0.13 mm in diameter, excluding the outer layer of large follicle cells. The inner follicle cells are small and brown. Both gut and gonads are embedded in the body wall on the left side of the body. Spherical renal vesicles with a brown or colourless crystalline inclusion are conspicuous in the body wall around the gut wall and extending out into the body wall on both sides of the body. They obscure both gut and gonads.

REMARKS: The structures of the individuals referred to above from southern temperate locations resemble those described from the eastern Atlantic and Mediterranean Sea in every respect, and do not justify separation of these isolated populations as distinct species.

Brewin (1946) reported small vascular processes on the internal longitudinal vessels of the New Zealand specimens. These are not present in the Australian material. Kott's (1971) proposal that *Ascidia meridionalis* from Antarctic waters is synonymous with the present species, based on the presence of similar excretory vesicles and the assumption that vascular processes described by Brewin are homologous with the branchial papillae of *Ascidia* spp., is not tenable.

Genus **Ascidia** Linnaeus, 1767

Type species: *Ascidia mentula* Mueller, 1776

The branchial sac is without folds and the stigmata are straight. Internal longitudinal branchial vessels are supported by a papilla at their junctions with the transverse vessels. The papillae project into the lumen of the pharynx above the level of the internal longitudinal vessels. The gut is on the left side of the branchial sac. The gonads are in the gut loop. A tubular ovary is branched at its proximal end. Testis follicles spread over the gut loop and the vasa efferentia join to a long, thick vas deferens that accompanies the oviduct and rectum to open at the base of the atrial aperture. There are usually 6 to 10, and sometimes up to 15, branchial lobes and 6 or 7 atrial lobes. There are pigmented ocelli between the lobes of the apertures. When the apertures are closed, the border is drawn together to form a frill, the lobes being drawn into the centre and the interlobal area standing out to leave the ocelli exposed. The position of the neural gland varies from above the dorsal tubercle to the base of the atrial siphon, but there are no accessory openings from its duct. The dorsal lamina is usually double anteriorly between the neural ganglion and the dorsal tubercle and the left half of the double embrane often passes to the left of the peritubercular area. Excretory vesicles are often conspicuous in the body wall over the gut.

The test of most species is firm, naked, gelatinous and translucent, although sometimes it is thin and papery, and occasionally sand is embedded. Body musculature is well developed as transverse or branching bands that form an irregular mesh on the right side of the body, usually crossing the dorsal mid-line. There are no muscles over the gut, and on the left side of the body, musculature is present only anterior to the gut. Longitudinal and circular bands are present on the siphons. The branchial sac is often very finely pleated between the internal longitudinal vessels; this pleating is emphasised when the branchial sac is contracted. Most species lie on their left side and are fixed to the substrate by a large part of that side of the body. Many species have up to 7 minute papillae fringing each lobe of the apertures, similar to those found in *Phallusia julinea*. Some species of *Ascidia* also share with *Phallusia* a tendency to accumulate vast quantities of mud in the descending limb of the gut loop and in the rectum. In large specimens, this distends the gut to such an extent that it occupies a large part of the left side of the body, and often appears to occlude the pharynx.

Ascidia is distinguished from *Phallusia* only by the absence of the accessory openings of the neural gland into the atrial cavity that characterise the latter genus; and by the (usually) less numerous lobes of the atrial aperture (fewer than 8, while *Phallusia* spp. have 8 or more). The differences between these two genera are slight, however, and in the absence of secondary neural openings, young specimens of *Phallusia* can readily be confused with species of the present genus.

The morphology of species in the genus *Ascidia* is not diverse, and taxonomy of the genus is far from satisfactory. Between 1885 and 1915, Sluiter recorded 28 species of this genus from the Indonesian region. Until the present review, only 4 of these were previously known to be synonyms and only 14 have been recorded more than once. From the Siboga collection (Sluiter 1904), 14 species were taken only once, each being represented only by from 1 to 4 specimens. On the other hand, 3 to 5 species of the genus were taken at certain stations (stations 24, 213 and 144). This suggests either that intraspecific variability has confused attempts to define species parameters; or that species diversity is unusually high, populations are relatively sparse and geographic range is limited. Although all these factors may have contributed to some extent to the apparently unusual pattern of distribution, it is probable that the former explanation is the correct one.

Examination of Sluiter's type material has established that many of the described species are conspecific. Many of these occur in Australian waters. Thus, there are species of this genus that have the same wide geographic ranges as those of other tropical genera.

In the present review, the characters that appear to be reliable indicators of species are: the presence or absence of a fringe on the border of the apertures and their position; the arrangement of body muscles; the test vascularisation; the position of the neural ganglion in relation to the dorsal tubercle; the length and number of stigmata between the internal longitudinal branchial vessels; and the length (and to some extent the orientation) of the gut loop. The number of branchial tentacles, number of lobes around the apertures, shape of the slit of the dorsal tubercle, and pigmentation of the test all seem to be variable and to alter with growth. Their reliability for purposes of identification is generally only very limited.

Some of the species of *Ascidia* recorded from Australia fall into the following apparently natural groups:

1. *Sydneiensis* group: species with fringed lobes of apertures. With the exception of *A. occidentalis* n.sp., these species have the muscles on the right side of the body arranged in regular transverse bands, confined to the dorsal half of the body in *A. liberata*, but usually forming a border of short, parallel muscles along the dorsal and ventral margin of the right side. In this group, the anterior end of the dorsal lamina is assymmetrical, the left half of the double membrane passing to the left of the peritubercular area.
   Members of the group are *Ascidia sydneiensis, A. liberata, A. munda, A. parasamea* n.sp., and *A. occidentalis* n.sp.

2. *Gemmata* group: species in which the body muscles on the right form an irregular mesh. This group includes *Ascidia decepta* n.sp. and *A. latesiphonica* (in which terminal ampullae of test vessels are expanded into large, spherical ampullae) and *A. kreagra* and *A. capillata* (in which the test projects into the body wall around the gut). Other members of the group are *A. empheres, A. gemmata, A. glabra, A. thompsoni* and *A. challengeri*.

Ascidia archaia (with an open gut loop and pinnate branches on the proximal half of the ovarian tube), *A. pandora* n.sp. (with a brittle, sandy test) and *A. prolata* n.sp. (with a short, flat intestinal loop and long branchial siphon) all have their body musculature on the right organised into transverse bands in the dorsal half of the body. However, their other characters do not indicate a natural group of species.

Ascidia nerea n.sp. has bands of short transverse muscles along the dorsal and ventral margin of the right side of the body as in the *sydneiensis* group, but is separated from that group by the absence of a fringe on the apertures.

Ascidia scaevola is a highly adapted sand-dwelling species, its flattened intestine and rectum resembling that of *A. prolata* n.sp., but it is isolated from all other known *Ascidia* spp. by many characters.

The affinities of the majority of species of the genus *Ascidia* in Australian waters are with the tropical fauna, although there are indigenous species in both temperate and tropical waters. On present records many species do seem to have a quite limited geographic range.

Key to the Species of *Ascidia* Recorded from Australia

1. Muscles form irregular mesh on right side of body 2
   Muscles do not form irregular mesh on right side of body 10
2. Extensions of inner wall of test projecting into body wall around gut 3
   No extensions of inner wall of test projecting into body wall around gut 4
3. Dorsal ganglion near dorsal tubercle .... *A. capillata*
   Dorsal ganglion not near dorsal tubercle ....*A. kreagra*
4. Tentacular fringe on apertures ....*A. occidentalis* n.sp.
   No tentacular fringe on apertures 5
5. Large spherical terminal ampullae in surface test 6
   No large spherical terminal ampullae in surface test 7
6. Atrial aperture in anterior half of body; some sand in test .... *A. decepta* n.sp.
   Atrial aperture in posterior half of body; no sand in test .... *A. latesiphonica*
7. Atrial aperture in anterior one-third of dorsal surface .... *A. challengeri*
   Atrial aperture not in anterior one third of dorsal surface 8

8. Intermediate branchial papillae .... *A. thompsoni*
No intermediate branchial papillae.... 9
9. Anal opening posterior to pole of gut loop 10
Anal opening more or less level with pole of gut loop.................................. *A. glabra*
10. Up to 4 stigmata per mesh ....*A. gemmata*
More than 4 stigmata per mesh . *A. empheres*
11. Branchial fold on left side of dorsal lamina... ....*A. scaevola*
No branchial fold 12
12. Tentacular fringe on apertures 13
No tentacular fringe on apertures 17
13. Border of short, parallel muscles encircling right side of body.............................14
No border of short, parallel muscles encircling right side of body...................*A. liberata*
14. Anal border lobed................*A. sydneiensis*
Anal border not lobed...........................15
15. Atrial aperture in posterior one-third of body 16
Atrial aperture not in posterior one-third of body ....*A. parasamea* n.sp.
16. 2 or 3 stigmata per mesh....... *A. nerea* n.sp.
More than 3 stigmata per mesh .... *A. munda*
17. Gut loop wide open; proximal half of ovarian tube branched ....*A. archaia*
Gut loop narrow, closed; less than half of proximal end of ovarian tube branched..18
18. Test brittle with sand; branchial siphon short ....*A. pandora* n.sp.
Test not brittle with sand; branchial siphon very long......................*A. prolata* n.sp.

The following species are known from the Indonesian region but are not yet recorded from Australia:

Ascidia bifissa Sluiter, 1887 has a terminal branchial siphon, and a sessile posteriorly positioned atrial aperture. Externally, it resembles *A. thompsoni*, but does not have intermediate branchial papillae, and has a smaller number of stigmata than the latter species. It also resembles some of the larger specimens of *A. kreagra* and *A. latesiphonica* but is distinguished by the interrupted opening of the dorsal tubercle.

Ascidia kuneides Sluiter, 1887 (ZMA V.TU239) has sessile apertures and only 2 short stigmata in each mesh. Longer stigmata appear to be in the process of subdivision by the parastigmatic vessels. The branchial sac resembles that of *A. nerea* n.sp.

Ascidia limpida Sluiter, 1904 has side branches on the branchial papillae. Only the thin, sand-encrusted test of the type specimen (ZMA V.TU246) remains. It is similar to the test of *A. nerea* n.sp.

Ascidia melanostoma Sluiter, 1885 resembles *A. kreagra* in its branchial sac, although it has darkly pigmented sessile apertures (which are not present in the latter species). The type specimen is lost (Spoel 1969).

Ascidia nodosa Sluiter, 1887, 1890 has 2 or 3 stigmata in each mesh and an 8-lobed branchial aperture. It appears not to have branchial papillae. It is known from 2 specimens, which appear to be juveniles rather than specimens of the genus *Ascidiella*. The holotype specimen of this species (ZMA V.TU255) contained a label, *A. munda* (see Spoel 1969). In fact, the specimen is one of *A. munda*. It may be the missing specimen of *A. translucida* Sluiter, 1890 (< *A. munda* Sluiter, 1898a nom. nov.).

Ascidia perfluxa Sluiter, 1904 (ZMA V.TU357) is a richly vascularised species. There are the same number of stigmata per mesh as in *A. kreagra*, however, the branchial sac is strengthened with intermediate longitudinal vessels in the meshes.

Ascidia spinosa Sluiter, 1904 (ZMA V.TU262) is covered with conical points about 5 mm high, thus resembling *A. samea* Oka, 1935 from Japan and the Philippines (*A. sydneiensis samea* : Tokioka 1967a). The body musculature is transverse and there are numerous glandular folds in the stomach lining.

Ascidia tricuspis Sluiter, 1904 has side branches on the branchial papillae, and only 2 stigmata per mesh. The gut forms a simple open loop. The type specimen has been lost.

Ascidia archaia Sluiter, 1890
(Fig. 7)

Ascidia archaia Sluiter, 1890, p.346; 1904, p.29.
Ascidia aperta Sluiter, 1904, p.38. Van Name, 1918, p.119. Tokioka, 1954a, p.257; 1962, p.9; 1967a, p.143. Millar, 1975, p.269. Nishikawa and Tokioka, 1976, p.389.
Ascidia rhabdophora Sluiter, 1904, p.45. Hartmeyer and Michaelsen, 1928, p.280. Tokioka 1953a, p.220. Kott, 1981, p.197 (part, specimens from Suva Barrier Reef and one from Dravuni).
Phallusia corelloides Van Name, 1924, p.27.
Ascidia corelloides: Van Name, 1945, p.187.

DISTRIBUTION

NEW RECORDS: Western Australia (Rowley Shoals, WAM 944.83). New South Wales (Norfolk I., QM GH2698). Queensland (Mudjimbah, QM GH2445; Hervey Bay, QM GH2545; Heron I., QM GH1343

Species	[1]Range outside Australia	[2]Range in Australian waters	[3]Distance between apertures	Branchial lobes	Lobes of apertures	Features of test	Opening of neural gland	Ganglion - dorsal tubercle	Body muscles, right side	Stigmata / mesh	Distal limb gut loop	Additional features
A decepta n.sp.	—	SA–Townsville	1/3–1/2	8	smooth	firm, sand embedded	entire	apart	mesh	8–10	cylindrical	spherical terminal ampullae
A. latesiphonica	—	Broome–Gladstone	1/2–2/3	7–10	"	firm, smooth	"	"	"	6–8	"	"
A thompsoni	—	SA	2/3	8	"	firm, some sand	entire to interrupted	"	"	6–8	"	intermediate branchial papillae
A. gemmata	WP	Broome–Townsville	"	8–11	"	firm, smooth	entire	"	"	3–4	sometimes distended	long stigmata
A. glabra	—	NSW–Cockburn Sd	1/3	9–10	"	"	"	"	"	6–8	cylindrical	—
A. kreagra	WP	Heron I.	1/2	8–10	"	"	"	"	"	4–5	"	internal test projections
A. empheres	WP	Heron I. - Abbot Pt.	2/3	7–8	"	finely papillated	"	"	"	6–8	"	stripes in siphon lining
A. capillata	WP	NSW–Albany	1/3	6–10	"	"	"	close	"	2–3	"	"
A. challengeri	sub-Antarctic	Tas.	1/3	10	"	"	"	"	"	6	distended	sessile apertures
A. nerea n.sp.	—	Gladstone	1/2–2/3	"	"	thin, sandy	"	"	marginal band	2–3	cylindrical	gut occupies most of left side
A. munda	WP	NSW–Shark Bay	1/2–2/3	6	fringed	firm, smooth	convoluted	"	"	8–10	sometimes distended	long body
A. parasamea n.sp.	—	NE Qld	1/2	7	"	thin, smooth	"	"	"	12	distended	circular body; 2 branchial pleats per mesh
A. sydneiensis n.sp	pan-tropical	NW Aust.- NT	1/3–2/3	6–10	"	thin, irregular	"	"	"	6–12	"	lobed anus
A. occidentalis	—	Cockburn Sd	1/3	8	"	"	entire	"	mesh	8	"	thin, opaque test
A. liberata	WP	Norfolk I. Heron I.	1/3–1/2	7	"	pointed papillae on siphons	"	apart	dorsal band	6–8	cylindrical	pointed test papillae
A. pandora	WP	Heron I.	1/2	8	smooth	sandy, brittle	"	close	"	4–6	distended	sessile apertures
A. archaia	WP	Norfolk I. - Rowley Shoals	"	8–10	"	smooth glassy	"	"	"	4–6	cylindrical	intermediate branchial papillae; proximal half of ovary branched; open gut loop
A. prolata n.sp.	—	Tas.	"	10	"	some sand	"	apart	"	3	flat	long branchial siphon; short gut loop
A. scaevola	WP	SA - Townsville	1/3	8	"	sandy, brittle	entire to interrupted	close	3 dorsal	5	"	pseudosiphons; short gut loop

[1]WP, western Pacific. [2]Range is given anti-clockwise around the continent. [3]As a fraction of the body length.

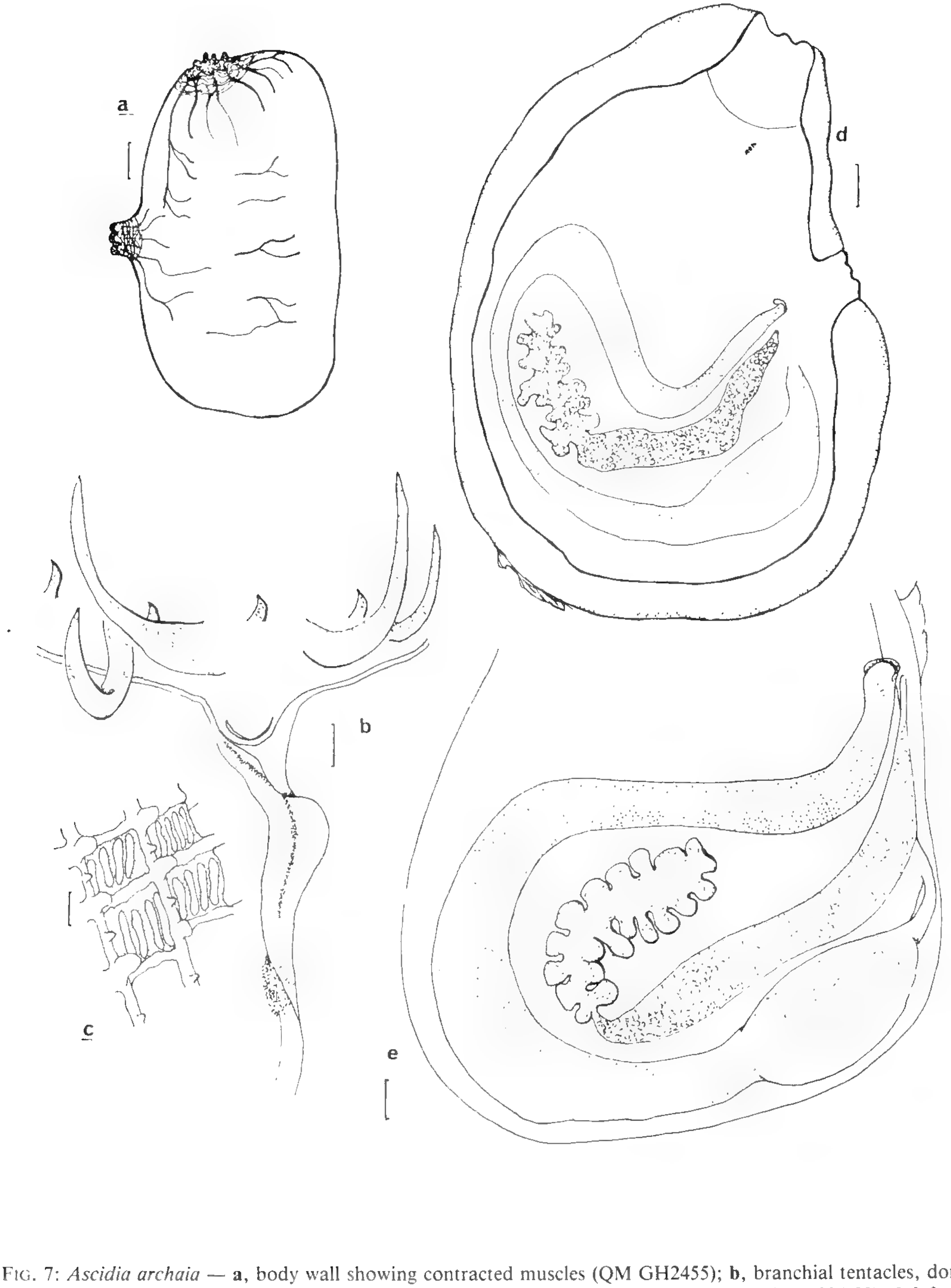


FIG. 7: *Ascidia archaia* — **a**, body wall showing contracted muscles (QM GH2455); **b**, branchial tentacles, dorsal tubercle and anterior part of dorsal lamina (QM GH3064); **c**, portion of branchial sac (WAM 994.83); **d**, left side of body showing gut and ovary (QM GH2445); **e**, gut and ovary showing variation in orientation of the ovary (QM GH3064). (Scales: **a**, 2.0 mm; **b**, **c**, 0.01 mm; **d**, **e**, 1.0 mm).

GH2542-4 GH2547-8 GH2550-2 GH2600 GH2615 GH2626 GH3000 GH3040 GH3064; Wistari Reef, QM GH2988; Lizard I., QM GH2546 GH2549 GH2553).

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Hartmeyer and Michaelsen 1928). Indonesia (*A. archaia* type ZMA V.TU212 Sluiter 1890, 1904; Millar 1975). Philippines (Van Name 1918). Fiji (Kott 1981). Marshall Is. (Tokioka 1967a). Japan (Tokioka 1953a; Tokara and Amami Is — Tokioka 1954, Nishikawa and Tokioka 1976; Izu Peninsula — Tokioka 1962). West Indies (Van Name 1924, 1945).

The species is commonly found under stones and rubble in shallow pools and crevices. One specimen from Heron I. (taken from an experimental plate that had been in the water for 6 months) is 5 cm long.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are oval and laterally flattened, fixed by the left side, and up to 5 cm in length. The outer border is firm and rounded. The apertures are sessile except in larger specimens when the atrial aperture is on a conical elevation. The 8 to 10-lobed branchial aperture is terminal, and the 6 to 8-lobed atrial aperture is about halfway along the dorsal surface. Red pigment spots are present between the lobes of the apertures and there is often a fine red line around the apertures. In living specimens the test is smooth and firm. Usually it is transparent and glassy, although some individuals taken from the eastern end of the Heron I. reef (QM GH3064) were maroon purple (Ridgeway 1886). It is thinner on the left side of the body than on the right, and is thickest around the apertures. Thick test on the right side of the body causes small specimens to appear almost hemispherical. The main test vessel enters the test about halfway along the ventral surface, and the 3 primary branches can be seen clearly in the test. There are rather sparse terminal branches at the surface.

Two commensal amphipods present in the atrial cavity can usually be seen through the glassy test of living specimens.

INTERNAL STRUCTURE: The body musculature is rather sparse. There are circular muscles around the apertures. On the right side of the body, there is a very open meshwork of muscles, which when contracted are gathered into a few, short, transverse bands that extend only halfway down the side of the body. Muscles do not extend beyond the base of the siphons on the left. There are about 40 sturdy branchial tentacles, large and small alternating, and these alternate with rudimentary tentacles. The anteriorly directed opening of the neural gland is transverse, or forms a wide U-shape curving around the base of a shallow peritubercular area. The dorsal ganglion is a short distance posterior to the tubercle. The dorsal lamina is a broad membrane, double anteriorly to a point just posterior to the neural ganglion. It is ribbed on both sides. Small, pointed projections extend from the ribs beyond the border of the membrane.

There are rounded papillae at the junctions of the internal longitudinal vessels with the transverse and parastigmatic vessels, and small intermediate papillae are present on the longitudinal vessels between the primary papillae. There are 4 to 6 stigmata per mesh. The branchial sac has only minute pleats.

The gut occupies the posterior half to three-quarters of the body. The primary loop is long and rather wide. The curvature of the loop varies with the contraction of the body. When it is strongly contracted, the rectum (which is sometimes short) can be bent back tightly against the descending limb of the intestine. When the body is relaxed, however, the gut loop is gently curved around the posterior end of the body, and the secondary loop is wide and open. The stomach is spherical or slightly elliptical, with 4 longitudinal folds. The anal border is smooth. Hartmeyer and Michaelsen (1928, Fig. 7) have shown the variation in the curve of the gut loop.

The gonads are in the primary gut loop. The ovary is tubular and has rather short, rounded and sometimes almost pinnate branches along the proximal one third of its length. The branching part of the ovary lies along the inner curve of the intestinal part of the ascending limb of the gut loop. The distal part of the ovary is a wide, thick tube extending parallel to the rectum to open near the anal opening. It is separated from the proximal part by a constriction. In some of the larger specimens (QM GH3064) the proximal branching part of the ovary curves dorsally parallel to the descending limb of the gut loop and the distal part of the ovary. The testis follicles are small and branching, spreading over the limbs of the gut loop and joining to a wide tubular vas deferens. The male and female gonads do not appear to mature at the same time.

REMARKS: The wide gut loop, glassy test, sessile apertures, sparse body musculature that is largely transverse, intermediate branchial papillae, and the relatively large part of the ovarian tube that is branched are all characteristics of this species. Living specimens are readily identified by the two active amphipods that are always visible through the glassy test.

Intermediate branchial papillae are reported to be present in *Ascidia decemplex* Sluiter, 1890.

However these are not present in the type (ZMA V.TU223), and the species are readily distinguished by other characters.

Ascidia archaia was reported (Sluiter 1890) to have the rectum tightly folded back against the descending limb of the gut loop, but this condition results from contraction of the dorsal part of the body. *A. archaia* (ZMA V.TU212), with its open primary gut loop, glassy test and ovary branched along the proximal half of its length, is inseparable from specimens of *A. aperta*.

Kott (1981) ascribed specimens with pointed papillae around the apertures and a narrow gut loop to *A. rhabdophora*. Reexamination of these specimens has confirmed that they are *A. liberata*.

Ascidia rhabdophora Sluiter, 1904 has an identical morphology to that of the present species. The calcareous spicules in the outer layer of test that were believed to distinguish it from the present species (Sluiter 1904, Hartmeyer and Michaelsen 1928) were, apparently, artefacts or foreign bodies (as suggested by Tokioka 1953a).

Tokioka (1953a) had suggested that *Ascidia corelloides* (Van Name, 1924) from the West Indies is conspecific with *A. rhabdophora*, a junior synonym of the present species. This relationship is confirmed.

Ascidia capillata Sluiter, 1887.
(Fig. 8a–d)

Ascidia capillata Sluiter, 1887, p.255.
Ascidia austera Sluiter, 1904, p.39. Hartmeyer, 1909, p.1401. Hartmeyer and Michaelsen, 1928, p.297. Kott, 1966, p.296.
Ascidia melanostoma: Kott, 1981, p.197.
? *Ascidia cylindracea* Herdman, 1882, p.216. Sluiter, 1904, p.32.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM GH2622 GH2997 GH3019 GH3082; Wistari Reef, QM GH3030; Abbot Bay, QM GH704).

PREVIOUSLY RECORDED: Western Australia (Oyster Harbour — Hartmeyer and Michaelsen 1928). ? New South Wales (Twofold Bay — Herdman 1882). Northern Territory (Darwin — AM Y1654 Kott 1966). Indonesia (*A. capillata* type ZMA V.TU219 Sluiter 1887, *A. austera* ZMA V.TU267.2 Sluiter 1904). Fiji (Kott 1981).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals up to 4.0 cm are known. The body is oval to elongate, tapering to the terminal branchial aperture. It is laterally flattened and fixed by the whole of the left side. Externally both apertures are sessile, although the surrounding test is ridged. The branchial aperture has 8 to 10 lobes and the atrial aperture, one-third of the way down the dorsal border, is 6-lobed. In preservative, the test is usually translucent, with inconspicuous clouds of minute dark pigment particles and more intense dark pigment around the apertures and in the siphon linings. In life, the body is pinkish vinaceous with darker siphons (Ridgeway 1886). The branches of the test vessels are numerous and there are numerous terminal branches at the surface. Sometimes the surface of the test is raised into minute pointed papillae over the terminal branches of test vessels. In other specimens, although the terminal branches of the test vessels can be seen near the surface, the test over them is smooth. The surface test of preserved material has rounded swellings and creases. The lobes of the apertures are smooth, with ocelli between them.

Sand particles are attached to the very thin test on the left side, where it is fixed to the substrate. This part of the test is very readily torn.

INTERNAL STRUCTURE: Generally the body is a whitish colour in preservative. Wide, flat membranes, terminating around their borders in irregularly branched processes, extend from the inside of the test and project into, but do not penetrate, the body wall around and in the centre of the gut loop. The effect is to partially isolate the gut from the remainder of the body, surrounding it with test to varying extents, and causing the left side of the body to be associated very closely with the test. The test vessel enters the test through one of the test membranes ventral to the gut loop. The body wall is very delicate. The very short and exceptionally narrow siphons have longitudinal and circular muscles. An open, irregular mesh of muscles is present on the right side, but muscles on the left are present only anterior to the gut loop. There are about 40 rather long and crowded branchial tentacles. The narrow prebranchial zone is finely papillated. The dorsal tubercle is a large, circular cushion with a large U-shaped slit. It fills the V-shaped peritubercular area. The neural ganglion is close behind the dorsal tubercle. The left half of the double anterior part of the wide, ribbed dorsal lamina passes to the left of the peritubercular area. Posteriorly, the ribs of the dorsal lamina are produced into short projections from the edge of the membrane.

The branchial sac has shallow pleats. Large rounded papillae are present at the junctions of the transverse and internal longitudinal vessels. There is a single pleat to each mesh with 2 or 3 rectangular stigmata.

The gut forms a deeply curved double loop. There are four internal folds in the short, elliptical, dark stomach. The oesophagus is long, originating

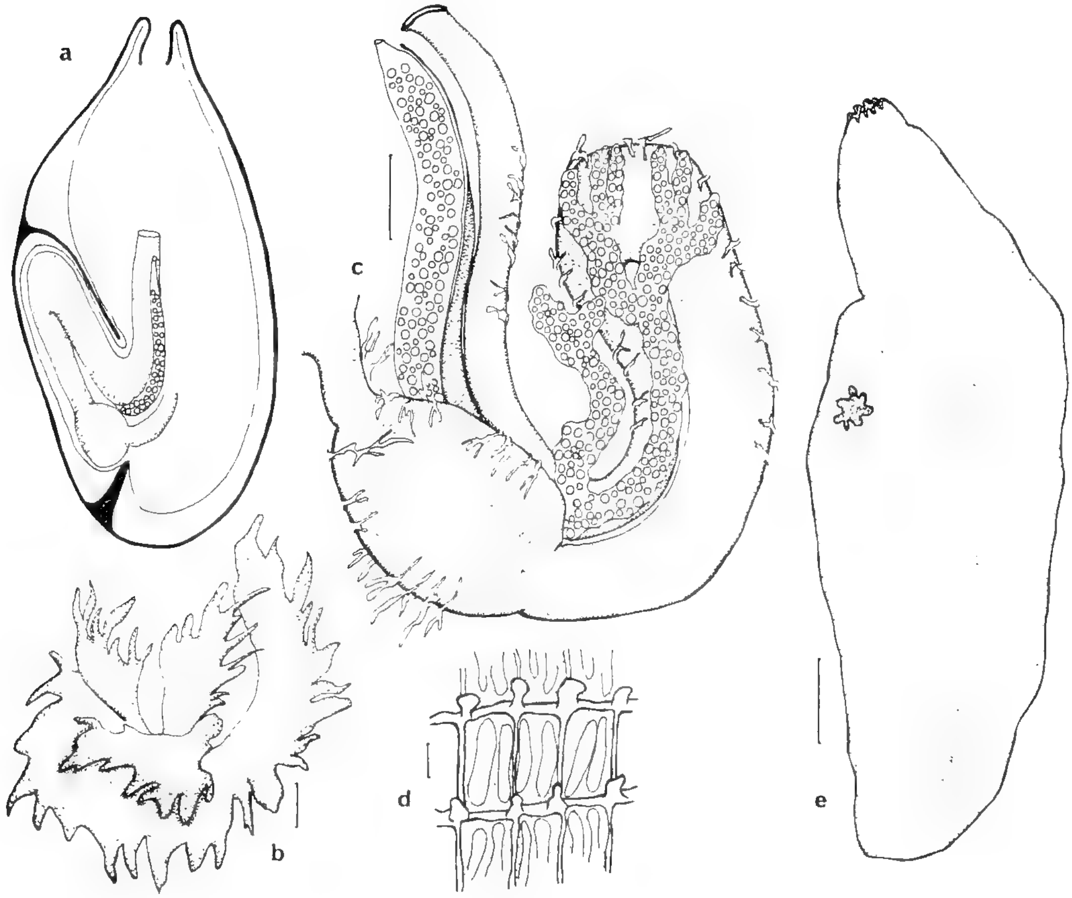


FIG. 8: *Ascidia capillata* (QM GH2622) — **a**, profile of body from dorsal surface showing test partially enclosing gut (diagrammatic); **b**, membranes from inner surface of test; **c**, gut and gonads showing terminal tips of test membranes curving around the gut; **d**, portion of the branchial sac. *Ascidia challengeri* — **e**, external appearance. (Scales: **b**, **c**, 1.0 mm; **d**, 0.1 mm; **e**, 1.0 cm).

from about two-thirds down the branchial sac. The rectum is a very long flat tube extending anterior to the pole of the gut loop (which curves dorsally). The branchial sac projects posterior to the stomach, which extends transversely across the body.

The ovary has long, narrow branches. Some join the thick oviduct at the level of the stomach. The terminal branches curve around the outside of both limbs of the gut loop.

The ragged edges of the test membrane that partially isolate the gut from the body wall can sometimes be seen on the mesial surface of the gut, curving around the outside of the loop, especially the descending limb, and around both sides of the stomach.

REMARKS: This is a unique species, in which the test becomes rather intimately associated with the body wall, partially isolating the gut and gonad from the remainder of the body wall. This is a condition reminiscent of *Microgastra* n. gen., although the body wall projects out into the test in the latter species. The species is otherwise similar to other species of *Ascidia*, with its gonads enclosed in the long, narrow, deeply curved gut loop. The flattened rectum is also reminiscent of that of *Microgastra* spp., although it is very much longer.

The double dorsal lamina extending up to the left of the dorsal tubercle is similar to that found in species of the *sydneiensis* group, although other characteristics of that group are not present.

The species is also characterised by the dark pigmentation in the linings of the short, narrow, anteriorly situated siphons; almost flat branchial sac with very shallow pleats and few stigmata in each mesh; long rectum extending anterior to the pole of the gut loop to reach the anterior atrial siphon; and dorsal curve of the intestinal loop. The dark pigmentation persists in the siphons of alcohol-preserved specimens.

Ascidia capillata is distinguished from *A. glabra* and *A. gemmata* by its more numerous test vessels, internal test membranes, rather narrow internal siphons and anteriorly positioned atrial aperture. In *A. kreagra* there is an internal ridge of test that fits under the descending limb of the gut loop. It is more solid and less extensive than the test membranes of the present species. *Ascidia kreagra* is also more robust, with thicker test, more stigmata per mesh, more conspicuously pleated branchial sac. Its bright canary yellow colour clearly distinguishes the living specimens from those of the present species.

Ascidia challengeri Herdman, 1882
(Fig. 8e; Pl.Ia)

Ascidia challengeri Herdman, 1882, p.202; 1923, p.28. Arnback, 1938, p.46. Van Name, 1945, p.192. Kott, 1954, p.148; 1969a, p.90; 1971, p.40. Millar, 1960b, p.89. Vinogradova, 1962, p.198.
Phallusia challengeri: Hartmeyer, 1912b, p.283.
Ascidia charcoti Sluiter, 1905b, p.471; 1906, p.34. Herdman, 1912b, p.314; 1915, p.96; 1923, p.29.
Phallusia charcoti: Hartmeyer, 1911, p.466; 1912, pp.286, 287. Sluiter, 1914, p.26.
Ascidia dispar Arnback, 1938, p.48.

DISTRIBUTION

NEW RECORD: Tasmania (Port Davey, QM GH2012).

PREVIOUSLY RECORDED: Tasmania (Herdman 1923, Kott 1954). Kerguelen Is., Heard I. (Herdman 1882, Hartmeyer 1912b, Kott 1954, Vinogradova 1962). Antarctic Peninsula and Scotia Ridge (Sluiter 1905b 1906 1914, Arnback 1938, Millar 1960b, Kott 1969a). Antarctic Continent (Hartmeyer 1911, Herdman 1923, Vinogradova 1962, Millar 1960b, Kott 1969a).

The species is one of the few from the sub-Antarctic that extends north of the subtropical convergence. It has a wide circumpolar range and is found in waters down to 600 m in depth in the southern part of its range.

DESCRIPTION

EXTERNAL APPEARANCE: The newly recorded specimen is 9 cm long, more or less cylindrical over most of its length, narrowing to the terminal branchial aperture. The atrial aperture is small and inconspicuous, about one-third of the distance down the dorsal surface. Both apertures are sessile. There are 10 branchial lobes and 8 atrial lobes. Ocelli are present between the lobes, which are not fringed. The test is firm and only very slightly translucent. The test vessels branch profusely. Terminal branches are not expanded into spherical ampullae.

INTERNAL STRUCTURE: Muscles form an irregular mesh on the right side of the body but these straighten into a band of parallel, transverse muscles across the dorsal mid-line. On the left, the muscles are limited to the part of the body anterior to the gut loop. There are about 100 crowded branchial tentacles, their bases extending around a muscular velum to form ribs around it. The prebranchial area is conspicuously papillated. A large, circular dorsal tubercle has a U-shaped slit, but there is no V-shaped peritubercular area. The dorsal ganglion is a short distance posterior to the dorsal tubercle, about halfway between the tubercle and the base of the anteriorly positioned atrial siphon. The dorsal lamina is ribbed, and the ribs project beyond the edge of the membrane. It is a double membrane anteriorly.

The branchial sac has only very shallow pleats and long meshes with about 6 long stigmata in each mesh. The branchial papillae are large and rounded; occasionally very small intermediate papillae are associated with parastigmatic vessels that cross the stigmata.

The gut forms a long, deeply curved loop. The descending limb of the intestine, and the rectum are considerably distended with mud. The anal border has a few, irregularly placed indentations, but is otherwise smooth. The gonads are in the usual position in the very tight gut loop.

REMARKS: The external appearance of this specimen very closely resembles individuals from south of the sub-tropical convergence. Its branchial tentacles are more numerous, however, and they appear to be arranged in a single circle rather than in two as previously described (Millar 1960b; Kott 1969a). It is possible that the apparent arrangement of the branchial tentacles is obscured by the contraction of the muscles at their base.

As in the present specimen, those from Antarctic locations are often found with mud-distended gut, and the branchial sacs are also similar. The external appearance and the branchial sac, with its occasional intermediate papillae and parastigmatic vessels, shallow pleats and relatively long stigmata, provide the principal characters by which the species can be distinguished from others occuring in Australian waters.

Ascidia decepta n.sp.

(Fig. 9)

Ascidia thompsoni: Kott 1975, p.10.

DISTRIBUTION

TYPE LOCALITY: Queensland (Fraser I., 1 km from mouth of Moon Creek, off wreck, coll. P. Davie. 20.7.75, holotype QM G10076).

NEW RECORDS: Tasmania (Spring Bay, QM GH2027), South Australia (St Vincent Gulf, paratype QM G9629; Kangaroo I., paratypes QM G10002), Queensland (Moreton Bay, QM G4976 GH349 GH2573; Fraser I., paratype GH2581; Burnett Heads, QM GH2578; Gladstone, QM G9713 GH271 GH11881 GH11883–4 GH2574 GH2579; Abbot Point, paratypes QM GH2571–2 GH2575–7 GH2580; Townsville, QM GH2566).

PREVIOUSLY RECORDED: South Australia (Upper Spencer Gulf — Kott 1975).

The species has been taken in shallow water on mud or sandy substrates.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are oval, up to 5 cm long. They are usually dorso-ventrally or, occasionally, laterally flattened. Both apertures are on short, cylindrical, often but not always ridged, siphons of equal length that are relatively close to one another in the anterior half of the body. They are often parallel to one another, at right angles to the long axis of the body, the branchial siphon arising from the anterior end of the dorsal surface. However, the branchial siphon is sometimes terminal and turned dorsally. There is sand, sometimes sparse but often in quite a dense coat, embedded in the test, but the rather fleshy siphons are always naked. Lamellibranch molluscs are sometimes embedded in the test, causing some swellings and irregularity in the otherwise even surface. The test is firm and gelatinous and glassy, and there are conspicuous bladder cells between the large, spherical, terminal ampullae of test vessels that are characteristically present in the surface test and especially conspicuous on the siphons. They are of variable size and probably function as chromatophores. In some specimens these are less conspicuous and appear to have broken or are collapsed.

There are 8 branchial lobes and 6 or 7 atrial lobes around the respective apertures. Ocelli are present between the lobes of the apertures. In some specimens, there are pigmented stripes in the siphon lining.

INTERNAL STRUCTURE: Outer longitudinal and inner circular muscles are present on the siphons. On the right, they extend over the side of the body to form an irregular meshwork of branching longitudinal and transverse muscles that terminate parallel to one another at right angles to the ventral border. Dorsally, they cross the mid-line onto the left side of the body. On the left, the longitudinal bands are conspicuous anterior to the gut loop, but muscles are absent over the gut. The internal branchial siphon is relatively short. The internal atrial siphon always arises from about halfway down the body and is always long. Both siphons have a conspicuous layer of circular muscles.

There are 60 to 80 very fine branchial tentacles. The dorsal tubercle is a large, circular cushion in the narrow prebranchial area. A peritubercular area is present occasionally, but is very shallow. The slit is almost circular, its open interval directed anteriorly; sometimes one or both of its horns are turned in or overlap. The ribbed dorsal lamina is double anteriorly, becoming single in the vicinity of the neural ganglion, which is about half the distance between the atrial siphon and the tubercle. The ribs of the dorsal lamina project from the membrane along the middle part of its length, and there is often a small intermediate projection between the primary ones. In one specimen (from Bowen) the slit on the dorsal tubercle is interrupted.

The branchial papillae are curved, with a protruberance near the base of their dorsal concave border. The meshes are wide and short, the stigmata being very short and oval. The pleats in the branchial sac are shallow and rather wide, usually less than one per mesh. There are about 12 stigmata per pleat, but only 8 to 10 per mesh.

The gut forms a deeply curved loop, rather open at the pole. The intestinal part of the loop curves dorsally toward the tip of the rectum, which projects up into the base of the atrial siphon and terminates in a smooth-rimmed or very inconspicuouly scalloped anus.

The gonads are present in the gut loop. About the proximal quarter of the ovarian tube is irregularly branched. Male follicles underlie the ovary and extend out over the gut loop.

REMARKS: The sand-embedded test, the short, cylindrical and often upright and naked siphons, and the ovarian tube that is branched for up to half the length of the intestinal part of the gut loop are characteristic, and present even in juvenile specimens. Specimens in which the spherical terminal ampullae are broken or collapsed can be distinguished from most other species by the glassy test, usually with embedded sand.

Ascidia glabra has similarly short and wide meshes in the branchial sac, but lacks the spherical chromatophores in the surface test (which should not be confused with the stellate chromatophores

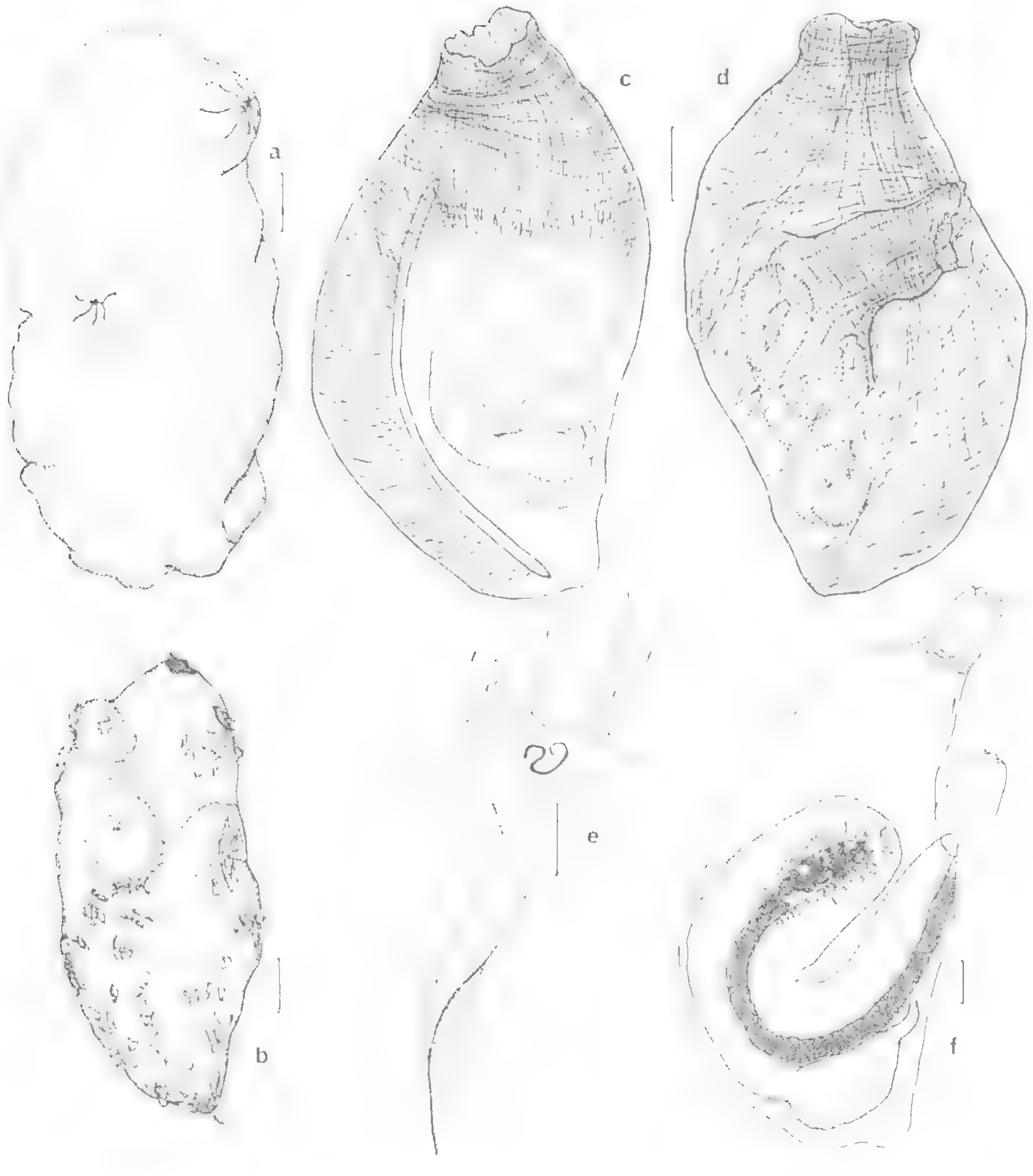


FIG. 9: *Ascidia decepta* n.sp. — **a**, **b**, external appearance (QM GH2573, G9629); (**c**, **d**, body musculature (QM G9629) (**c**, from ventral surface; **d**, from dorsal surface); **e**, dorsal tubercle and anterior part of dorsal lamina (QM GH9629); **f**, left side of body showing gut loop, ovary and some male follicles (QM G10076). (Scales: **a**, 2.0 mm; **b**, 5.0 mm; **c**, **d**, **f**, 2.0 mm; **e**, 1.0 mm).

of *Phallusia julinea*). Although the accessory openings of the neural gland are not always present and the test chromatophores are faded, the latter species can be distinguished from *A. decepta* by its thicker, firmer, opaque and smooth-surfaced test, and tentacular fringe on the lobes of the apertures.

Specimens of *Ascidia latesiphonica* in the present collection have spherical terminal ampullae that resemble those of the present species. The species are distinguished primarily by the shape of the body, *A. latesiphonica* being long and narrow, usually with a long, terminal branchial siphon and the atrial siphon at varying distances along the dorsal surface. *Ascidia decepta* has a shorter, more rectangular body with short atrial and branchial siphons, more numerous stigmata in each pleat of the branchial sac and some sand embedded in the test (while *A. latesiphonica* is usually naked).

Ascidia empheres Sluiter, 1895
(Fig. 10a–d)

Ascidia empheres Sluiter, 1895, p. 177; 1904, p. 31.

DISTRIBUTION

NEW RECORDS: Queensland (Heron Is., QM GH2461 GH2463 GH3068 GH3074 GH3472-3; Wistari Reef, QM GH3108; Don River, QM GH703). PREVIOUSLY RECORDED: Indonesia (ZMA V.TU227 Sluiter 1895, 1904).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are club-shaped, rounded posteriorly and narrowing to a terminal 7 or 8-lobed branchial aperture. The posteriorly oriented, 6 or 7-lobed atrial aperture is two-thirds of the body length distant from the branchial aperture. In smaller specimens both apertures appear to be sessile, but larger specimens (up to 6 cm) have short, ridged siphons.

The body is slightly laterally flattened and fixed by almost the whole of the left side, where the test is very thin. Elsewhere, the test is firm, gelatinous and cloudy. The surface is very finely papillated. Test vessels are relatively sparse and there are no expanded terminal ampullae.

The living specimens are slate-grey, with dark pigment particles dispersed through the test. The colour is more intense anteriorly. The test vessels contain masses of very bright yellow corpuscles, which become dark in preservative.

INTERNAL STRUCTURE: The internal siphons are distinct even in very small specimens. The body wall has a mesh of muscles on the right side of the body. On the left, muscles are present only anterior to the gut loop. In freshly preserved specimens, dark corpusles are present in the body wall, the branchial tentacles and the vessels and papillae of the branchial sac. Dark longitudinal stripes are present in the siphon lining. There are 12 to 24 branchial tentacles, not very crowded and only of moderate length, alternating with rudimentary tentacles. The prebranchial area is narrow and finely papillated. There is no peritubercular V, and the small dorsal tubercle is in the prebranchial area, at the anterior end of the dorsal lamina. The opening of the neural gland is a simple U-shape with one or both horns turned out. The open interval between the two folds of the dorsal lamina is displaced slightly to the left of the dorsal mid-line. The dorsal lamina is ribbed, and from about halfway down the body, the ribs project from the free edge of the membrane as small languets. The dorsal ganglion is halfway between the dorsal tubercle and the atrial siphon.

The branchial sac has conspicuous pleats, slightly less than one in each mesh, and there are about 8 long rectangular stigmata in each pleat. The papillae at the junctions of the longitudinal and transverse vessels are large, and have a membrane extending out along the transverse vessels from their concave side.

The deeply curved, but relatively short gut loop is in the posterior half to one-third of the body, the pole of the loop being only slightly anterior to the anus which curves out into the posteriorly oriented atrial siphon.

The gonads are in their usual position in the gut loop. Long branches from the proximal end of the ovarian tube curve around onto the outside side of the pole of gut loop.

REMARKS: The posteriorly oriented atrial siphon and general shape of the body, together with its musculature are the same as in *Ascidia gemmata*. Living specimens can be distinguished by the dark slate colour of the present species and its profuse yellow blood corpuscles in the test vessels. In preservative, the deep branchial pleats, more numerous stigmata, shorter and less numerous branchial tentacles, shorter gut loop and cloudy, sometimes dark test distinguish the present species. Externally, individuals also resemble *Ascidia capillata* but can be distinguished by the posterior position of the atrial aperture in *A. empheres*.

Sluiter (1895) records only 4 stigmata in each branchial mesh. The holotype (ZMA V.TU227) has the usual tight branchial pleats which possibly obscured the 6 to 8 stigmata that are present in each mesh.

FIG. 10: *Ascidia empheres* — **a**, external appearance (QM GH3068); **b**, body wall from left side (QM GH3068); **c**, portion of branchial sac (QM GH3472); **d**, dorsal tubercle (QM GH3472). *Ascidia gemmata* — **e**, external appearance (QM GH2457); **f**, right side of body showing muscles; **g**, left side of body showing gut and gonads (QM GH2466); **h**, border of apertures standing out in a frill that leaves the ocelli exposed on contraction (diagrammatic); **i**, portion of the branchial sac. (Scales: **a**, **b**, **e–g**, 2.0 mm; **c**, **d**, **i**, 0.1 mm).

Ascidia gemmata Sluiter, 1895
(Fig. 10 e-i)

Ascidia gemmata Sluiter, 1895, p.177; 1904, p.29. Herdman, 1899, p.15. Hartmeyer, 1919, p.95. Hartmeyer and Michaelsen, 1928, p.292. Tokioka, 1950, p.131; 1952, p.103; 1961, p.107. Kott, 1952, p.308; 1966, p.296; 1976a, p.74; (not: 1972a, p.26, < ? *A. latesiphonica*).
Phallusia gemmata Hartmeyer, 1909, p.1402.

DISTRIBUTION

NEW RECORDS: Western Australia (Broome, WAM 941.83; Cockburn Sound, WAM 133.75). Victoria (Bass Strait, NMV H733). Queensland (Hervey Bay, QM G9360 GH2430 GH2468 GH2481; Heron I., QM GH1436-7 GH1439 GH2458-9 GH2462 GH2464-7 GH2623 GH2625; Northwest I., QM GH2457; Townsville, QM GH2564 GH2495; Magnetic I., QM GH2460).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Shark Bay, Cockburn Sound, Albany — Hartmeyer and Michaelsen 1928). Victoria (Port Phillip Bay — Kott 1976a). New South Wales (Port Jackson — Herdman 1899). Arafura Sea (Tokioka 1952). Indonesia (Sluiter 1895, 1904). Palau Is (Tokioka 1950). Noumea (Tokioka 1961).

DESCRIPTION

EXTERNAL APPEARANCE: The body is long (up to 10 cm) and relatively narrow. It is dorso-ventrally flattened and is usually fixed by a large part of the left side of the test, which is often spread out from the sides of the body where it is fixed to the substrate. The branchial and atrial apertures are sessile or on conical to cylindrical ridged siphons that sometimes increase in length with the size of the individual. One specimen from Hervey Bay (QM GH360) has a branchial siphon that is half the total length of the body (10 cm). The branchial aperture is terminal, or curved up to open on the dorsal or upper surface. The atrial aperture is directed at right angles to the long axis of the body, or posteriorly. It arises about two-thirds of the body length from the atrial aperture. There is often no external atrial siphon, although the branchial siphon is usually present. There are 8 to 13 branchial lobes, and 6 or 7 atrial lobes, with ocelli between the lobes. The test is translucent and cloudy. The branched test vessels are conspicuous, although the terminal ampullae are very small. The test is firm and especially thick on the right side of the body. Its surface is smooth without tubercles, papillae or epibionts. In preserved specimens, some dark pigment is present in the test around the apertures, and stripes are sometimes present in the siphonal lining. Living specimens are vinaceous pink or citron yellow (Ridgeway 1886), shading to orange around the apertures.

INTERNAL STRUCTURE: Longitudinal and transverse muscles form an irregular mesh on the right side of the body. These form into a regular band of parallel transverse muscles around the ventral margin. The body wall is almost opaque, with a vascular network that is greenish yellow in preservative. There are over 100 crowded branchial tentacles on the edge of a muscular velum. There is a narrow papillated prebranchial area. The large dorsal tubercle in a V-shaped peritubercular area has an almost closed C-shaped slit. The neural ganglion is distant from the dorsal tubercle, about halfway between the widely separated apertures. The dorsal lamina is a double membrane as far back as the neural ganglion. It is strongly ribbed on the left; the ribs project from the border of the membrane.

The stigmata are long and narrow, and there are only 3 or 4 in the very shallow pleats of the branchial wall. The branchial meshes are square, or longer than their width. The branchial papillae at the junctions of the transverse and longitudinal vessels have a conspicuous projection at the base of their dorsal concave border.

The gut forms a long, narrow, deeply curved loop, open at the pole. The rectum curves dorsally to the posteriorly positioned atrial aperture. The anal border is smooth. The descending limb of the gut loop, and the rectum are often distended with mud. The pole of the gut loop is always anterior to the anus and the loop itself is either parallel to the long axis of the body, or curved over toward the dorsal surface.

The gonads are of the usual ascidiid type. The tubular oviduct has long branches from its proximal end that cover the mesial side of the gut loop and sometimes project beyond it where they can be seen from outside the left side of the body.

REMARKS: The species is characterised by its small number of long stigmata, orange pigmentation and posteriorly oriented atrial siphon. It is distinguished from *A. glabra* by the posterior position of its neural ganglion and atrial aperture, and the lesser number of shorter stigmata in each mesh.

Ascidia kreagra is distinguished by its internal test lamella, more anteriorly positioned atrial aperture and neural ganglion and by the very numerous terminal branches of test vessels.

Ascidia glabra Hartmeyer, 1922
(Fig. 11)

Ascidiella aspersa: Hartmeyer, 1920a, p.210.
Ascidia glabra Hartmeyer, 1922, p.305. Hartmeyer and Michaelsen, 1928, p.304.

FIG. 11: *Ascidia glabra*: a, external appearance; b, left side of body showing terminal branches of ovarian tube curving around the outside of the gut loop; c, portion of branchial sac. (Scales: a, b, 2.0 mm; c, 0.1 mm.)

DISTRIBUTION

NEW RECORDS: New South Wales (Arrawarra, QM GH2533). Queensland (Moreton Bay, QM GH2540; Cape Vernon, QM GH2539; Heron I., QM GH2532 GH2534-7 GH2628-31 GH2975 GH3003 GH3007 GH3041 GH3044 GH3059-63 GH3067 GH3427; Wistari Reef, QM GH2983 GH2987 GH2989 GH2993 GH2996 GH2998-9 GH3008 GH3428; Gladstone, QM G10058; N.W. Bowen, QM GH2531; Townsville, GH3428).

PREVIOUSLY RECORDED: Western Australia (Fremantle — Hartmeyer and Michaelsen 1928).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are long and relatively narrow: up to 7 cm long, and about 1.5 cm wide posteriorly (where the body is rounded) and narrowing anteriorly. They are attached by the whole of the left side. The apertures are on very short, conical, ridged siphons, the branchial aperture terminal and the atrial aperture about one-third to one-half of the distance down the dorsal surface. There are 9 to 12 branchial lobes and 6 to 8 atrial lobes. Conspicuous ocelli are present between the lobes of the apertures. The test is firm and translucent. There are occasional minute papillae on the surface, and some test hairs by which individuals may adhere to one another. Living individuals are wax yellow to citron yellow (Ridgeway 1886). They are faded and translucent in preservative, with red ocelli. There are small terminal vessels at the surface of the test, but these are not expanded into conspicuous ampullae. Some red blood cells are present in these vessels, especially around the apertures and occasionally forming a network of red in the surface test. Sometimes the surface test is slightly granular; in larger specimens it has some longitudinal creases.

INTERNAL STRUCTURE: The body wall has a mesh of muscles on the right, but on the left there is no musculature over the gut. Only longitudinal muscles radiating from the branchial siphon are present in the anterior part of the left side of the body. The muscles which form an irregular mesh in the centre of the right side of the body straighten to form a border of parallel bands around the border. About 100 branchial tentacles are crowded onto a muscular velum. There is a very shallow papillated prebranchial area, but no peritubercular V at the anterior end of the dorsal lamina. The dorsal tubercle is a large cushion just behind the ring of branchial tentacles. It has a large C-shaped slit, sometimes with one horn turned in. The neural ganglion is just posterior to the dorsal tubercle.

The branchial sac has very shallow pleats, with 6 to 8 oval stigmata in each. The meshes are short but very wide, and the transverse and longitudinal vessels are robust.

The gut forms a deeply curved loop. The intestinal part of the primary loop is especially long, and curves dorsally. The rectum extends anteriorly to open at the base of the sometimes anteriorly oriented atrial aperture, and the smooth-rimmed anus is level with or slightly anterior or posterior to the pole of the gut loop.

The gonads are present in the primary gut loop. Branches of the ovary from the proximal end of the tube are long, and extend over the mesial surface of the loop, project beyond its border, and curve around the sides of both ascending and descending limbs of the intestine.

REMARKS: The species resembles *Ascidia gemmata* and *A. liberata* in its habit and the nature of the test. It lacks the tentacular fringe on the lobes of the apertures and the pointed papillae (along the outside of the siphonal ridges) that are characteristic of *A. liberata*. It is further distinguished from the latter species by having more branchial lobes, more branchial tentacles, shorter stigmata in each branchial mesh, and a mesh of muscles on the right side of the body. It also resembles *A. gemmata* in the number of branchial lobes and branchial tentacles, and mesh of muscles on the right side of the body. It is distinguished from *A. gemmata* by its shorter and more numerous stigmata, more anteriorly positioned atrial aperture, and absence of stripes in the siphons.

Larger specimens closely resemble the Japanese species *Ascidia longistriata* Hartmeyer, 1906; Tokioka 1953a. However, the latter appears to have more conspicuous and consistent longitudinal creases in the test than the present species.

Ascidia kreagra Sluiter, 1895
(Fig. 12; Pl.1b)

Ascidia kreagra Sluiter, 1895, p.18.
? *Ascidia decemplex* Sluiter, 1890, p.343.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM GH1433 GH1435 GH1440 GH3073 GH3080–1 GH3459–60).

PREVIOUSLY RECORDED: Indonesia (ZMA V.TU238 Sluiter 1895, ? *A. decemplex* holotype V.TU223 Sluiter 1890).

DESCRIPTION

EXTERNAL APPEARANCE: The body is very variable (probably as a result of its habitat in crevices in the reef), from elongate (up to 4 cm long) to short and more or less square, often with the longitudinal axis of the body curved. The apertures are on short, thick, cylindrical siphons, the branchial aperture terminal and sometimes curved dorsally; the atrial half way down the dorsal surface and sometimes turned to the right. There are 8 to 10 branchial lobes and 7 atrial lobes. The lobes are pointed and each contains a median blood vessel. These pointed lobes alternate with small, rounded projections, each with a particularly bright ocellus in the centre. The test is firm and relatively thick on the right side. It is thinner on the left where the animal is usually fixed to the substrate. The surface is naked, always smooth and rather shiny, although in preserved specimens it is often creased and swollen here and there. The test is well vascularised, with branching vessels ending in terminal branches at the surface of the test. These terminal branches are not expanded into ampullae.

Internally, there is a long, flat ridge of test with a straight, even edge, that fits into a groove in the body wall along and under the descending limb of the gut loop and probably holds the gut in place.

The most striking characteristic of living specimens is their colour: canary yellow test, red siphons and red thorax seen through the test. In freshly preserved material yellow blood cells can be seen in the test vessels, especially around the apertures. The test becomes whitish and translucent in preservative.

INTERNAL STRUCTURE: In freshly preserved material, the right side of the body is opaque dark brown and the left side is equally opague bright red. Elliptical patches of bright red pigment, one corresponding to each lobe of the apertures, are somtimes present in the siphon linings. Conspicuous red and brown blood cells are also present in the branchial vessels, papillae and dorsal lamina. Although this colour fades, there is usually a trace of pigment in some part of the body wall.

There is a mesh of muscles on the right side of the body. On the left musculature is present only anterior to the gut. The branchial tentacles are not crowded. There are 12 to 15 longer tentacles alternating with from 1 to 3 of smaller sizes. The prebranchial area is narrow and papillated. The dorsal tubercle is circular, with a U-shaped slit. The dorsal ganglion and gland are halfway between the tubercle and the base of the atrial siphon. The dorsal lamina is double anteriorly, as far as the dorsal ganglion. It is conspicuously ribbed, the ribs projecting from the margin of the membrane. Both the papillae in the prebranchial area and the ribs of the dorsal lamina are bright red in freshly preserved material.

The branchial sac has fine internal longitudinal vessels, flattened papillae and is finely pleated. The meshes are short, there is one pleat per mesh with 4 or 5 oval to elliptical stigmata in each.

The oesophageal opening is about two-thirds of the distance down the branchial sac. The gut loop curves dorsally, the descending limb close and parallel to the rectum. The anal opening is slightly anterior to the pole of the gut loop.

Gonads are present in the gut loop. Long branches of the ovarian tube project around the mesial aspect of both ascending and descending limbs of the loop.

REMARKS: Living specimens of this species are very striking in appearance and are readily identified. Freshly preserved material is also characteristic with conspicuous red and brown blood cells. However, long term preservation removes the pigment. The presence of the internal test ridge fitting into a groove under the descending limb of the gut loop, finely pleated branchial sac with short meshes, the well spaced branchial tentacles and the well vascularised test without ampullae help to distinguish the species.

The holotype (and unique) specimen of *A. decemplex* (ZMA V.TU223) has all the characteristics of the present species and lacks the intermediate branchial papillae reported (and figured) by Sluiter (1890). It is probably a synonym of the present species.

FIG. 12: *Ascidia kreagra* — **a**, body wall from left showing pocket to receive ridge of test under descending limb of gut loop (QM GH3081); **b**, portion of branchial sac (QM GH3459); **c**, internal body wall on left (QM GH3459). (Scales: **a**, 5.0 mm; **b**, 0.1 mm; **c**, 2.0 mm).

Ascidia latesiphonica Hartmeyer, 1922
(Fig. 13)

Ascidia latesiphonica Hartmeyer, 1922, p.307. Hartmeyer and Michaelsen, 1928, p.301.
? *Ascidia malaca*: Hartmeyer and Michaelsen, 1928, p.277.
? *Ascidia gemmata*: Kott, 1972a, p.26.
? *Ascidia bisulca*: Millar, 1975, p.269.

DISTRIBUTION

NEW RECORDS: Western Australia (Broome, WAM 955.83; Cockburn Sound, WAM 10.75). South Australia (Kangaroo I., QM GH2612). Victoria (Deal I., QM G11853 GH2489). Queensland (Tallebudgera, QM G10070; Moreton Bay, QM GH340 GH2617; Mooloolaba, QM GH2613; Gladstone, QM G9784).

PREVIOUSLY RECORDED: Western Australia (Shark Bay, Swan River — Hartmeyer and Michaelsen 1928).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are long (up to 8 cm), almost cylindrical and robust. The smallest specimen recorded is 3 cm long (WAM 10.75). The branchial aperture is terminal, on a fairly short siphon that is usually ridged, although the ridges are not always conspicuous. Seven to 10 lobes border the branchial apertures. The 6-lobed atrial aperture is half to two-thirds of the body length along the dorsal border. It is often sessile, but sometimes is on a short, ridged more or less cylindrical siphon. The atrial aperture is directed anteriorly, or posteriorly, or to the side. The test is firm, gelatinous, smooth and without epiphytes. Its most conspicuous feature is the large, spherical terminal ampullae of the test vessels that abound beneath the surface. These are especially crowded on the siphons and around the anterior end of the body. They are of variable diameter (from 0.1 to 0.2 mm). In life, these terminal ampullae form yellow spots on the surface, although they are sometimes collapsed and inconspicuous.

INTERNAL STRUCTURE: The body wall has a mesh of muscles on the right side. On the left, the muscles are confined to the part of the body anterior to the gut loop. The atrial siphon, from half to two-thirds of the distance down the body, is sometimes long and projected laterally. In other specimens it is short and posteriorly oriented. There are about 40 fine branchial tentacles. The dorsal tubercle is a large cushion in a fairly shallow peritubercular area. It has a large C- or U-shaped slit, with one or both horns turned in or out. The dorsal ganglion is well separated from the dorsal tubercle, being present about halfway to the base of the atrial siphon. The dorsal lamina is ribbed, the ribs projecting from the free margin of the membrane. It is double anteriorly, becoming a single membrane in the vicinity of the dorsal ganglion.

The branchial sac has rather deep, tight pleats. Both longitudinal and transverse vessels are rather thick, with conspicuous papillae at the junctions of the vessels. The transverse vessels are very close together, and there are 6 to 8 short oval stigmata in each mesh.

The gut forms a deeply curved loop in the posterior half of the body. The intestinal part of the loop curves dorsally, parallel to the rectum.

The gonads are in the usual position in the gut loop. The ovarian tube has rather short branches at its proximal end.

REMARKS: The terminal ampullae at the surface of the test, the large dorsal tubercle, the gut loop confined to the posterior half of the body, the mesh of muscles on the right, and the very short branchial meshes characterise this species. The orientation of the atrial siphon is variable, as is its presence or absence. These variations can be observed in the one population (QM G10070 from Tallebudgera). However, the texture of the test is also variable, that of the South Australian specimens (QM GH2612) having firmer test with less conspicuous siphonal ridges than the other specimens. There were no other features observed to justify their division into two or more species.

Hartmeyer and Michaelsen (1928) did not observe the large terminal ampullae. However, the proportions of the body, its size, the firm test and cylindrical siphons are similar to those of the present specimens.

The terminal ampullae resemble those of *Ascidia decepta* n.sp., from which the present species is distinguished by its slightly more posteriorly positioned atrial aperture, naked test, fewer stigmata in each mesh, and longer, more cylindrical body.

The position and course of the gut resemble *Ascidia gemmata* and *Phallusia arabica*. Again, the spherical terminal ampullae, together with the short branchial meshes, distinguish the present species.

Ascidia bisulca: Millar, 1975 differs from the present species only in the reportedly deep groove at the base of the peritubercular area. This report possibly results from misinterpretation of the groove between the two membranes of the double anterior half of the dorsal lamina, as in *A. bisulca* Sluiter (< *A. sydneiensis*).

Ascidia malaca: Hartmeyer and Michaelsen, 1928 from the Swan River has an unusually long siphon, but resembles the present species in its internal characters.

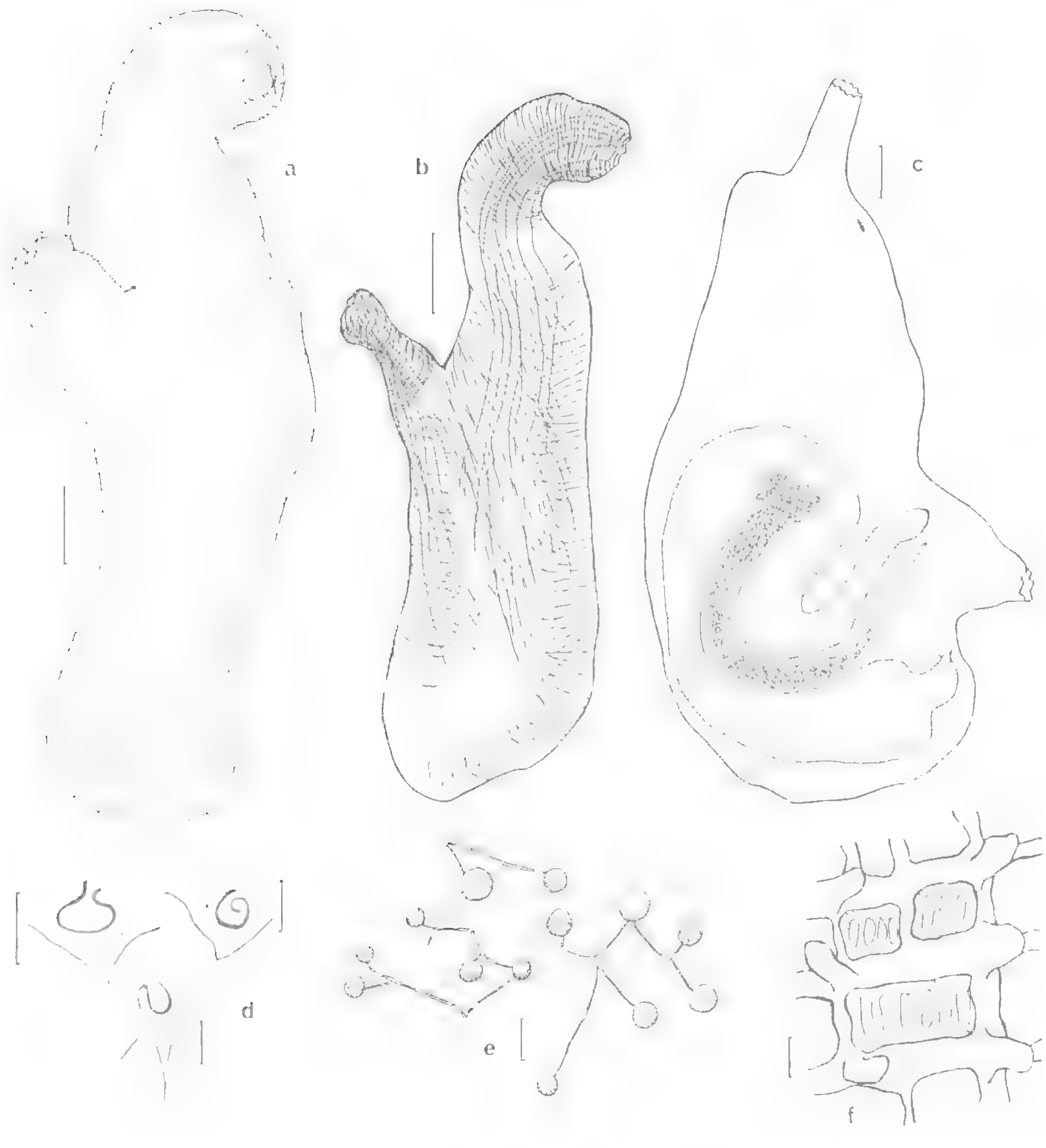


FIG. 13: *Ascidia latesiphonica* — **a**, external appearance (WAM 955.83); **b**, right side of body showing musculature (WAM 955.83); **c**, left side of body showing gut and ovarian tube (WAM 10.75); **d**, a variety of openings on the dorsal tubercle; **e**, terminal ampullae of test vessels; **f**, portion of branchial sac. (Scales: **a** – **c**, 2.0 mm; **d**, 0.5 mm; **e**, 0.2 mm; **f**, 0.1 mm).

Ascidia liberata Sluiter, 1887
(Fig. 14; Pl.1c)

Ascidia liberata Sluiter, 1887, p.251.
Ascidia rhabdophora: Kott, 1981, p.197 (part, specimens from Makaluva and part Dravuni).

DISTRIBUTION

NEW RECORDS: New South Wales (Norfolk I., QM GH2699). Queensland (Heron I., QM GH2482 GH2484-6 GH2518-22 GH2524-30 GH2968 GH2973 GH2979 GH3004 GH3012 GH3043 GH3045 GH3070 GH3072; Wistari Reef, QM GH2523 GH2618-2620 GH2986 GH3075).

PREVIOUSLY RECORDED: Indonesia (ZMA V.TU244 Sluiter 1887). Fiji (QM GH146 and part GH82 Kott 1981).

The species has been taken down to 5 m, on the under surface of rubble.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are up to 2 cm long and 1.5 cm wide, with an oval body flattened on the left or ventrally where it is fixed to the substrate. The upper surface is highly arched. The borders of the body are rounded, and the test is very thin on the left side. There is a deep crease across the antero-dorsal corner of the body to the right of the apertures, and a long, rounded ridge along the dorsal half of the right side. Apertures are on the upper surface toward the left side. When the body is fixed by the whole of the left side, they are on the dorsal border near the substrate. The branchial aperture is sub-terminal and the atrial aperture is one-third to half of the distance down the dorsal surface. The apertures are usually sessile in smaller specimens, but short, ridged siphons develop with growth. There are always 7 branchial lobes and 6 atrial lobes, always with small, conical, pointed papillae on their outer surface. As the siphons develop the pointed papillae extend in a row along the length of each siphonal ridge. The external test is otherwise smooth, without papillae, although it is slightly irregular, with some wrinkles in the preserved specimens. The lobes around the apertures are fringed with about 7 small, fine, tentacular projections (iridescent in life), and there are pigmented spots (ocelli) between the lobes.

The test is firm but thin and transparent. Terminal ampullae of the test vessels are very small indeed. In living specimens the body, seen through the colourless, translucent test, is maroon purple, isobella with liver brown around siphons, mars or wood brown or citron yellow (Ridgeway 1886). The colour is most conspicuous around the siphons. In preservative, the anterior end of the body, including the siphons, is often bright red, although occasionally only vestiges of the red pigment are present. The ocelli are yellow. The right parietal vessel, filled with yellow blood cells, is often conspicuous in the test of living specimens. There are sometimes some epibionts, including *Perophora multiclathrata* on the surface.

INTERNAL STRUCTURE: The body wall is delicate. There are circular muscles on the siphons. Longitudinal muscles extending along each siphon consist of a single band associated with each lobe around the apertures, which divides at the base of the siphon. The longitudinal muscles on the left side of the atrial siphon extend only a short distance from the base of the siphon. Transverse muscles cross the mid-line between the siphons and posterior to the atrial siphon. Together with longitudinal muscles from the atrial siphon, they form a continuous band of parallel muscles that extends along the dorsal half to three-quarters of the right side of the body and is associated with the deep longitudinal crease in the test that occurs to the right of the mid-dorsal line. The body wall adheres closely to the test in the vicinity of these muscles. The main test vessel enters the test from the body wall just to the left of the mid-line about halfway up the ascending limb of the gut loop. In living specimens, the heart can be seen forming a wide arc around, but slightly separated from, the ventral curve of the ascending limb of the gut loop.

There are no more than 50 branchial tentacles on the edge of a muscular velum. The dorsal lamina is double for a short distance anteriorly, and ribbed. The left half of the double membrane passes to the left of the peritubercular area. More posteriorly, the ribs extend out from the border of the membrane. There is a very narrow, prebranchial area. The opening of the neural gland is a simple, curved slit directed anteriorly. The neural ganglion is separated from it, being located about halfway between the dorsal tubercle and the base of the atrial siphon.

The branchial sac has small, narrow pleats between the longitudinal vessels, with 6 to 8 regular oval to elongate stigmata in each pleat.

The gut is present in the posterior half of the body. It consists of a narrow, deeply curved loop. The intestinal part of the loop is slightly curved dorsally. The intestine and rectum are of even diameter throughout their length. The anus opens at the base of the atrial siphon, anterior to the pole of the gut loop. Its border is smooth.

The gonads are enclosed in the gut loop and are of the usual ascidiid type, with small, branched male follicles that spread over the gut loop. A tubular ovary has long branches from the proximal end of the tube. The branches of the ovary spread

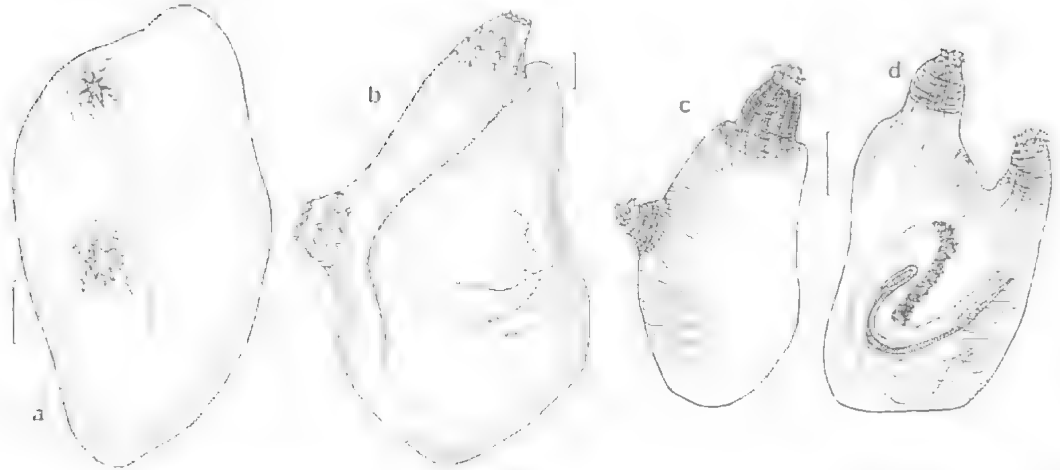


FIG. 14: *Ascidia liberata* — a, b, external appearance showing pointed papillae on siphonal lobes (juvenile QM GH2486, adult QM GH3043); c, right side of body showing musculature and fringe on apertures (QM GH2486); d, left side of body showing terminal branches of ovarian tube curving around outside of gut loop (QM GH2484). (Scales: 2.0 mm).

over the mesial side of the gut loop, partly obscuring it. Sometimes the tips of the branches are visible from outside the body wall where they overlap and curve around the outside of the gut loop.

REMARKS: The species is common at Heron I. and Wistari Reef. Its small size and cryptic habit may have caused it to be overlooked in other locations. The latter view is supported by the fact that both *Ascidia glabra* and *A. gemmata*, wide ranging species that occupy a similar habitat to the present species, have been taken most often at Heron I. where collecting has been most intensive.

Externally, *A. liberata* resembles *A. glabra* and *A. gemmata*, but is distinguished from those species by the presence of the tentacular fringe on the lobes of the apertures and a lesser number of lobes; the deep, oblique groove to the right of the apertures; pointed papillae on the siphons; and parallel transverse musculature on the right side of the body. Although a similar tentacular fringe is present in *Phallusia julinea* and in *Ascidia sydneiensis* and related species (*A. munda, A. parasamea* n.sp., and *A. samea*), the present species differs in having musculature on the right confined to the dorsal half of the body, a simple dorsal tubercle and the neural ganglion distant from it. *Ascidia sydneiensis* is further distinguished by its anal lobes.

Living specimens can also be distinguished by the wide arc of the heart that projects slightly from the ventral border, and sometimes by the conspicuous right parietal vessel.

Ascidia munda Sluiter, 1898
(Fig. 15a–d)

Ascidia translucida: Sluiter, 1890, p.344. (Not: Herdman, 1882, p.215).

Ascidia munda Sluiter, 1898a, nom. nov. p.5. Hartmeyer, 1919, p.97. Hartmeyer and Michaelsen, 1928, p.295. Harant and Tuzet, 1932, p.3. Vasseur, 1967a, p.111.

Ascidia munida (sic): Sluiter, 1905a, p.8.

Phallusia munda: Hartmeyer, 1909, p.1403.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 174.75 220.75). New South Wales (Tweed Heads, QM G4974). Queensland (Tallebudgera, QM GH2490).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Shark Bay — Hartmeyer and Michaelsen 1928). Indonesia (ZMA V.TU255 Sluiter 1890, 1898a; Harant and Tuzet 1932). Indian Ocean (Vasseur 1967a).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are long and narrow, up to 8 cm. The body narrows to a long, terminal branchial siphon. The atrial siphon is usually from the middle, or in the posterior half of the dorsal surface, and directed posteriorly. Amongst the number of specimens from Tallebudgera (QM GH2490), some have an anteriorly directed atrial siphon from the middle

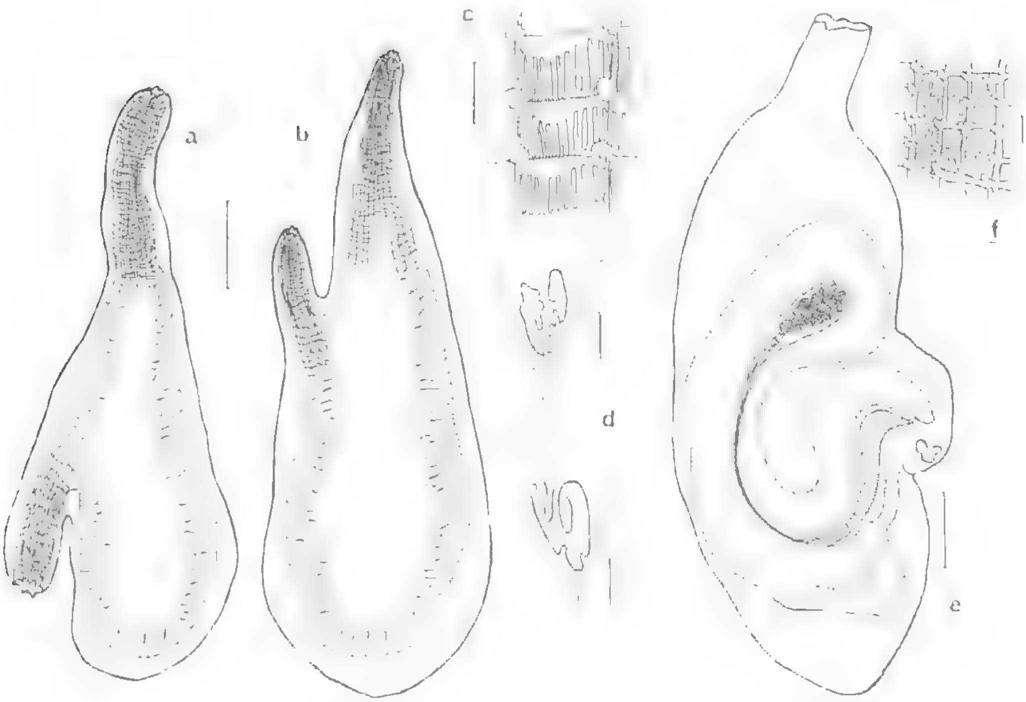


FIG. 15: *Ascidia munda* — **a**, **b**, two different specimens from right side showing body musculature (QM GH2490); **c**, portion of branchial sac; **d**, dorsal tubercles. *Ascidia nerea* n.sp. (QM GH2563) — **e**, left side of body showing gut and gonads; **f**, portion of branchial sac. (Scales: **a**, **b**, 1.0 mm; **c**, **d**, 0.25 mm; **e**, 2.0 mm; **f**, 0.1 mm).

of the body. The external atrial siphon is not very long, and development of the test on its anterior or posterior border effects its posterior or anterior orientation respectively. The siphons have 6 longitudinal ridges corresponding to the 6 lobes around each of the apertures. The border of each of the lobes is fringed with 7 fine tentacular projections. Ocelli are present between the lobes of the apertures. The test is smooth, although there are some creases and ridges on the surface. It is firm, and almost glassy and transparent.

INTERNAL STRUCTURE: The siphons have a layer of internal circular muscles. Longitudinal muscles are in bands, each band corresponding to one of the lobes around the apertures. The longitudinal muscles of the atrial siphon extend only a very short distance from the base of the siphon. A band of short, parallel muscles completely encircles the right side of the body, crossing onto the left side only along the dorsal mid-line. Very delicate, quite inconspicuous, transverse muscles connect the dorsal and ventral bands across the centre of the right side. There is no musculature over the gut. The internal atrial and branchial siphons are long, and the former always arises from halfway along the dorsal surface.

The branchial tentacles are very long and crowded. The dorsal tubercle completely fills the V-shaped peritubercular area, and the slit is very convoluted. The neural ganglion is just behind the tubercle. The dorsal lamina is a single, ridged membrane for the whole of its length. The ribs do not extend beyond the edge of the membrane. It is double for a short distance anteriorly, and the left half of the double membrane originates just to the left of the peritubercular area.

The branchial sac is narrow, with no more than 40 internal longitudinal vessels on each side. The meshes are twice as wide as long, and there is more than one pleat of the branchial sac in each mesh. About 8 elongate stigmata are present in each pleat and up to 10 in each mesh. There are no intermediate papillae.

The gut forms a deeply curved double loop. The descending limb of the gut loop, and the rectum are usually (but not always) very expanded with fine mud. The anal border has some (4 or 5) indentations, but is not lobed. The gonads, of the usual ascidiid type, are present in the gut loop.

REMARKS: The species closely resembles *Ascidia sydneiensis* in its ridged siphons, relatively small number of branchial lobes, fringes on the lobes of the apertures, convoluted dorsal tubercle, position of its neural ganglion, expanded mud-filled gut, and band of muscles framing the right side of the body. It is these characters that distinguish the species from specimens of *Ascidia gemmata* that have a similarly oriented atrial aperture. It is distinguished from *A. sydneiensis* by its consistently narrow body, more posteriorly situated atrial siphon, and the absence of lobes on the anal border.

Ascidia sumea Oka, 1935 from Japan and the Philippines (*Ascidia sydneiensis samea*: Tokioka, 1967a) is distinguished from the present species by its broader, almost sessile apertures, anteriorly placed atrial siphon, and (usually) tubercles and processes on the upper surface of the test.

Ascidia nerea n.sp.
(Fig. 15e-f)

DISTRIBUTION

TYPE LOCALITY: Queensland (Gladstone Harbour, 8.3 km upstream from mouth of the Calliope river, 4.4. m, silty sand, coll. P. Saenger, November 1979, holotype QM G2562, paratype QM GH2563).

DESCRIPTION

EXTERNAL APPEARANCE: The two available specimens are oval, about 2 cm long. The test is absolutely glassy and very thin and flexible, with sand grains embedded in the surface, obscuring the outline of the animal. The branchial aperture is terminal on a very short, ridged siphon. The atrial aperture is 6-lobed, almost sessile, and posteriorly directed from more than halfway along the dorsal surface. There are no tentacular fringes on the lobes of the apertures.

INTERNAL STRUCTURE: The body wall is very thin. Fine bands of longitudinal muscles radiate from each aperture, terminating only a short distance from the base of the siphon on each side of the body. On the right, they fill the gap between the bands of short transverse muscles along the ventral and dorsal border, leaving the centre of the right side of the body free of muscles.

There are some delicate, circular muscles around each aperture and at the base of the tentacles, but nowhere else. The transverse muscles forming a band along the dorsal border of the right side extend across the dorsal mid-line onto the left side. There are about 200 crowded and rather long branchial tentacles. The dorsal tubercle has a simple, U-shaped slit. The neural ganglion is just posterior to the dorsal tubercle.

The branchial sac is flat, without pleats, and with only 2 or 3 stigmata in each mesh. Generally these are very short, but occasionally a long stigma extends the full length of 2 meshes. The branchial papillae are conspicuous and curved.

The gut is very large, and forms a deeply curved loop that occupies most of the left side of the body wall. The intestinal part of the loop is especially long; its pole curves dorsally. The rectum is also curved parallel to the intestinal loop; its distal end bends posteriorly into the base of the atrial opening. The anal border is smooth.

The gonads are crowded into the loop of the gut in the usual way. The ovarian tube is branched at its proximal end in the pole of the loop, the branches extending posteriorly on the mesial side of the intestinal part of the loop.

REMARKS: This species resembles *Ascidia sydneiensis* and related species in the position of the neural ganglion near the tubercle and the presence of a border of transverse muscles around the right side of the body. *Ascidia munda* has a similarly oriented rectum. However, the present species is distinguished by the greater delicacy of its musculature, the absence of a tentacular fringe on the lobes of the apertures, very numerous branchial tentacles, a very large gut occupying most of the right side of the body, the absence of a mud-distended intestine, the absence of pleats in the branchial sac, and the small number of stigmata in each mesh.

Ascidia kuneides Sluiter, 1887 (ZMA V.TU239) from Indonesia has a similar arrangement of stigmata; however it is distinguished from *A. nerea* by its naked, firm test, upright body with both apertures anteriorly positioned, and mesh of muscles on the right side of the body.

Ascidia occidentalis n.sp.
(Fig. 16)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Cockburn Sound, off Rockingham, Coll. F. Wells and C. Bryce, St. 164, 28.2.78, holotype WAM 912.83).

FURTHER RECORDS: Western Australia (Swan River estuary, paratypes WAM 118.72 915-6.83 939.83).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are more or less egg-shaped, pointed anteriorly and rounded posteriorly. The apertures are on short, ridged siphons. The 8-lobed branchial aperture is terminal; the 6-lobed atrial aperture is from one-third to one-half of the body length distant from it along the dorsal surface. The lobes around the

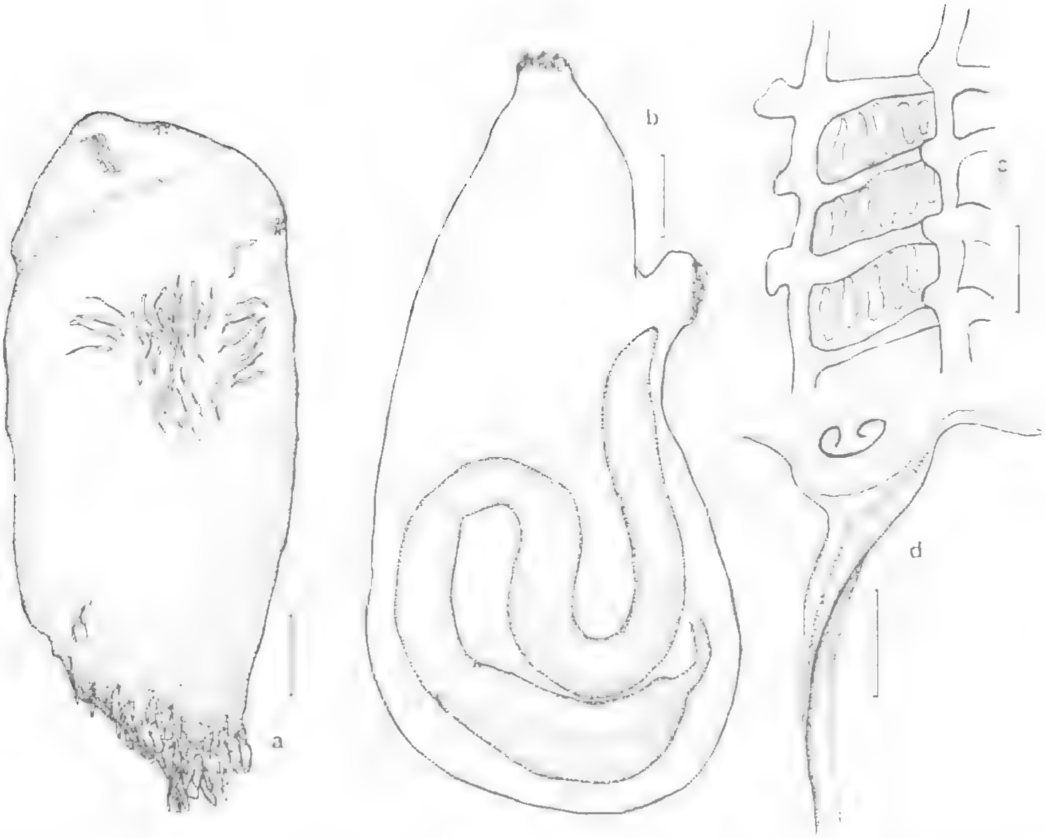


FIG. 16: *Ascidia occidentalis* n.sp (WAM 912.83) — **a**, external appearance, with some epibionts; **b**, left side of body; **c**, portion of branchial sac; **d**, dorsal tubercle and anterior part of dorsal lamina. (Scales: **a**, 5.0 mm; **b**, 2.0 mm; **c**, 0.2 mm; **d**, 0.25 mm).

border of each aperture have a fringe of minute tentacular papillae, and there are ocelli between the lobes. The test is thin and almost opaque and grey in preserved specimens. There are some small spots of red pigment around the siphons. Sand and mud adhere to slight surface irregularities. Epibionts, including some worm tubes also adhere to the surface.

INTERNAL STRUCTURE: The body wall has longitudinal muscle-bands radiating from the siphons. They terminate anterior to the gut on the left, but on the right form a rather crowded and irregular mesh of fine, branching and coalescing muscle bands. These straighten out around the dorsal and ventral borders to form a band of transverse muscles. There are about 30 branchial tentacles of varying sizes, neither long nor very crowded. The dorsal tubercle is a large circular cushion in a very shallow peritubercular area. There is a pronounced U-shaped slit on the tubercle, with both horns turned in. The dorsal ganglion is just behind the tubercle. The dorsal lamina is double for a very short distance anteriorly. It is asymmetrical, and the left half of the double membrane extends anteriorly to the left of the peritubercular area.

The branchial sac has pronounced pleats, each with about 10 short, oval stigmata. However, there are only about 8 stigmata in each mesh, there being about 3 pleats to every 4 internal longitudinal vessels.

The gut forms a deeply curved loop in the posterior half of the body. The rectum extends anterior to the pole of the gut loop to open at the base of the atrial siphon. Neither the descending limb of the gut loop nor the rectum is distended with gut contents. The anal border is smooth.

The gonads are in the usual position in the loop of the gut, the male follicles being spread over the gut, and the tubular ovary branching at its proximal end.

REMARKS: Externally, the species very much resembles *Ascidia sydneiensis* with its thin, translucent test with irregular processes on its surface to which mud and sand adhere; short, ridged, anteriorly positioned siphons; tentacular fringe on the lobes of the apertures; assymmetrical dorsal lamina; and red pigment spots anteriorly. *Ascidia occidentalis* is distinguished from *A. sydneiensis* by the mesh of muscles on the right side of the body; undivided slit on the dorsal tubercle; smooth anal border; and absence of a mud-distended gut. The species is distinguished from *Ascidia liberata* (which also has a tentacular fringe around the apertures) by the mesh of muscles on the right side of the body and the thin but almost opaque test. The asymmetrical dorsal lamina also occurs in *Ascidia kreagra*. However, there are other conspicuous differences between these two species.

Ascidia occidentalis appears to be a species with a limited range in Cockburn Sound, Western Australia

Ascidia pandora n.sp.
(Fig 17)

DISTRIBUTION

TYPE LOCALITY: Queensland (Wistari Reef, low tide, 3m, coll. P. Kott, March 1975, holotype QM GH2045).

DESCRIPTION

EXTERNAL APPEARANCE: The individual is oval and slightly dorso-ventrally flattened. The very thin test is rigid with sand. There are root-like protruberances on the ventral surface, also heavily invested with sand. Both apertures are sessile, the branchial aperture terminal and the atrial aperture mid-dorsal. There are 7 very delicate lobes around the atrial aperture. Lobes could not be seen around the distended branchial aperture in the single specimen known.

INTERNAL STRUCTURE: The body wall is delicate, except across the dorsal surface, where there is a layer of parallel transverse muscles extending from the level of the prepharyngeal groove to the posterior end of the body, interrupted only by the atrial aperture. There is a narrow, circular sphincter muscle around each aperture. Some short longitudinal bands radiate from the atrial aperture beneath the transverse bands. Very fine, inconspicuous, longitudinal bands also radiate from the branchial aperture over the anterior end of the body. There are about 40 fine tapering tentacles just inside the branchial aperture. The prepharyngeal area is very narrow indeed. The prepharyngeal groove extends straight across the dorsal mid-line behind the simple transverse opening of the neural gland, and does not form a V-shaped peritubercular area at the anterior end of the dorsal lamina. The neural ganglion and gland are over the anterior end of the narrow, plain-edged dorsal lamina.

The branchial sac is flat, without pleats. Small, rounded papillae are present at the junctions of the internal longitudinal vessels with the transverse vessels. There are 4 to 6 stigmata of moderate length in each mesh.

The gut forms a J-shaped loop, slightly open at the pole and occupying a large part of the left side of the body. The oesophageal opening is about two-thirds of the body length along the dorsal surface, almost level with the atrial opening. The stomach is fragile and elliptical, with 4 longitudinal grooves in its lining. It is present in the posterior curve of the ascending limb of the gut loop. The long and voluminous intestine extends anteriorly before curving back on itself to form a long, narrow loop in the longitudinal axis of the body. The narrow rectum lies along the anterior border of the stomach and curves dorsally (close to the anterior border of the stomach) and anteriorly (close to the anterior border of the oesophagus) to open near the atrial aperture. The anal border has a few shallow indentations. The descending limb of the intestine is distended into a large pouch filled with mud. The gonads are tightly crowded into the primary gut loop. Very numerous, short branches of the ovarian tube are conspicuous in this specimen, but no male follicles were observed.

REMARKS: The species resembles *A. scaevola* in having a stiff, rigid test and sessile apertures, but is distinguished from the latter species by the absence of false siphons, absence of a branchial fold, and its gently curved, long J-shaped gut loop and mud-filled intestinal pouch. Its distinctions from *A. prolata* n.sp. are its sessile apertures, short body, long gut loop, and more numerous stigmata in each mesh. The band of short transverse muscles across the dorsal border of the body resembles *A. liberata*, from which it is distinguished by its sandy test and the position of its neural ganglion (near the dorsal tubercle).

The species is extremely inconspicuous, owing to its sand-embedded test.

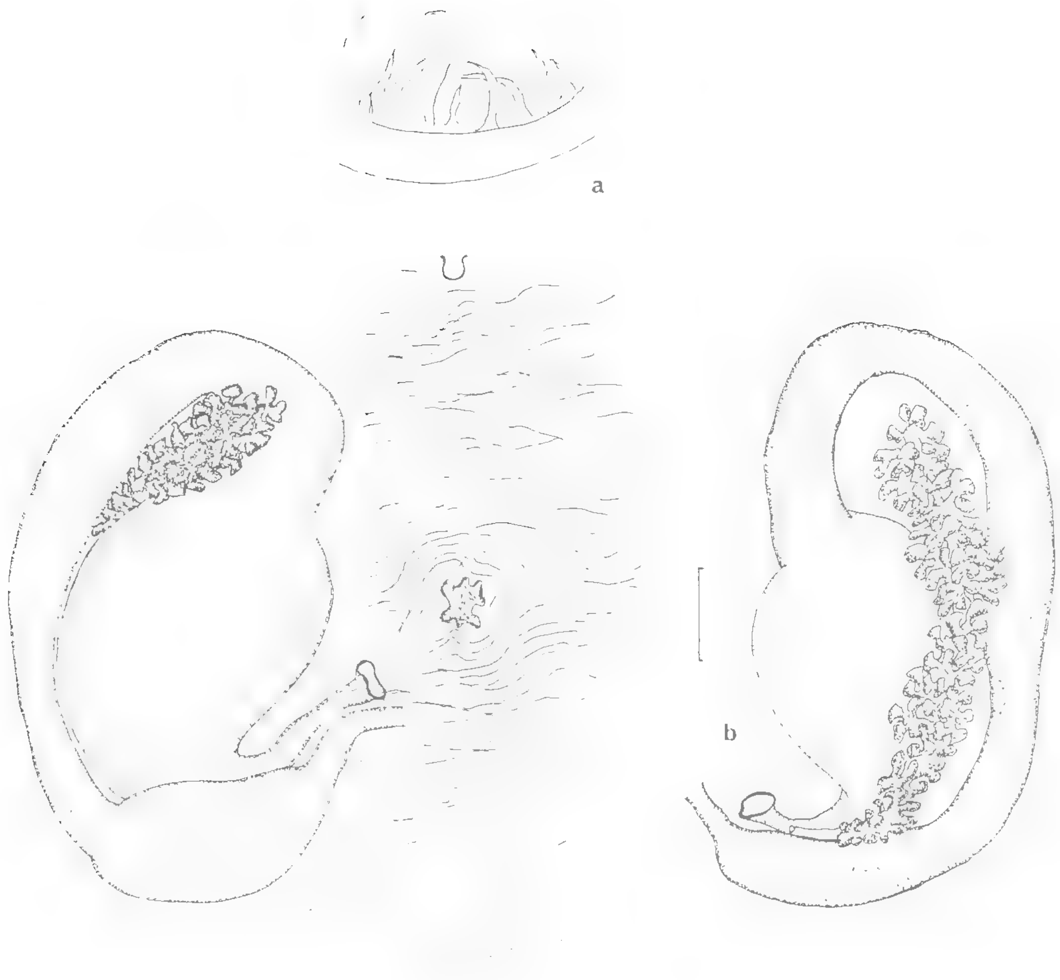


FIG. 17: *Ascidia pandora* n.sp (QM GH2598) — **a**, dorsal and left side of body showing musculature and gut loop; **b**, gut and ovary. (Scales: 2.0 mm).

Ascidia parasamea n.sp.
(Fig. 18)

DISTRIBUTION

TYPE LOCALITY: Queensland (off Gordonvale, 17°3′S, 145°55.6′E,coll. Queensland Fisheries Service, holotype QM GH776).

FURTHER RECORDS: Queensland (off Innisfail, paratypes QM GH2521; Barrow Point, QM GH2514; Cape Weymouth, QM GH2515; Trinity Bay, paratypes QM GH2516).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are almost circular, and up to 10 cm in diameter. In life they probably form a hemisphere that is fixed or lies on the substrate on the flat ventral half of the body. The branchial aperture is terminal, and the atrial aperture is halfway down the upper surface. Both apertures are sessile. The cloudy, translucent test, grey in preservative, is thicker on the upper surface than on the flat base, but is never other than paper-like, flexible and smooth, without wrinkles, outgrowths, epibionts or adhering or embedded particles of any sort.

There are 7 branchial lobes and 6 atrial lobes. The lobes have a fringe of fine tentacular projections, and alternate with ocelli.

INTERNAL STRUCTURE: The internal siphons in all these specimens are very short and darkly pigmented. The musculature consists of a margin of short, parallel bands around the right side of the body, those on the dorsal margin crossing over the mid-line between the siphons, and posterior to the atrial siphon. The longitudinal muscles on the short siphons never extend posterior to the base of the siphons. There are a very few delicate muscle bands forming a wide open mesh across the centre of the right side of the body.

There are about 20 robust branchial tentacles filled with dense, yellow blood corpuscles. These alternate with 2 or 3 smaller, delicate, coiled, fine and colourless tentacles. The prebranchial area is very narrow. The dorsal tubercle, which has a very convoluted opening, completely fills the peritubercular V-shaped area and extends anteriorly to the base of the tentacles. The body wall over the dorsal tubercle forms some rather irregular pockets over the openings. The neural ganglion is just posterior to the tubercle. The ribbed dorsal lamina is not toothed on the border. Anteriorly, it extends just to the left of the peritubercular area, but it is not a double membrane.

Branchial papillae are relatively small. There are no intermediate papillae. There are 2 pleats of the branchial sac in each mesh, each pleat with about 6 very short, almost egg-shaped, stigmata.

The gut forms a deep double loop, with the descending limb of intestine and rectum distended with mud. The anal border is indented 4 or 5 times, but is not lobed.

The gonads are crowded in the gut loop. Narrow branches of the ovary extend over the distended descending limb of the intestinal loop. Small, sometimes branched male follicles are also present on the gut loop.

REMARKS: In its fringed lobes of the apertures, convoluted dorsal tubercle, position of the neural ganglion, margin of short muscles around the right side of the body, and mud-distended gut, the present species resembles *Ascidia munda, A. sydneiensis* and *A. samea* Oka, 1935. It is distinguished from those species by its naked, smooth and extremely thin test, circular shape, and very small internal siphons. It is further distinguished from *A. sydneiensis* by the absence of regular lobes on the anal border, and from *A. samea* by having 2 (rather than a single) branchial pleats in each mesh.

Ascidia prolata n.sp.
(Fig. 19)

DISTRIBUTION

TYPE LOCALITY: Tasmania (Ninepin Point, 10 m, coll. D. Cropp, 12.1.83, holotype QM GH2023).

The single specimen was taken from 10 m, firmly wedged in a crevice.

DESCRIPTION

EXTERNAL APPEARANCE: The individual is long (9 cm), narrow (1 cm at its wide posterior end) and almost cylindrical. The terminal branchial aperture is on a long, cylindrical siphon that is almost half of the body length. There are 10 pointed, triangular lobes around the rim of the aperture. The atrial aperture, almost sessile, on a very short siphon, with about 7 rounded lobes on its border is about two-thirds of the body length distant from the branchial tentacles. The test is cartilaginous and translucent but thin and flexible, especially on the left side of the body. It is thickened into a rod, containing embedded sand or shell particles, along both dorsal and ventral borders. There is also some sand adhering to the test posteriorly. Orange pigment is present in the siphonal lining around the apertures.

INTERNAL STRUCTURE: The body wall is delicate and closely adherent to the test. It has a layer of strong parallel, transverse muscles over the whole of the right side, terminating anteriorly at the level of the prepharyngeal groove. Musculature on the

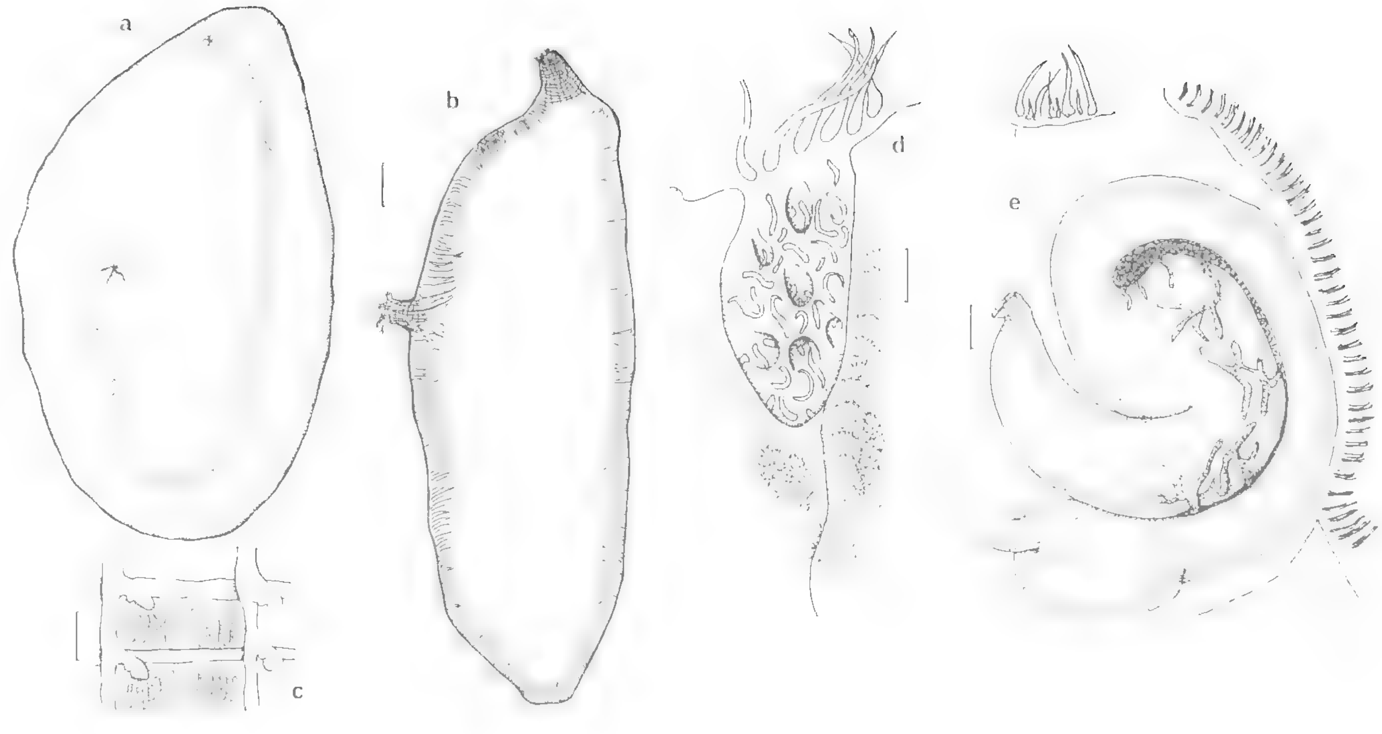


FIG. 18: *Ascidia parasamea* n.sp. **a**, external appearance (QM GH776); **b**, right side of body showing musculature (QM GH2515); **c**, portion of branchial sac (QM GH776); **d**, branchial tentacles, dorsal tubercle and anterior part of dorsal lamina (QM GH776); **e**, left side of body showing gut, some terminal branches of the ovarian tube and short muscles to the right of the ventral mid-line (QM GH776). (Scales: **a**, **b**, 5.0 mm; **c**, 0.2 mm; **d**, 0.5 mm; **e**, 2.0 mm).

FIG. 19: *Ascidia prolata* n.sp. (QM GH2023) — left side of body showing branchial velum, tentacles, gut and gonads. About 4 cm has been cut out of the branchial siphon. (Scale: 5.0 mm).

left is inconspicuous. At the base of the atrial siphon, a muscular velum protrudes into the lumen in front of the branchial tentacles. There is also a circular sphincter around the margin of the apertures. Inconspicuous longitudinal muscles along the branchial siphon extend to the border of the aperture beneath the circular muscles. There are about 24 tapering branchial tentacles alternating with rudimentary ones. The prebranchial area is relatively narrow. There is a large dorsal tubercle in a V-shaped peritubercular area. The aperture on the dorsal tubercle is U-shaped, with both horns turned out. The dorsal lamina is a double membrane for about the anterior quarter of its length. The dorsal ganglion is separated from the tubercle by about one-fifth of the length of the dorsal lamina.

The branchial sac is long and narrow, with only about 50 internal longitudinal vessels on each side of the body. At their junctions with the transverse and parastigmatic vessels are small, rounded papillae. There are about 3 long, elliptical stigmata per mesh.

The oesophageal opening is about four-fifths of the distance down the branchial sac. The oesophagus is short and narrow. The stomach is oval, with longitudinal folds, and extends anteriorly parallel to the long axis of the body. The distal one-third of the intestine is bent back against its middle third to form a short, narrow, vertical loop that makes a slight angle with the antero-dorsally directed rectum. The anal border at the base of the atrial aperture is smooth. The branchial sac extends posterior to the gut, which occupies the anterior two-thirds of the posterior one-third of the body (excluding the branchial siphon). There are no mature gonads in this specimen, although some immature male follicles are present on the mesial surface of the gut, and gonoducts are visible extending from between the gut loop, along the anterior border of the stomach and curving anteriorly across the space between the stomach and rectum to open with the anus at the base of the atrial opening.

REMARKS: *Ascidia lagena* Michaelsen, 1922, from Stewart I. (New Zealand), has the same long branchial siphon, narrow branchial sac, parallel transverse muscles on the right, and small number of stigmata in each mesh as the present species. However, the gut loop in the New Zealand species occupies almost the whole length of the left side of the body and the species appear to be distinct. A single specimen from the Atlantic has an equally long branchial siphon (*A. interrupta*: Monniot 1970c) but is distinguished by its long and distended gut loop.

The short gut loop of *A. prolata* resembles that of *Microgastra* n.gen. *granosa*, as do the parallel transverse muscles. However, a relationship with the latter species is not implied by these similarities. *Ascidia scaevola* also has a short gut loop, but is readily distinguished by its specialised musculature, pseudosiphons, brittle test and branchial fold.

Ascidia malaca: Hartmeyer and Michaelsen, 1928 from the Swan River, Western Australia, resembles the present species in its long branchial siphon and almost sessile atrial siphon; however, it is readily distinguished by its mesh of muscles on the right side of the body and its more numerous stigmata.

Ascidia prolata is probably a temperate species. Its habit — tightly wedged in the substrate, visible only through its projecting orange branchial siphon — is probably the reason for the lack of records. The species is characterised by its long branchial siphon; thickened, sand-embedded rod of test along the dorsal and ventral mid-lines; and its layer of parallel transverse muscles on the right.

Ascidia scaevola (Sluiter, 1904)
(Fig. 20)

Styelopsis scaevola Sluiter, 1904, p.89.
Ascidia aclara Kott, 1952, p.309; 1972a, p.27; 1972c, p.236; 1975, p.11. Millar, 1963, p.721

DISTRIBUTION

NEW RECORDS: Victoria (Sale, NMV H633). Queensland (Gladstone, QM G9799 G12705 GH2155; NW Bowen, QM GH679 GH709 GH2353-2360; Townsville, QM GH721; Nymph I., QM GH2352).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1975; St Vincent Gulf — Kott 1972a). Victoria (Lakes Entrance — Kott 1952; Port Phillip Bay — Millar 1963). Queensland (Moreton Bay — QM G5931-50, Kott 1972c). Indonesia (Sluiter 1904).

Specimens are found on, and buried in, sandy sediments.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are longer than wide and dorso-ventrally flattened. The largest specimens reported are from southern Australia; they are up to 17 cm long and 10 cm wide (Kott 1972a). The most conspicuous features of the body are the two false siphons — cylindrical extensions of the thin rigid, sand-impregnated test — projecting out from the area around each sessile aperture. Sand is absent only from the membranous test surrounding each aperture at the base of each false siphon. There are 8 small, delicate lobes around the branchial aperture, and 6 around the atrial aperture. The false siphons are sometimes close together on the upper surface of the body, directed vertically. However, sometimes the branchial tube is almost terminal and the atrial tube diverges from it. In most specimens, an inner layer of membranous test around the atrial aperture separates from an outer, rigid, sandy layer to divide the sandy capsule into two compartments: the larger antero-ventral compartment contains the body of the animal; the smaller postero-dorsal compartment opens to the exterior through the atrial tube and receives the opening of the atrial aperture. It is possible that this latter chamber forms as a result of contraction

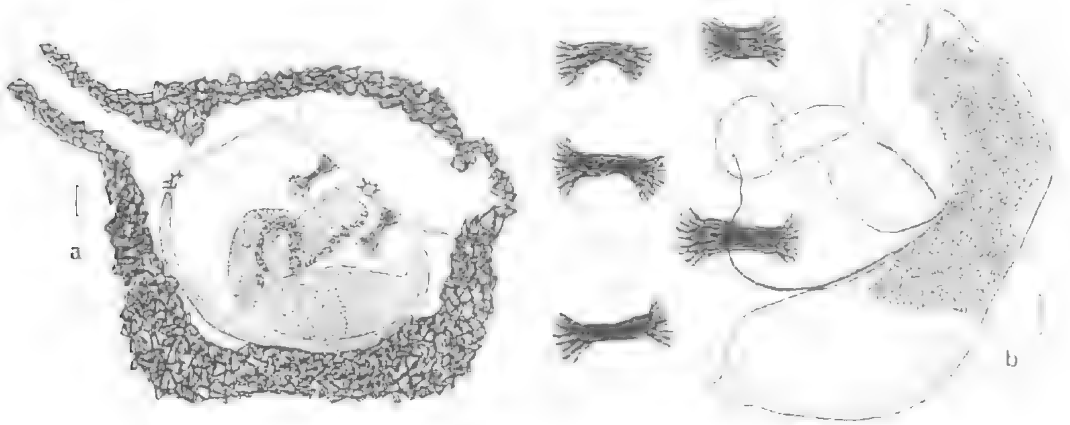


FIG. 20: *Ascidia scaevola* (QM GH772) — **a**, body lying in the test showing external chambers outside the sessile apertures, the two short muscle bands across the dorsal mid-line and the flattened, ribbon-like gut loop; **b**, muscle bands on right side and over dorsal mid-line, gut and gonads on left. (Scales: 1.0 mm).

of the body causing an inner layer of test to pull away from the outer, sandy layer.

INTERNAL STRUCTURE: There are narrow, circular sphincter muscles around each aperture. The only other body muscles are 3 short, strong bundles of transverse muscles evenly spaced down the right side of the body, and 2 across the mid-dorsal line, anterior and posterior to the atrial aperture respectively. There is a circle of about 200 long, crowded branchial tentacles of very even length. The prepharyngeal groove loops across from the left in front of the V-shaped peritubercular area, creating a wide branchial fold in the dorsal part of the left side of the branchial sac that covers the peritubercular area and the dorsal lamina. The neural gland is immediately dorsal to the large dorsal tubercle, which is sometimes in the peritubercular area and sometimes to its right, where it is not covered by the branchial fold. There is a large S- or reverse C-shaped slit on the dorsal tubercle. In specimens from Port Phillip Bay (Millar 1963), the slit on the dorsal tubercle is interrupted, and numerous elongate openings perforate the surface of the tubercle. The neural ganglion is posterior to the base of the peritubercular area over the anterior end of the dorsal lamina. There are 5 oval stigmata per mesh in the branchial sac.

The oesophageal opening is near the posterior end of the branchial sac. The oesophagus is of moderate length. The large, thin-walled, egg-shaped to elliptical stomach tapers slightly to the wide, flat, ribbon-like intestine. The distal third of the intestine bends back against the ascending limb to form a short, narrow loop. The rectum extends dorsally straight to the anal opening, which has a border divided into shallow lobes. The gut is embedded in the body wall.

The branches of the tubular ovary are crowded into the tight gut loop, where they mingle with small male follicles that are also scattered over the mesial surface of the ascending limb of the gut loop. The gonoducts extend along the anterior border of the stomach before curving anteriorly and extending along the left side of the dorsal mid-line to the atrial aperture.

REMARKS: The species is characterised by its sandy, brittle test; false siphons around the apertures (that presumably give partially buried individuals access to the surface of the sea bed); specialised and very localised body musculature; presence of a branchial fold; and the position of the neural gland (closely associated with its opening on the dorsal tubercle rather than with the dorsal ganglion that is some distance posterior to it). Sluiter's (1904) account of separate polycarp-like gonads appears to have resulted from misinterpretation of the branches of the ovarian tube projecting out beneath the gut loop.

The species resembles *Ascidia prolata* n.sp. and *Ascidia pandora* n.sp. in some of it characters. It is distinguished from both by its discrete muscle bundles and sessile apertures. The latter species is further distinguished by its simple, curved gut loop; large, distended rectum and very branched ovarian tube.

The sandy, brittle test and branchial fold in this species resemble species of the family Plurellidae, although, in addition to the distinction afforded by the familial characters, the gut loop of the present species is embedded in the body wall rather than being very lightly attached to it.

Ascidia sydneiensis Stimpson, 1855
(Fig. 21; Pl.1d)

Ascidia sydneiensis Stimpson, 1855b, p.387. Whitelegge, 1889, p.295. Herdman, 1891, p.593; 1899, p.11. Hartmeyer, 1915a, p.313; 1919, p.98. Hartmeyer and Michaelsen, 1928, p.285. Van Name, 1945, p.189. Tokioka, 1950, p.133; 1952, p.105; 1953a, p.223; 1954b, p.84. Kott, 1952, p.310; 1964, p.147; 1966, p.296; 1972a, p.24; 1972b, p.182; 1972c, p.237; 1972e, p.49; 1976a, p.73. Millar, 1955a, p.190; 1956, p.411; 1960b, p.91; 1962a, p.173; 1963, p.720; 1966, p.366. Kott and Goodbody, 1982, p.526.

Phallusia sydneiensis: Hartmeyer, 1909, p.1405.

Ascidia canaliculata Heller, 1878, p.2. Sluiter, 1885, p.176; 1898a, p.41. Herdman, 1891, p.593. Hartmeyer, 1911, p.576. Michaelsen, 1918, p.59.

Phallusia canaliculata: Hartmeyer, 1909, p.1401.

Ascidia rudis: Schmeltz, 1879, p.89.

Ascidia pyriformis Herdman, 1882, p. 219; 1899, p.15.

Phallusia pyriformis: Traustedt, 1885, p.15. Hartmeyer, 1909, p.1403.

Phallusia longitubis Traustedt, 1882, pp.277, 283; 1885, p.16. Traustedt and Weltner, 1894, p.10. Sluiter, 1898b, p.8. Herdman, 1899, p.594. Hartmeyer, 1909, p.1402.

Ascidia limosa Sluiter, 1887, p.257. Hastings, 1931, p.81.

Ascidia diplozoon Sluiter, 1887, p.249

Ascidia divisa Sluiter, 1898a, p. 43; 1904, p.30. Hartmeyer, 1906, p.21. Tokioka, 1951b, p.171.

Ascidia bisulca Sluiter, 1904, p.43. (Not: Millar, 1975, p.269 ?).

DISTRIBUTION:

NEW RECORDS: Western Australia (Cockburn Sd., WAM 133.75). Tasmania (Eaglehawk Neck, TM D717; Bruny I. NMV F51818; Sarah I., QM GH2021; Kingston, TM D707; Triabunna Jetty, QM GH 2541). Victoria (Bass Strait, NMV H384 H409 H468 H914; Hobson's Bay, QM GH11860; off Lake's Entrance, QM G11853). New South Wales (Arrawarra, QM G9628; North Solitary I., QM G9656). Queensland (Moreton Bay, QM G10079; Tallebudgera Creek, GH2448; Hervey Bay, QM

FIG. 21: *Ascidia sydneiensis* — **a**, typical appearance; **b**, body from right side showing musculature; **c**, margin of apertures showing fringe, longitudinal and circular muscles and ocelli; **d**, portion of branchial sac; **e**, dorsal tubercle and anterior part of dorsal lamina; **f**, variability in anal lobes. (Scales: **a**, 1.5 cm; **b**, 2.0 mm; **c**, 0.5 mm; **d**, 0.25 mm; **e**, **f**, 1.0 mm).

G9408; Gladstone, QM G9675 G9678 G9717 G9719-20 G9786-7 G9784 G9796 G10057-8 G12706 GH2513; Yeppoon, QM GH2493; Wistari Reef, QM GH1355 GH2507 GH2511 GH2991; Heron I., QM GH2512 GH3058 GH3066; Townsville, QM GH307 GH745 GH1385; Trinity Bay, QM GH774; Lizard I., QM GH2476 GH2508-10).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Shark Bay — Hartmeyer and Michaelsen 1928; Cockburn Sound — Hartmeyer and Michaelsen 1928, Kott 1952, Millar 1963; Albany — Kott 1952, Millar 1963). South Australia (St Vincent Gulf — Kott 1952 1972a,b). Tasmania (Spring Bay — Kott 1952). Victoria (Port Phillip Bay — Kott 1952, Millar 1960b 1963 1966; Westernport — Kott 1976). New South Wales (Port Jackson — Herdman 1882 1899, Stimpson 1885). Queensland (Caloundra, Moreton Bay, Hervey Bay, Yeppoon, Townsville — Kott 1964 1966; Moreton Bay — Kott 1972c; Bowen — Schmeltz 1879). Northern Territory (Darwin — Kott 1966). Arafura Sea (Tokioka 1952). Indonesia (*A. limosa* type ZMA V.TU245 Sluiter 1885, *A. diplozoon* type ZMA V.TU224 Sluiter 1887, *A. bisulca* type ZMA V.TU267.3 Sluiter 1904). New Caledonia (Vasseur 1967b). Palau Is. (Tokioka 1950). Japan (Hartmeyer 1906, Tokioka 1953a 1954). Indian Ocean (Seychelles — Michaelsen 1918; Isles Maurice — Vasseur 1967a; eastern Africa — Traustedt and Weltner 1894, Millar 1956). South Africa (Heller 1878, Hartmeyer 1911, Millar 1955 1962). Atlantic Ocean (Traustedt 1882, Sluiter 1898b, Rennie and Wiseman 1906, Hartmeyer 1911, Van Name 1945).

This is one of the most frequently recorded species of the Ascidiacea. Its wide latitudinal range, mainly in the southern hemisphere, where it extends into temperate southern waters of the African and Australian continents, may at least partly explain its almost completely pan-tropical range. It is absent only from the eastern Pacific (see Van Name 1945).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are longer than wide and laterally flattened. Very large specimens are up to 20 cm long. The siphons are short, cylindrical and always ridged. The branchial siphon is terminal, and the atrial siphon is one-third to two-thirds of the body length distant from it. The atrial aperture is often turned posteriorly. The test is often paper-thin, translucent and cloudy, but in large specimens is often moderately thick and firm. It usually has some short, sparse and irregular processes on the surface, to which sand and mud adhere. There are usually 6 branchial lobes and 6 atrial lobes, although more branchial lobes (up to 10) are sometimes present. One 3 cm long specimen from Bass Strait (NMV 384) has only 5 lobes on each of the apertures. The lobes are fringed, with ocelli between them. Living specimens have a slate to black body that shows through the cloudy, translucent test.

INTERNAL STRUCTURE: The right body wall has a border of short, parallel transverse muscles. The dorsal band of parallel muscles crosses the mid-dorsal line between the apertures and posterior to the atrial siphon. The muscles across the centre of the right side of the body are few and very fine and inconspicuous. Muscles on the left terminate anterior to the gut loop. There are strong, circular muscles around each aperture. There are about 40 rather short branchial tentacles, which are reduced in number in very large specimens. The dorsal tubercle fills the V-shaped peritubercular area and has a complex convoluted to interrupted slit, although in small specimens it is U-shaped, with both horns turned in. The neural ganglion is above and immediately posterior to the dorsal tubercle. The prepharyngeal space is very narrow. The dorsal lamina is wide and ribbed on the left. Posteriorly, the ribs terminate in narrow projections from the free edge of the wide membrane, double anteriorly. The left half of the double anterior part of the dorsal lamina extends anteriorly to the left of the peritubercular area.

The branchial sac has one deep, tight pleat in each mesh, between the internal longitudinal vessels. There are 6 to 12 moderately long stigmata in each pleat. Parastigmatic vessels are seldom present. The branchial papillae are large and rounded.

The gut forms a deeply curved, narrow loop. The descending limb of the gut loop and the proximal part of the rectum are always distended with mud, often occluding the ascending limb and the whole of the left peribranchial cavity. There are up to 30 rounded anal lobes. The gonads are crowded together in the gut loop.

REMARKS: The species is variable in regard to the position of the apertures, number of branchial tentacles, degree to which the opening of the neural gland is convoluted and interrupted, number of stigmata in each branchial pleat, and number and length of the anal lobes. However, its characteristic features are the border of short transverse muscles around the right side of the body, lobed anal border, position of the neural ganglion close behind the dorsal tubercle, assymmetrical dorsal lamina, fringed lobes around the apertures, and a mud-distended gut. *Phallusia julinea* and *Ascidia liberata* n.sp. have similarly fringed lobes around the apertures; but both species lack the anal lobes and ventral band of short transverse muscles. *Ascidia parasamea* n.sp. and *Ascidia munda* also have fringes on the lobes of the apertures and the same border of short transverse muscles on the right. They are distinguished from *A. sydneiensis* by their smooth anal borders.

Ascidia limosa Sluiter (ZMA V.TU245), *A. diplozoon* Sluiter (ZMA V.TU224) and *A. bisulca* Sluiter (ZMA V.TU267.3) share all the characteristics of the present species. In *A. bisulca* the deep groove at the base of the peritubercular area, is, in fact, the groove between the two halves of the double anterior part of the dorsal lamina.

Ascidia thompsoni Kott, 1952
(Fig. 22)

Ascidia thompsoni Kott, 1952, p.312; 1972a, p.27; (not: 1972b, p.180; 1975, p.10, < *A. decepta* n.sp.).

DISTRIBUTION

NEW RECORDS: South Australia (St Vincent Gulf, QM G9311 G9325).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1952 1972a,b). Tasmania (Great Taylor Bay — Kott 1952).

The species appears to have a range restricted to a relatively small area of south-eastern Australia.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are up to 10 cm long, widest (up to 4 cm) at their rounded posterior end and gradually narrowing to the terminal 8-lobed branchial aperture, which is on a short, slightly expanded, smooth, cylindrical siphon. The 6-lobed atrial aperture, about two-thirds of the distance down the dorsum, is either sessile and inconspicuous or on a short, posteriorly oriented siphon. The test is firm and gelatinous, only slightly translucent, and smooth, but with some irregular swellings and creases on the surface. The siphonal linings have longitudinal pigmented bands corresponding to the lobes. The branchial aperture is often curved dorsally, and the body is concave dorsally. Some sand grains are embedded in the test.

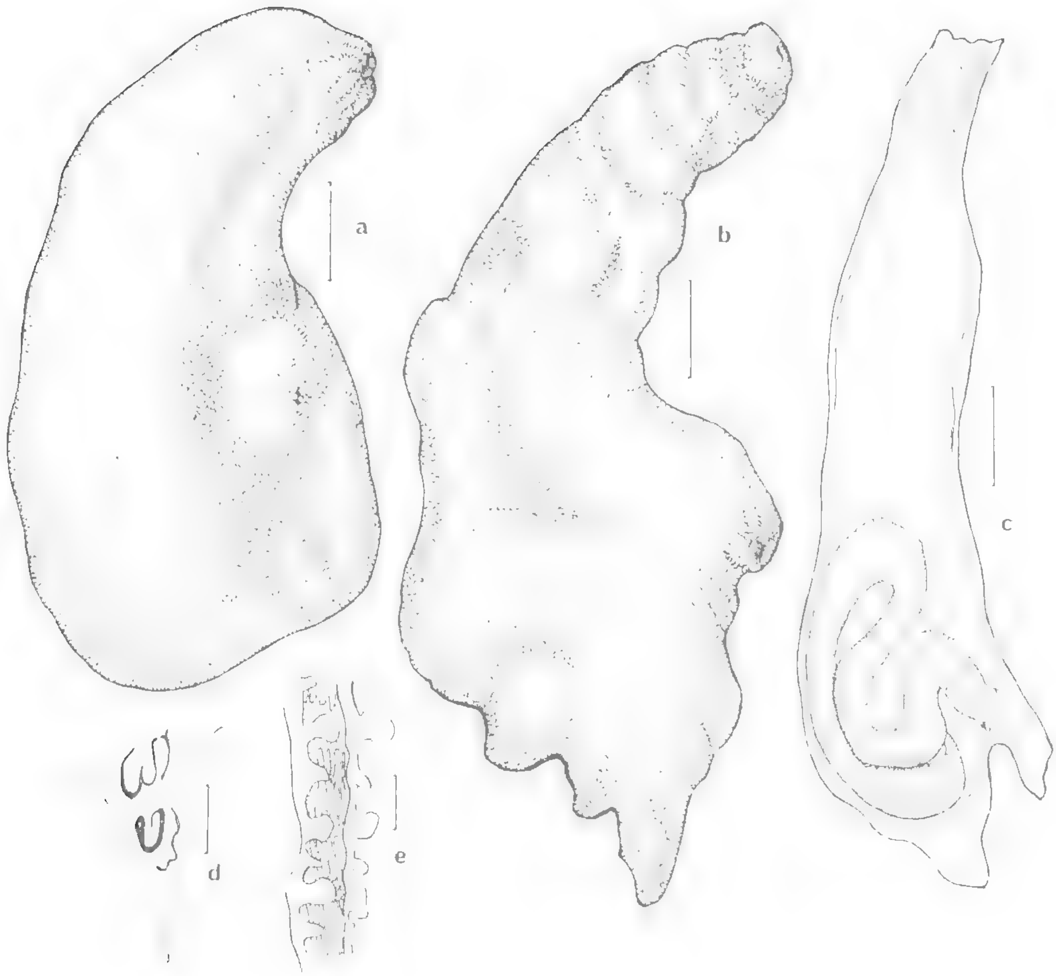


FIG. 22: *Ascidia thompsoni* — **a**, **b**, external appearance (QM G9311, G9325); **c**, left side of body (QM G9325); **d**, double opening of neural gland (QM G9325); **e**, portion of branchial sac (QM G9325). (Scales: **a** – **c**, 1.0 cm; **d**, 0.5 mm; **e**, 0.2 mm).

INTERNAL STRUCTURE: There are short internal siphons, each with an internal layer of circular muscles and externally longitudinal bands extending posteriorly from each of the lobes. The musculature on the left terminates anterior to the gut loop. On the right, longitudinal and transverse muscles form an irregular mesh over the side of the body. There are about 20 very fine, crowded tentacles. The dorsal tubercle is large, in an unusually long peritubercular area. One specimen (QM G9325) has two dorsal tubercles, one behind the other. The opening of the neural gland is U- or S-shaped or sinuous, and often is interrupted. The neural ganglion is about halfway between the dorsal tubercle and the base of the atrial siphon. The dorsal lamina is a broad, ribbed membrane, double as far back as the neural ganglion. There are small pointed projections from the free edge of the dorsal membrane in its posterior extent. The prebranchial zone is not papillated.

The branchial sac has a moderately deep pleat with 6 to 8 long stigmata in each mesh. There are large, rounded primary papillae at the junctions of the transverse and internal longitudinal vessels. These have a protruberance near the base of the dorsal concave border. Small, conical intermediate papillae alternate with the primary papillae on the narrow, internal longitudinal vessels.

The gut forms a deeply curved loop, and the rectum often forms an extra loop, curving posteriorly into the base of the atrial siphon. The anal border has small, inconspicuous scallops.

The gonads are of the usual ascidiid type in the loop of the gut.

REMARKS: The species most resembles *A. munda*, *A. gemmata* and *A. bifissa* Sluiter, 1895 in external appearance and in the course of the gut. It is distinguished from those species and many others by the intermediate branchial papillae. These are present in *A. archaia* which distinguished by its open gut loop and characteristic ovarian tube. *Ascidia bifissa* has an interrupted slit on the dorsal tubercle, as sometimes occurs in the present species. However, it is reported to have only 3 to 5 stigmata per mesh in the branchial sac (Sluiter 1895).

Genus **Phallusia** Savigny, 1816

Type species: *Ascidia mammillata* Cuvier, 1815

Species are large with a thick, firm, cartilaginous and usually naked test. The dorsal ganglion is always posterior to the dorsal tubercle, separated from it by at least a quarter of the length of the branchial sac. The duct of the neural gland extends along the mid-dorsal line above the dorsal lamina between the ganglion and dorsal tubercle. It usually opens into the atrial cavity on each side of the dorsal lamina by many secondary openings, accessory to the primary opening on the dorsal tubercle. The dorsal tubercle is usually small. There are rarely fewer than 8 lobes around each aperture; ocelli are present between these lobes. The gut is on the left. Usually the rectum, and sometimes also the descending limb of the intestinal loop, become distended with fine mud. The test is well vascularised with a system of vessels that can often be seen through the translucent test. Terminal ampullae, sometimes forming chromatophores, are conspicuous at the surface of the test.

The external appearance of many of the species in this genus is often variable. This is partly the result of variations in the orientation of the apertures, probably the result of growth in response to environmental pressures, since the thick, firm test has no flexibility. Orientation of the apertures is likely to be of paramount importance to these large, solitary individuals. Intraspecific variations in the surface of the test (the development of tubercles, papillae and ridges) and the distribution of pigment may be partly the result of age, although some genetic diversity is probable.

Test vessels are large and conspicuous. The pattern of their branching is remarkably constant throughout the genus. The main test vessel branches off the ventral sinus and enters the test. It divides into 3 main branches usually near its point of entry. The course of these vessels and their main branches (branchial, atrial and ventral) are set out in Fig. 23.

In one species (*Phallusia julinea*), the accessory openings of the neural gland are not always present in smaller specimens, and specimens can be mistaken for members of the closely related genus *Ascidia*.

The genus *Phallusia* is not diverse, although most known species have a wide geographic range. Five species are known from Australia, of which 2 are probably indigenous: *P. obesa* from the southern half of the continent; and *P. barbarica* n.sp. from Moreton Bay.

KEY TO SPECIES OF THE GENUS *PHALLUSIA* RECORDED FROM AUSTRALIA

1. Anal border with few shallow indentations . 2
   Anal border deeply divided into numerous lobes 3

2. Stellate chromatophores in surface test .... *P. julinea*
No stellate chromatophores in surface test .... *P. barbarica* n.sp.
3. Distance between base of atrial siphon and branchial siphon one-third of body length 4
Distance between base of atrial siphon and branchial siphon one-half to two-thirds of body length .... *P. arabica*
4. Main test vessel enters test at posterior end of body, all branches extending anteriorly parallel to one another ...... *P. millari* n.sp.
Main test vessel enters test halfway up ventral surface branches radiating from its point of entry .... *P. obesa*

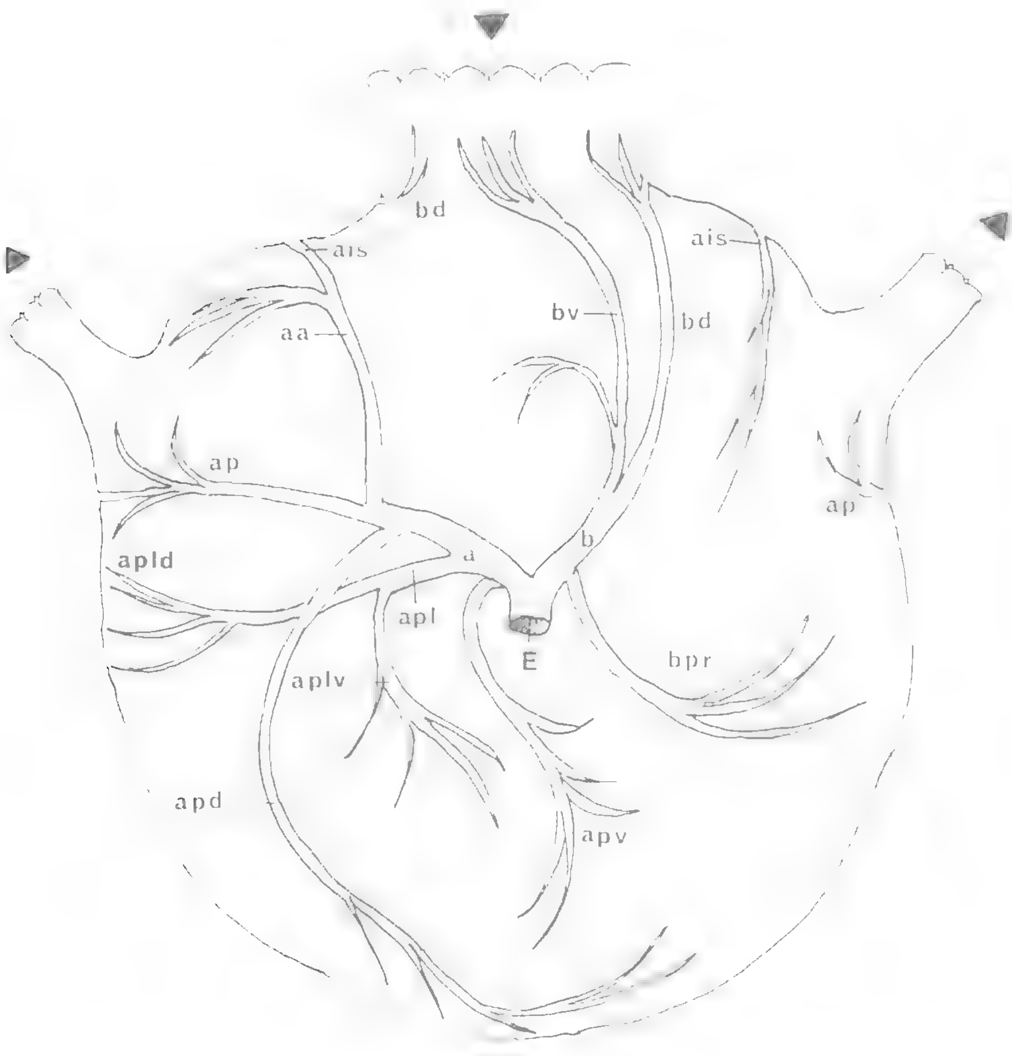


FIG. 23: Diagram of test dissected along the mid-dorsal line to show test vessels in *Phallusia* spp. (**a**, atrial vessel; **aa**, anterior atrial vessel; **ais**, intersiphonal vessel — a branch of the anterior atrial vessel; **ap**, posterior atrial vessel; **apd**, postero-dorsal vessel—a branch of the atrial vessel; **apl**, left parietal vessel—a branch of the atrial vessel; **apld**, dorsal branch of the left parietal vessel; **aplv**, ventral branch of the left parietal vessel; **apv**, postero-ventral vessel; **b**, branchial vessel; **bpr**, right parietal vessel—a branch of the branchial vessel; **bv**, ventral branch of the branchial vessel; **bd**, dorsal branch of the branchial vessel; E, main test vessel, point of entry into test Arrows show the incurrent aperture and the bisected atrial aperture).

TABLE II — SUMMARY OF CHARACTERS OF SPECIES OF *PHALLUSIA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Distance between apertures	Origin of test vessels	Branching of terminal test vessels	Surface test	Mud distended gut	Anal border	Additional features
P. julinea	WP	Moreton Bay - Cape Jaubert	1/3–2/3	mid-ventral	umbellate	smooth; minute papillae	usually	irregular indentations	fringe on apertures; chromatophores in surface test
P. obesa	—	circum Aust.	1/3	"	"	smooth; with swellings	always	lobed	tubercles and pigment spots sometimes present; neural gland spreads along duct
P. arabica	IWP	Heron I. - Arafura Sea	1/2	"	sparse; even	smooth; minute papillae	usually	"	fringe on apertures; more than 12 stigmata per mesh
P. millari n.sp.	WP	Bowen - Cockburn Sd	1/3	postero-ventral	sparse; random	smooth	not present	"	parallel test vessels; sandy posterior holdfast
P. barbarica n.sp.	—	Moreton Bay - Hervey Bay	1/2–2/3	"	profuse; random	creased wrinkled	"	smooth	bands of pigment line siphons; sand, epibionts

[1]WP, Western Pacific; IWP, Indo-West Pacific. [2]Range given anti-clockwise around the continent. [3]As a fraction of body length.

Phallusia arabica Savigny, 1816
(Fig. 24a-d; Pl.Ie)

Phallusia arabica Savigny, 1816, p.164. Hartmeyer, 1915b, p.414. Michaelsen, 1919, p.113.
? *Ascidia depressiuscula* Heller, 1878, p.5. (Not: Herdman, 1906, p.305, < *Ascidia* sp.)
Phallusia julinea Sluiter, 1915, p.7. Hartmeyer, 1919, p.99. Hastings, 1931, p.81. Tokioka, 1950, p.133; 1952, p.107 (part, specimens 94 mm and 80 mm long 'without anal lobes'); 1961, p.110; 1967a, p.147; (not: 1952, p.107 specimen with anal lobules, < *P. arabica*). Kott, 1964, p.148; (not: 1952, p.305, < *P. millari* n.sp.; 1966, p.295, < *P. barbarica* n.sp.). Vasseur, 1967b, p.129; 1969, p.924. (Not: Millar, 1963, p.722, < *P. millari* n.sp.).

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM G10028 GH3084-5; Erskine I., QM G10116; Lizard I., QM GH3424; Trinity Bay, QM GH773).

PREVIOUSLY RECORDED: Queensland (Northwest I. — Kott 1966). Arafura Sea (Tokioka 1952). Philippines (Van Name 1918, Tokioka 1970, Millar 1975). Sri Lanka (Heller 1878). Red Sea, Gulf of Suez (Savigny 1816, Hartmeyer 1915b, Michaelsen 1919).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are robust, up to 20 cm long. They are often narrow and almost cylindrical, but occasionally wider and slightly laterally flattened, the dorsal test being thickened around the atrial aperture. The surface is naked and usually marked with some longitudinal creases or depressions. The apertures are usually conspicuous, the branchial aperture terminal on a thick, cylindrical and sometimes slightly ridged siphon, and the atrial aperture usually on a similar siphon from halfway along the dorsal surface and directed anteriorly, laterally or posteriorly. However, thickened test along the dorsal surface of the body around the atrial siphon may surround it for some or all of its length, obscuring it and its point of origin and reducing the external aperture to a sessile condition. The branchial siphon is often turned to one side but specimens with the branchial siphon turned posteriorly have not been recorded. There are 8 to 10 branchial lobes and 8 or 9 atrial lobes around the respective apertures; small projections between these lobes have ocelli on them. Sometimes (QM GH3424) there is a very inconspicuous tentacular fringe on the rim of the apertures, but this was not always detected. Individuals are fixed by the posterior end of the body, or by the posterior part of to most of, the left side. The test is thinner where the body is fixed to the substrate, but everywhere else it is thick, firm and rigid with a smooth surface. Living specimens are translucent and yellowish to milky white and the open, cylindrical siphons can be often seen protruding from crevices. In preservative, the test is translucent and smoky brown, grey, or almost colourless. The colour is usually deeper anteriorly than posteriorly.

The main test vessel enters the test from one-third to halfway down the body to the left of the ventral line. Branchial vessels extend anteriorly from it, while atrial and right parietal branches extend horizontally, and the ventral vessel extends posteriorly from the point of entry of the main vessel. Small terminal branches from these vessels are fairly evenly, but sparsely, distributed at the surface of the test.

INTERNAL STRUCTURE: The atrial siphon, from a level halfway down the dorsum, is a most conspicuous feature of the animal removed from its test. Musculature is strong on the right side of the body, with external longitudinal bands curving ventrally and terminating posteriorly at right angles to the ventral border. There they lie parallel to the ventral part of irregular and transverse bands that form a meshwork with the longitudinal bands over most of the right side and anterior to the gut loop on the right. There is no conspicuous musculature on the left over the gut loop, and the body wall is very delicate. Circular and longitudinal muscles are present around the siphons. There are 30 to 40 rather robust branchial tentacles with yellow blood corpuscles conspicuous in them. These alternate with rudimentary tentacles. The prebranchial area is very narrow and is finely papillated. There is a C- or U-shaped slit on a very small dorsal tubercle at the anterior end of the dorsal lamina. There is no V-shaped peritubercular area. The dorsal lamina is a double membrane for about half of its length, ribbed along both sides. Posteriorly, where the membrane is single, there are small tentacular projections continuous with each rib from the border of the membrane. The long dorsal ganglion is just anterior to the base of the atrial siphon. A long, irregular line of small accessory openings of the neural duct is present between the dorsal ganglion and the dorsal tubercle. These open into the peribranchial cavity to the left of the dorsal sinus.

There are deep plications in the branchial wall, one corresponding to each rather square mesh, with about 12 stigmata in each pleat. At the junction of the internal longitudinal vessels with the transverse vessels there are large, spoon-shaped, antero-posteriorly flattened papillae. These have a prominence on their concave dorsal surface and a small basal expansion anteriorly and posteriorly.

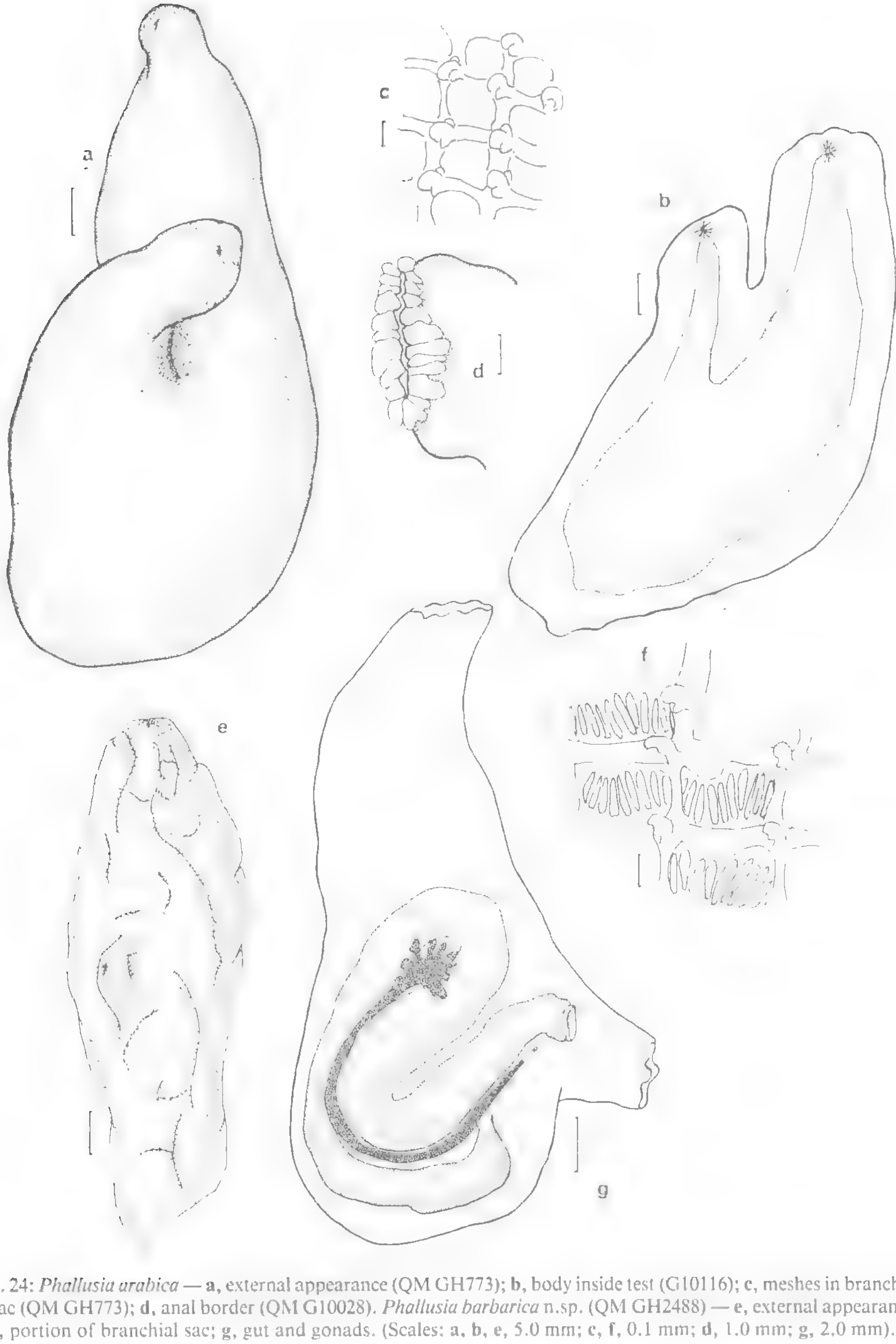


FIG. 24: *Phallusia arabica* — **a**, external appearance (QM GH773); **b**, body inside test (G10116); **c**, meshes in branchial sac (QM GH773); **d**, anal border (QM G10028). *Phallusia barbarica* n.sp. (QM GH2488) — **e**, external appearance; **f**, portion of branchial sac; **g**, gut and gonads. (Scales: **a**, **b**, **e**, 5.0 mm; **c**, **f**, 0.1 mm; **d**, 1.0 mm; **g**, 2.0 mm).

The oesophageal opening is about halfway down the dorsal lamina. The gut, which is confined to the posterior half of the body, forms a tight vertical or slightly oblique double loop. The pole of the primary loop is open. The rectum is distended with mud. The anal border has from 16 to 20 very conspicuous, sometimes bipartite, rounded lobes that curve back around the end of the rectum.

Testis follicles are present around the ovary and over the mesial surface of the gut. The ovary is a branched, convoluted tube, crowded in the loop of the duct. Thick gonoducts extend in a U-shape between the limbs of the deeply curved primary gut loop to the base of the atrial opening. The rectum, crowded between the oesophagus and the pole of the primary loop, is often distended with mud.

REMARKS: The long body, with its posteriorly placed atrial siphon resembles *Phallusia julinea*. It is distinguished from the latter species by the absence of chromatophores, the presence of the neural ganglion at the base of the atrial siphon rather than halfway between it and the dorsal tubercle, the presence of numerous anal lobes and the conspicuous cylindrical siphons. Further, the gut loop of the present species is more deeply curved, the oesophageal opening being in the middle of the branchial sac rather than posteriorly. There are also basal expansions on each side of the branchial papillae, and the branchial tentacles are more robust than in *P. julinea*.

A specimen of *P. arabica* from the Red Sea has been examined (ZMC 7/1 1903, ident. Hartmeyer); the present specimens cannot be separated from it by any known character.

The secondary openings of the neural gland are not reported in the original description of *Ascidia depressiuscula* Heller, 1878 from Sri Lanka, and the dorsal tubercle is described as having a slit with horns spiralling inwards. However, the general shape of the body and nature of the test do appear to be those of a *Phallusia* species. The position of the atrial siphon and absence of chromatophores suggest that Heller's specimen is conspecific with *P. arabica*.

As Millar (1975) observed, however, *Ascidia depressiuscula*: Herdman, 1906 appears to be a species of *Ascidia* rather than of *Phallusia*.

Phallusia philippinensis Millar, 1975 (excluding specimens from Singapore) and *Phallusia depressiuscula*: Van Name, 1918 and Tokioka, 1970 both have the atrial siphon and oesophageal opening from the middle of the dorsal surface, a tight U-shaped gut loop, pointed papillae absent from the surface test, basal expansions on the branchial papillae and a lobed anal border. They appear to be synonyms of the present species.

Some of the white, opaque specimens of *Phallusia julinea*: Tokioka, 1952 (45 to 80 mm specimens) from the Arafura Sea belong to the present species, having a lobed anal border and side branches on the branchial papillae. However, at least one other specimen (without anal lobes) is probably *P. julinea*.

Phallusia barbarica n.sp.

(Fig. 24e–g)

Ascidia nigra: Kott, 1964, p.148.
Phallusia julinea: Kott, 1966, p.295.

DISTRIBUTION

TYPE LOCALITY: Queensland (Moreton Bay, Cleveland Point, coll. A. Rozefelds, 3.7.77, holotype QM GH3086, paratype QM GH2488).

NEW RECORDS: Queensland (Moreton Bay, QM GH2678).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — QM G4982 Kott 1964; Hervey Bay — Kott 1966).

DESCRIPTION

EXTERNAL APPEARANCE: Preserved specimens (up to 8 cm long) are irregular externally and usually have sand, mud and some ephiphytes adhering to the surface. The body is rounded posteriorly (up to 3.5 cm wide), narrows to the terminal branchial aperture and is usually laterally or dorso-ventrally flattened. The atrial aperture is from half to two-thirds of the distance down the dorsal surface and projects from the body on a conical siphon of varying length. The siphons are faintly ridged externally and the surface of the test has fine creases and wrinkles.

The dark black-grey colour of the otherwise translucent test is caused by clouds of minute dark pigment cells scattered in it. The dark pigmentation is especially conspicuous anteriorly, fading toward the posterior end of the body. The main test vessel enters the test about two-thirds of the distance down the ventral border and the principal vessels radiate from the point of entry. The vessels, which also contain dark pigment cells in the preserved specimens, branch prolifically and form a fine three-dimensional network through the thickness of the test. The terminal branches are not expanded into ampullae. There are longitudinal bands of dark pigment in the siphonal linings. There are 8 branchial and 6 atrial lobes, all without a tentacular fringe.

INTERNAL STRUCTURE: Longitudinal muscle bands extend from the siphons obliquely across the right side of the body where they branch to form an irregular mesh. On the left the muscles are present only anterior to the gut loop. The prebranchial area is narrow and papillated. The dorsal tubercle is C-shaped in a shallow V-shaped perituberculat area. The dorsal lamina is wide, ribbed and double anteriorly, becoming a single membrane in the vicinity of the dorsal ganglion which is from one-half to two-thirds of the distance between the dorsal tubercle and the base of the atrial siphon. There are delicate tongue-like projections from the edge of the posterior part of the dorsal lamina. The oesophageal opening is about two-thirds of the distance down the dorsal border of the branchial sac. Large, C-shaped to almost circular, secondary openings from the neural gland into the peribrancial cavity are scattered along the length of the duct between the ganglion and dorsal tubercle.

The branchial sac has about one and a half deep, tight folds per mesh, with about 10 stigmata in each fold. The meshes are wider than long. There are spoon-shaped papillae at the junctions of the longitudinal and transverse vessels, but no intermediate papillae.

The gut loop is long, narrow and deeply curved, occupying more than half, and sometimes up to two-thirds of the left side of the body. The orientation of the loop varies with the position and orientation of the atrial aperture. The gut loop is vertical when the atrial siphon projects anteriorly. When the atrial siphon projects posteriorly the gut loop inclines dorsally. The pole of the loop is always anterior to the smooth rimmed anus. Neither the descending limb of the gut loop nor the rectum are distended with foecal material as they are so often in species of this genus.

Branches of the oviducts are present in the pole of the gut loop. They are short and are confined to the proximal end of the ovary.

Remarks: The most striking characteristic of this species is its rough, irregular and creased surface test with some sand and epiphytes, which resembles specimens of *Ascidia sydneiensis* and contrasts with the smooth naked test of other *Phallusia* spp.

The position of the neural ganglion between the dorsal tubercle and atrial siphon and the smooth anal border resembles *P. julinea*. However, in addition to the nature of its test, *P. barbarica* is distinguished by the absence of both expanded terminal ampullae of test vessels and fringes on the lobes of the apertures. The dark pigmentation of preserved specimens results from oxidation of blood pigments and does occur in other *Phallusia* spp. *Phallusia depressiuscula*: Hastings, 1931 does not have a distended gut and in that respect resembles the present species. However the smooth test, cylindrical siphons and general shape of the body distinguish it from the present species.

Phallusia julinea Sluiter, 1915
(Fig. 25; Pl.1f)

Phallusia julinea Sluiter, 1915, p.7. Hartmeyer, 1919, p.99. Hastings, 1931, p.81. Tokioka, 1950, p.133; 1952, p.107 (part, specimens 94 mm and 80 mm long 'without anal lobes'); 1961, p.110; 1967a, p.147; (not: 1952, p.107 specimen with anal lobules, < *P. arabica*). Kott, 1964, p.148; (not: 1952, p.305, < *P. millari* n.sp.; 1966, p.295, < *P. barbarica* n.sp.). Vasseur, 1967b, p.129; 1969, p.924. (Not: Millar, 1963, p.722, < *P. millari* n.sp.).

Distribution

New Records: Western Australia (Port Hedland, WAM 227.83). Queensland (Moreton I., QM GH363; Mooloolaba, QM GH2538; Kawana Waters, QM GH2480; Heron I., QM G4950 G10090 GH1440 GH2429 GH2431–4 GH2437 GH2452 GH2471–2 GH2479 GH2627; North-west I.; Yeppoon, QM G9465; Townsville, QM GH2604; Lizard I., QM G9775 GH2431; Cape Tribulation, QM GH2470; Mossman, QM GH2469).

Previously Recorded: Western Australia (Cape Jaubert — Hartmeyer 1919). Queensland (Heron I. — Kott 1964). Arafura Sea (Tokioka 1952). New Caledonia (Tokioka 1961, Vasseur 1967b). Palau Is (Tokioka 1950, USNM 11406 11416 Tokioka 1967a). Indonesia (Sluiter 1915). Madagascar (Vasseur 1969).

The species has been recorded down to 30 m depth, although most records refer to specimens taken in shallow water, wedged amongst coral and rubble from which they are often difficult to dislodge.

Description

External Appearance: Individuals are variable in shape, sometimes long and club-shaped, or curved and slightly irregular and often laterally flattened. The body is rounded posteriorly. The branchial aperture is usually terminal on a short conical siphon. The atrial aperture is from one-third to two-thirds of the length of the body along the dorsal surface and is anteriorly, laterally or posteriorly directed, often on a siphon but sometimes sessile. There are sometimes longitudinal furrows along the siphons and a few along the length of the body. The branchial siphon is often curved to the side and posteriorly. The test is firm, gelatinous and translucent. Its most conspicuous feature in the living animals are the yellow chromatophores in the surface of the otherwise brownish test that contains clouds of brown pigment cells which are absent from an area immediately around the chromatophores. The chromatophores are formed

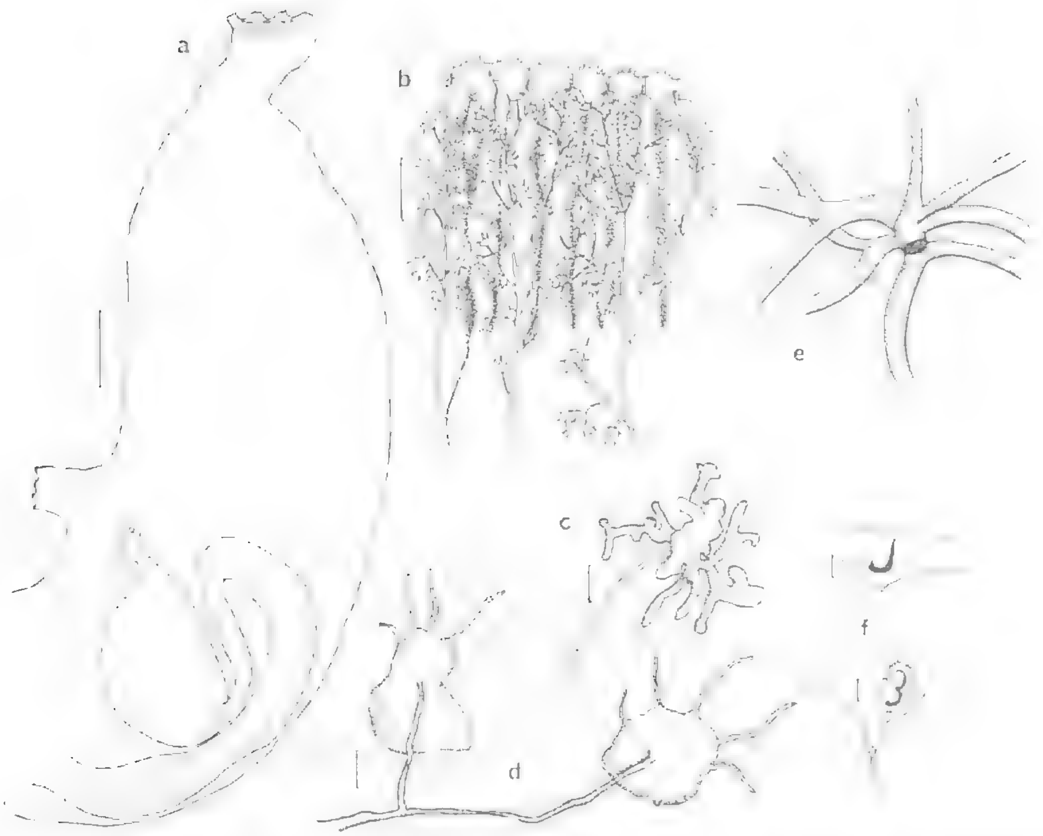


FIG. 25: *Phallusia julinea* — **a**, body from left side; **b**, test vessels and terminal ampullae in siphons with fringe on the border of the apertures and ocelli; **c**, terminal ampulla contracted; **d**, terminal ampulla expanded; **e**, origin of test vessels (diagrammatic); **f**, dorsal tubercles. (Scales: **a**, 5.0 mm; **b**, 2.0 mm; **c**, **d**, 0.2 mm; **f**, 0.25 mm).

by rounded reservoirs in the test vessels near the surface, from which short terminal vessels radiate in a circle at the surface. When the terminal vessels are expanded with blood they form, with the central vesicle, a star-shaped mass of yellow. Over the centre of each chromatophore is a minute pointed papilla, into which a central terminal vessel projects at its base. In preservative or when the chromatophores are not expanded, the pattern of pigmentation of the test is often inconspicuous or obscured. The thin terminal vessels radiating from a point beneath the surface papillae can still be seen in the test, however, and often the clear areas where brown pigmentation is absent from the area around the chromatophore can also be identified, especially on the anterior end of the body. The papillae and the associated chromatophores are fairly evenly distributed, but become more sparse posteriorly. The main test vessel enters the test halfway up the body to the left of the mid line. Atrial and right parietal branches extend horizontally from the point of entry of the test vessel; the branchial vessel extends anteriorly; and the ventral vessel extends posteriorly.

There are 8 to 10 small lobes around the branchial aperture and 8 to 10 around the atrial aperture in the present specimens, although Tokioka (1950) has recorded 9 to 16 lobes for the atrial aperture. Sometimes about 7 inconspicuous, tongue-like projections form a fringe on the border of each lobe. A comma-shaped ocellus is present between the lobes. Vertical bands of pigment are present in the siphon lining.

INTERNAL STRUCTURE: The body is long and narrow when removed from the test. The atrial siphon arises from one-third to one-half of the distance along the dorsal surface. Musculature is well developed on the right but not on the left. It consists of external longitudinal bands that curve toward the ventral border of the body posteriorly. There are transverse and irregular muscles that, together with the longitudinal bands, form a meshwork over the side of the body and also terminate against the ventral border at right angles to it. There are up to 50 branchial tentacles, although sometimes only half that number are present. They are relatively short and inconspicuous and very variable in size. The prebranchial area is very narrow, and the peritubercular area is a very shallow V. There is a large low dorsal tubercle with a V-, J-, E-, or H-shaped slit. The neural ganglion is at about one-half to two-thirds of the distance between the dorsal tubercle and the atrial siphon. Accessory openings of the neural gland into the peribranchial cavity occur to the left of the dorsal sinus. These are neither very numerous nor crowded, and are often absent altogether. The maximum number recorded is 19 (Tokioka 1950). The dorsal lamina is very wide. It is double in the anterior one-sixth to one-quarter of its length. It is ribbed on both sides. Posteriorly the ribs continue as small pointed projections from the margin of the membrane. The oesophageal opening is in the posterior one-third of the body.

The branchial sac is finely pleated, with 6 to 8 stigmata per mesh. There are small, narrow, antero-posteriorly flattened branchial papillae, with a rounded prominence on their dorsal concave border, but no basal prominences anteriorly or posteriorly.

The gut forms a tight double loop in the posterior half of the body. The stomach lies across the body and the distal half of the primary loop is open and curves dorsally. The rectum, which is usually distended with mud, extends antero-dorsally. The anal border is rounded, with 2 or 3 shallow indentations but no conspicuous rounded lobes.

The gonads are crowded in the loop of the gut. The ovary has short branches, and the small, elongate male follicles spread over the surface of the intestine.

Remarks: The characteristics of *P. julinea* are its chromatophores; fringed lobes around the apertures; rather large dorsal tubercle and slit; relatively few accessory openings of the neural gland; short, robust and relatively few tentacles; oesophageal opening toward the posterior end of the dorsal lamina; rectum well separated from the oesophagus; narrow branchial papillae without basal prominences; and atrial siphon from mid-body level. In the absence of accessory openings of the neural gland the species can be recognised primarily by its stellate chromatophores, which should not be confused with the spherical terminal ampullae of *Ascidia latesiphonica* and *Ascidia decepta* n.sp. The fringes on the lobes of apertures occur in *P. arabica*, *A. sydneiensis* and related species and in *A. liberata*.

Amongst the specimens from the Arafura Sea (*P. julinea*: Tokioka, 1952), only one of the figured specimens (80 mm) has the anal border without lobes and the large dorsal tubercle that can be ascribed to the present species.

Phallusia millari n.sp.
(Fig. 26)

Phallusia depressiuscula: Tokioka, 1952, p.110; 1970, p.87 (part, specimen no 954). Kott, 1972c, p.49.
Phallusia julinea: Kott 1952, p.305. Millar, 1963, p.722.
Phallusia philippensis Millar, 1975, p.273 (part, specimens from Singapore).

Distribution

Type Locality: Queensland (Abbot Bay, Euri Creek, 16 m in sandy mud, coll. Roberts and Hammond, 19.3.81, holotype QM GH699).

New Records: Western Australia (Montebello I., WAM 959.83 1281–2.83; Port Hedland, WAM 1287.83; Dampier Archipelago, WAM 1284.83; Shark Bay, WAM 1285.83). Queensland (Heron I., QM GH2798; Townsville; NW of Bowen, paratypes QM GH700 GH2364-2370; Cairns, QM GH983 GH2504; Princess Charlotte Bay, QM GH2505 GH2494-69; Cape Tribulation, GH2497; Innisfail, QM GH796 GH2500; Bathurst Head, QM GH2501; Cape Kimberley, QM GH2502; Cape Weymouth, QM GH2495-9 GH2502-3).

Previously Recorded: Western Australia (Cape Jaubert — Kott 1952; Cockburn Sound — Millar 1963). Northern Australia (Gulf of Carpentaria — AM Y1045 Y1048 Y1054-5 Y1061 Y1072 Kott 1972e). Arafura Sea (Tokioka 1952). Philippines (Tokioka 1970). Singapore (Millar 1975).

Description

External Appearance: Individuals are narrow and elongate (to 15 cm long) to rectangular, and invariably laterally flattened. The body narrows only slightly anteriorly. There is often a large, rounded, sandy holdfast, separated from the rounded posterior end by a constriction. Sometimes the body tapers posteriorly to a short stalk, or is sessile, fixed by part of the left side. The external apertures are sessile in smaller specimens, with the branchial aperture at the ventral end of the oblique upper surface, and the atrial aperture at the dorsal end, slightly posterior to the branchial aperture. In large specimens the branchial siphon is produced forwards and often turned to the right and posteriorly. The atrial

FIG. 26: *Phallusia millari* n.sp. — **a**, external appearance (WAM 287.83); **b**, external appearance showing test vessels (QM GH699); **c**, test vessels from inside test (diagrammatic); **d**, anal border. (Scales: **a**, **b**, 1.0 cm; **d**, 1.0 mm).

siphon, only a short distance posterior to the branchial siphon, projects straight forward. The test is smooth, translucent and firm, especially around the apertures, each being surrounded by a rounded rim of test. When siphons are present, they are firm and cylindrical. There are only rare, shallow longitudinal depressions in the surface test. The usual small lobes occur around the borders of the apertures, visible only in dissected specimens. There are 8 to 12 branchial lobes and 6 to 10 atrial lobes, with the usual delicate projections supporting ocelli between the lobes.

The test is translucent and white with a bluish tinge in preserved specimens, although blue-black blood cells are present in the short terminal branches of the test vessels, which are crowded in the surface test. Terminal branching of the test vessels is irregular, and there is no umbellate branching pattern as in *P. julinea*. The main test vessel enters the test from near the posterior end of the body to the left of the ventral line. Sometimes the main vessel enters the test from two-thirds down the length of the body and extends posteriorly before subdividing into the usual branches. The branchial and right parietal vessels extend posteriorly and ventrally before curving to extend anteriorly parallel to one another and to the longitudinal axis of the body. The atrial and ventral vessels extend posteriorly and dorsally before curving to run anteriorly, also parallel to the long axis of the body and to the other vessels. These vessels are embedded in the surface of the inside of the test against the body wall; their branches penetrate the test towards its outer surface, where their terminal branches and ampullae are present. There are two conspicuous channels in each main vessel.

Freshly collected material is described as transparent and veined. Oxidation of the vanadium in the blood cells changes its colour to dark blue-black.

INTERNAL STRUCTURE: The body removed from the test is long and narrow. The atrial siphon, which is always directed anteriorly, arises from the anterior third of the body. The body wall has longitudinal and transverse muscle-bands forming an irregular meshwork on the right side of the body, as in other species of this genus. There are from 50 to 100 branchial tentacles that, like the blood vessels, contain dark blood cells. These tentacles are very variable in size, but are mostly rather small. The prebranchial area is narrow. The peritubercular V is very shallow indeed, and often the prepharyngeal groove extends straight across the anterior end of the dorsal lamina. The slit on the dorsal tubercle is small and U-shaped to large and E- or H-shaped. Occasionally no primary opening of the neural gland could be found (see also Millar 1963). The dorsal lamina is wide, a double membrane for the anterior one-third of its length. It is ribbed on both sides. Posteriorly, these ribs are produced into robust, tentacle-like projections from the free margin of the membrane. The neural gland has numerous conspicuous accessory openings into the peribranchial cavity dorsal to the dorsal lamina on both sides of the dorsal sinus, between the neural ganglion and the dorsal tubercle. The ganglion is near the base of the atrial siphon.

The branchial sac is finely pleated and has 8 stigmata per mesh. The branchial papillae are rather small, rounded and antero-posteriorly flattened, with a rounded swelling in their dorsal concave border.

The oesophageal opening is two-thirds of the way down the branchial sac. The gut forms a long, narrow double loop, the distal half of the primary loop extending in an oblique line antero-dorsally from the postero-ventral curve of the body. It reaches the level of the atrial siphon. The anal border is divided into at least 20 conspicuous lobes. The descending limb of the primary loop and the rectum are often filled with fine sediment, but are not distended into large pouches as in other species of the genus.

The gonads are crowded into the pole of the primary gut loop. When mature, either the male or the female duct is distended with gametes and is very conspicuous between the limbs of the gut loop, accompanying the rectum to the base of the atrial siphon.

REMARKS: The species is distinguished by its anterior atrial siphon, sandy posterior holdfast, remarkable parallel test vessels that extend the whole length of the body, absence of large mud-filled distended pouch in the distal part of the intestine and in the rectum, and robust, tentacle-like projections on the posterior part of the dorsal lamina. The absence of chromatophores, the sparse irregular branching of the terminal test vessels, the absence of a tentacular fringe on the lobes of the apertures, the more numerous accessory openings of the neural gland, and the presence of anal lobes represent additional distinctions from *P. julinea*. The absence of basal prominences on each side of the branchial papillae further distinguish the species from *P. arabica*. The temperate species *Phallusia obesa* has a similar, anteriorly placed atrial siphon and recurved branchial siphon, but its surface furrows, ridges and tuberosities and dark pigment spots never occur in the present tropical species.

Tokioka's (1970) problematical specimen no. 954 from the Philippines has the characteristic parallel vessels and other characteristics of the present species.

Phallusia obesa (Herdman, 1880)
(Pl. 1g)

Pachychlaena obesa Herdman, 1880, p.462; 1882, p.223; 1891, p.596; 1898, p.446.

Phallusia obesa: Traustedt, 1885, p.16. Hartmeyer, 1909, p.1403. Hartmeyer and Michaelsen, 1928, p.308. Millar, 1963, p.723.

Ascidia obesa: Kott, 1952, p.303.

Pachychlaena oblonga Herdman, 1880, p.461; 1882, p.221; 1891, p.596; 1898, p.446.

Phallusia oblonga: Traustedt, 1885, p.16. Hartmeyer, 1909, p.1403.

Ascidia phallusioides Herdman, 1898, p.446; 1899, p.12.

Phallusia phallusioides Julin and Roberts, 1913, p.296.

Ascidia nigra: Kott, 1952, p.305.

Phallusia depressiuscula: Kott, 1972a, p.23; 1972d, p.250; 1976a, p.73.

DISTRIBUTION

NEW RECORDS: Western Australia (Houtman's Abrolhos, WAM 1273.83; Dampier Archipelago, WAM 1275.83; Rosemary I., WAM 1276.83; Port Hedland, WAM 1277.83; Cockburn Sound, WAM 126.72 15.75 107.75 1270.83 1272.83, QM G9650; Albany, WAM 1274.83). South Australia (Port Noarlunga, QM G9324 G9305; Spencer Gulf, QM GH2621; Kangaroo I., QM G10000). New South Wales (Jervis Bay, QM G9464; Solitary I., QM G9631). Queensland (Tallebudgera, QM GH2473; Moreton Bay, QM GH362; Cape Melville, QM GH2344).

PREVIOUSLY RECORDED: Western Australia (Shark Bay to Albany — Hartmeyer and Michaelsen 1928, Kott 1952, Millar 1963). South Australia (St Vincent Gulf — Kott 1972a). Victoria (Bass Strait — Herdman 1880 1882; Westernport — Kott 1976a). New South Wales (Port Jackson — Herdman 1898 1899). Queensland (Moreton Bay — Kott 1972d).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens up to 16 cm long are known. They are longer than wide, and taper to a terminal branchial aperture which is on a short siphon, invariably curved to the right side and posteriorly. The atrial siphon arises from the anterior one-third of the dorsal surface, usually directed anteriorly. The surface of the firm, cartilaginous test is raised into rounded longitudinal ridges, which are often subdivided into rounded tubercles. The colour is very variable, being cream or brown or blue-grey, or often dark grey to black. There are often, but not always, dark pigment spots scattered over the surface, each on a small protruberance. These pigment spots each consist of a heavily pigmented area around a group of radially arranged terminal test vessels in each protruberance.

Branches of the vessels extend anteriorly, posteriorly and laterally from the point of entry of the main test vessel, about halfway up the body to the left of the ventral line.

There are 10 to 12 branchial lobes and 10 atrial lobes around the respective apertures, with ocelli between these lobes.

INTERNAL STRUCTURE: The internal branchial siphon arises from the anterior one-third of the body. The body musculature is conspicuous only on the right side and around the siphons. The musculature on the right consists of an irregular meshwork of longitudinal and transverse bands, as in other species of the genus. There are 50 to 80 branchial tentacles. The prebranchial area is very narrow. The peritubercular area is a very shallow V. The slit on the dorsal tubercle varies from a simple horizontal opening to an S- or U-shape with horns turned out. In very large specimens, it is often interrupted. The neural gland has very numerous accessory openings into the peribranchial cavity above the dorsal lamina. There is also conspicuous glandular material along the length of the neural duct between the neural gland (situated at the base of the atrial siphon) and the dorsal tubercle. The dorsal lamina is a double membrane anteriorly, ribbed on both sides. The ribs terminate on the free border of the membrane in delicate projections, which become larger and more conspicuous posteriorly.

The oesophageal opening is about two-thirds of the distance down the branchial sac. The branchial wall is finely pleated, and there are 4 to 6 stigmata per mesh. The branchial papillae at the junction of the longitudinal and transverse vessels curve dorsally and have a rounded prominence on their dorsal concave border.

The gut loop is large and deeply curved, but does not extend anterior to the atrial siphon. The descending limb of the gut loop and the rectum are always distended with fine sediment. The anal border is divided into at least 20 lobes.

Gonads are crowded in the primary gut loop. The ovary has short branches, and the branched testes follicles are scattered over the gut loop.

REMARKS: This species is particularly robust, and individuals become larger than most other species found in Australian waters. Kott (1964), confounded by its variability, proposed other tropical species of *Phallusia* as synonyms of *P. obesa*. Although the type of radial branching of the terminal test vessels appears to be similar in *P. julinea*, the pigment spots in the surface test of *P. obesa* are caused by pigment in the test, rather than in the vessels themselves as is the case in the former species. Further, the atrial siphon is always from the anterior third of the test rather than (as in *P. julinea*) the middle of the dorsal surface. The species are further distinguished by the absence of anal lobes in *P julinea*.

Pigment spots are not always present in *P. obesa*, however, and confusion with *P. millari* n.sp. can also occur, as the orientation of the siphons (the branchial siphon curved posteriorly and the atrial siphon directed anteriorly), a particularly consistent character in the present species, also occurs in larger specimens of *P. millari*. However, the latter species has a smooth surface and distinctive arrangement of its test vessels. In the absence of the longitudinal furrows and tubercles on the test (that are usually present in *P. obesa*), the species can be distinguished from *P. arabica* by the anterior position of its atrial siphon and the posterior curve of the branchial siphon. The large number of accessory openings of the neural gland and the conspicuous development of glandular tissue above the dorsal lamina are further characteristics of *P. obesa*.

The Atlantic species *Ascidia nigra* also resembles *P. obesa* in general morphology. Although it is often black, *P. obesa* is never the deep glossy black of *P. nigra*.

Family PLURELLIDAE Kott, 1973

The family contains both colonial and solitary species. The body along the dorsal mid-line, both anterior and posterior to the atrial aperture and including the neural complex and the gonads, is embedded in the test. The neural gland and ganglion are present in the test just anterior to the atrial aperture. The duct of the neural gland extends in the test along the dorsal mid-line and opens to the atrial cavity by very numerous minute, simple, ciliated pits along its length. The short oval ovarian sacs are embedded in the test around the posterior and left side of the base of the atrial siphon. The testis is also embedded in the test some distance behind the ovary just to the left of the dorsal mid-line. The vas deferens extends forward in the inner layer of test to open into the base of the atrial siphon alongside the short oviduct. The heart is a robust tube, also embedded in the test in an arc around the ventral border of the gut loop on the left side of the ventral mid-line. The intestine is flattened. A further characteristic of this family is the loop of the prepharyngeal groove from the left across the mid-line anterior to the dorsal lamina to create a fold of the branchial sac, its base just to the left of the dorsal lamina, which it covers. There are numerous rows of regular stigmata and entire longitudinal vessels with papillae at their junctions with the transverse vessels. The test is extremely thin and fragile, and brittle with sand. Body musculature consists of a layer of parallel transverse bands along the ventral half of the right side of the body.

The zooids of colonial species in this family (genus *Plurella*) are very similar to the solitary individuals of the monotypic genus *Microgastra* n.gen., although they are generally smaller and less variable in size, the maximum zooid size being determined by the vegetative process. In view of this close morphology, the vegetative habit is probably an apomorphic character resulting from environmental pressures; and it does not appear to justify separation of colonial and solitary species at the familial level.

Although the multiple openings of the neural duct are reminiscent of *Phallusia*, the closest relative to the Plurellidae in the extant fauna is probably *Ascidia scaevola*, which has a tight and reduced gut loop, very delicate body wall with transverse muscle bands even more specialised than those of the Plurellidae, and a fold in the branchial sac identical with that of the Plurellidae. The openings of the plurellid neural gland are on the end of long, narrow ducts. Their very minute ciliated pits do not resemble those of any other species of Phlebobranchia. The gonads of Plurellidae are also quite unique.

Although *Perophora hutchisoni* has a similar separation of ovary from testis, the ovary (with a short oviduct) being located near the dorsal line, this does not indicate a phylogenetic relationship between Plurellidae and the other vegetatively reproducing family of the Phlebobranchia, Perophoridae. The latter is distinguished by its small zooids joined only by basal stolons in which buds develop, and its very much reduced branchial sacs.

The location of the gonads in pouches embedded in the test is also known in the stolidobranch genus *Seriocarpa* (family Styelidae).

The family Plurellidae is represented by two tropical and one temperate species, *viz.* a solitary species from the western Pacific (*Microgastra granosa*), an undescribed colonial species of *Plurella* from the Philippines (QM GH542, GH829) and a colonial species from temperate Australian waters (*Plurella elongata*). The affinities of the family appear to be with tropical *Ascidia* spp.

KEY TO THE GENERA OF PLURELLIDAE

Solitary; single ovary .... *Microgastra* n.gen.
Colonial; more than a single ovary........ *Plurella*

Genus **Microgastra** n. gen.

Type species: *Ascidia granosa* Sluiter, 1904

The genus contains solitary species of the family Plurellidae. The gut loop is a very small, deeply curved loop embedded in connective tissue but only very lightly attached to the thin body wall which is closely associated with the test. A single ovarian sac is embedded in the test posterior to the base of the atrial aperture. The testis is a compact oval organ embedded in the test a short distance behind the ovary.

The single known species is found on sandy substrates. It appears to have a wide range in the Indo-West Pacific, but records are few, probably because it is inconspicuous and fragile, with an extremely delicate body wall and thin test that is brittle with sand.

Microgastra granosa (Sluiter, 1904)
(Fig. 27)

Ascidia granosa Sluiter, 1904, p.36. Hartmeyer, 1906, p.21. Hastings, 1931, p.80.
Ascidia lapidosa Sluiter, 1904, p.32.
Ascidia mikrenterica Sluiter, 1904, p.37. Herdman, 1906, p.306.
Ascidia polytrema Herdman, 1906, p.306.

DISTRIBUTION

NEW RECORDS: Queensland (NW of Bowen, QM GH664 GH668 GH678 GH685 GH689–92 GH694 GH701; Townsville, QM GH712; Innisfail, QM GH775; Murdoch Point, QM GH2363; Princess Charlotte Bay, QM GH2362; Gordonvale, QM GH775.

PREVIOUSLY RECORDED: Queensland (Low Is — Hastings 1931). Indonesia (*A. lapidosa* syntypes ZMA V.TU240-1 V.TU243 Sluiter 1904, *A. mikrenterica* syntypes ZMA V.TU254 Sluiter 1904). Sri Lanka (Herdman 1906). Japan (Hartmeyer 1906).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are laterally flattened and longer than they are wide (up to 8 cm long and 4 cm wide). They narrow to a terminal branchial aperture, and the dorsal surface also tapers to the atrial aperture about halfway along its length. The atrial aperture is sometimes on a long, cylindrical siphon extending at right angles to the longitudinal axis of the body. There is usually a strong, root-like process about halfway along the ventral border just to the right of the ventral mid-line. The thin test is very brittle with embedded sand. Across the ventral surface, the test appears to be separated into 2 layers. The inner layer consists of a strong membrane which extends across beneath the body of the animal to enclose a space bounded on the outside by brittle external layers of sand-embedded test. There are usually two lamellibranch molluscs enclosed in this space (Leptonacea, Laseidae, *Kellia* sp.).

INTERNAL STRUCTURE: The body wall is very delicate and is closely associated with the test, with the exception of the layer of parallel transverse muscles along the whole length of the right side. There are about 50 branchial tentacles at the base of a short siphon. They are robust, tapering to a very fine point, and of variable length. The branchial aperture is directed to the side or dorsally, possibly away from the substrate. It has about 16 small, triangular lobes around the border. The prepharyngeal groove loops across the dorsal mid-line in front of the dorsal lamina, so that a fold of the branchial sac, its base just to the

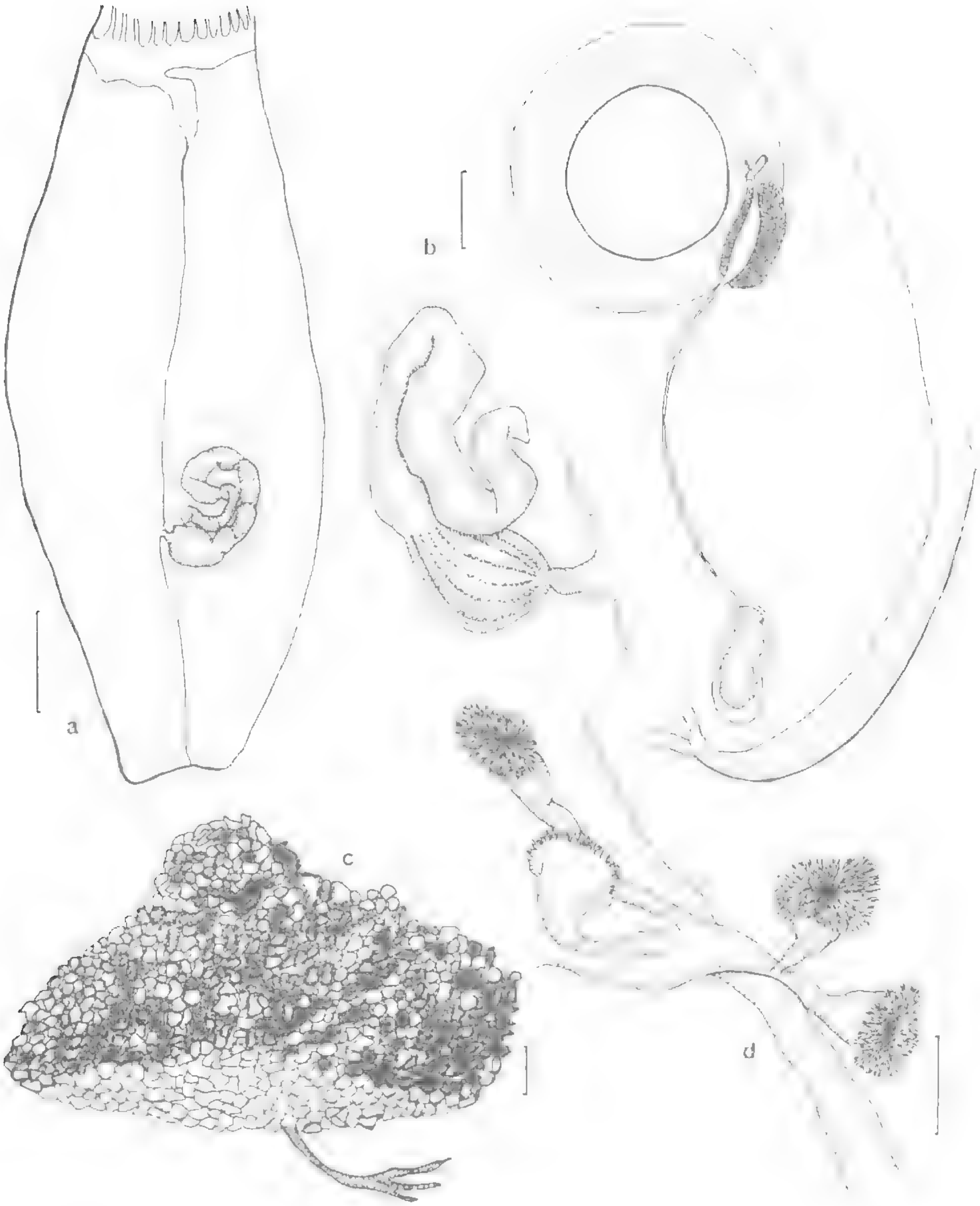


FIG. 27: *Microgastra granosa* — **a**, internal body wall, showing looped prepharyngeal groove and gut in position; **b**, internal body wall with gut displaced to the right showing heart, testis, vas deferens, seminal vesicle and ovary embedded in test at the side of the atrial opening; **c**, external appearance; **d**, part of neural duct, with cilated pits that open into the peribranchial cavity. (Scales: **a**, **c**, 1.0 cm; **b**, 0.25 cm; **d**, 0.05 mm).

left of the dorsal lamina, lies across the dorsal mid-line. Anteriorly the plain-bordered dorsal lamina is a double membrane. The dorsal ganglion and gland are embedded in the inner layer of test just anterior to the atrial aperture. Openings of the neural gland into the atrial cavity are very numerous, minute, trumpet-shaped, ciliated pits on narrow ducts that branch off the duct of the neural gland along its whole length between the gland and the anterior end of the dorsal lamina. The pits are only 0.05 mm in diameter at their widest where they open into the atrial cavity.

A very large shrimp, brooding eggs, is often present in the branchial cavity. The branchial sac is very delicate indeed. There are small papillae at the junction of the internal longitudinal and transverse vessels. Approximately 50 internal longitudinal vessels and 300 rows of short, oval stigmata (1 or 2 per mesh) are present on each side of the body.

The oesophageal opening is about two-thirds of the distance down the branchial sac. The deeply curved and very tight U-shaped gut loop forms a small, opaque mass of variable size in the dorsal part of the left side of the body adjacent to the oesophageal opening. The oesophagus is short. The thin-walled stomach has longitudinal folds and is almost spherical. The intestine is flat and almost ribbon-like. The loop is only very slightly open at the pole, which curves around towards the oesophageal end of the loop. The rectum is sometimes distended with mud. The anal border has irregular serrations. The whole gut is embedded in transparent, vascularised connective tissue, which holds it in a tight nucleus that lies free in the atrial cavity, attached only to the pharynx at the oesophageal end. Variation in size of the gut mass from one-seventh (or less) to one-third of the body length suggests that regeneration could occur. There is a single, flask-shaped ovarian sac embedded in the test at the base of the atrial siphon to the left of the mid-dorsal line. The short oviduct opens into the base of the atrial siphon distal to a wide tough velum of test (which has a thin covering of the body wall) that projects across the base of the aperture. The testis is a single, oblong mass of small, crowded follicles embedded in the test almost in the dorsal mid-line. The vas deferens extends from the distal end of the testis to the mesial surface of the ovary, where it expands into a seminal vesicle before opening with the oviduct into the base of the atrial siphon.

The body wall is firmly embedded in the test along the dorsal line, together with the gonads and the vas deferens. It is also embedded (with the heart) in a wide arc around the postero-ventral border of the gut loop from the testis to halfway along the ventral border of the body.

REMARKS: Dissected syntype material of *Ascidia lapidosa* Sluiter, 1904 (ZMA V.TU241) has been examined. The four specimens include a specimen of *Polycarpa chinensis*, one specimen of *Boltenia transversaria* (Sluiter, 1904), and only a single specimen of *Ascidia* which conforms with the description of the present species. This specimen, however, cannot be reconciled with Sluiter's description, possibly as a result of its confusion with the other specimens examined with it. *Ascidia granosa* Sluiter, 1904 has therefore been selected as the senior synonym for this species, and the type species for the genus *Microgastra*. It has page priority over *Ascidia mikrenterica* Sluiter, 1904. Its similarity to *Ascidia mikrenterica* was noted by Sluiter. The presence of gonads in the gut loop reported by Sluiter has not been confirmed. In the holotype, they are present embedded in the test, as they are in the newly recorded material. Sluiter also overlooked the branchial fold. It is surprising that Hartmeyer (1906), Herdman (1906) and Hastings (1931) also overlooked the position of the gonads and the presence of a branchial fold. It is possible that these characters were not detected because the body is extremely fragile and difficult to isolate from the sandy, brittle test, which also conceals the gonads and neural elements embedded firmly in it. Herdman (1906) did observe the neural gland openings, although his figure (Fig. 34) is out of scale.

The horny, spherical bodies between the test and body wall to which Sluiter (1904) referred, were apparently in the same position as the commensal lamellibranchs *Kellia* sp. found in the present specimens.

Ascidia recifensis Millar, 1977, from the Brazilian Shelf, has a small, tight gut loop, a sand-encrusted test, and secondary openings of the neural gland into the atrial cavity. No gonads were detected, but it is unlikely that specimens as long as 2.6 cm are juveniles, as Millar suggested. The possibility remains that *A. recifensis* is a species of *Microgastra*, distinguished from *M. granosa* by the absence of a branchial fold.

Genus **Plurella** Kott, 1973

Type species: *Plurella elongata* Kott, 1973

Vegetatively reproducing species of the family Plurellidae. The gonads consist of 4 or 5 ovarian sacs embedded in the test around the posterior and left side of the rim of the base of the atrial siphon.

The vas deferens branches, each branch expanding into a seminal vesicle on the surface of an ovarian sac. The gut is of moderate size and does not project free of the body wall as it does in *Microgastra*.

Colonies are massive and irregular, with zooids lying parallel to one another. They are separate for most of their length, although they adhere to one another and to the embedded sand in the test of adjacent zooids. Sand also collects between them. The posterior ends of the zooids are embedded in common test and here the colony is compact, with sand embedded in the surface but largely absent internally. Enlarged terminal ampullae are present in the common test at the posterior end of the body. They may be involved in the budding process. The form of these plurellid colonies most resembles those of *Polyandrocarpa lapidosa* and *P. watsonia* n.sp. (family Styelidae), although no phylogenetic relationship is implied by this resemblance. Similarly, division of a tubular ovary into sacs with separate openings and the presence of multiple openings of a single vas deferens are known only in Stolidobranchia (*Pyura littoralis* and *Molgula* spp. respectively).

The genus is not diverse. The two known species are inconspicuous. Colonies, which are embedded in sand, are difficult to dislodge. They have been collected only by SCUBA divers. Their projecting orange siphons are usually all that can be seen; it is probable that they occur more frequently than their present records suggest.

Plurella elongata Kott, 1973
(Fig. 28)

Plurella elongata Kott, 1973, p.258.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 170.75 1253.83, QM GH758). Victoria (Bass Strait, QM GH2230, NMV H411).

PREVIOUSLY RECORDED: South Australia (Investigator Strait — paratypes AM Y1163, NMV H165-6, holotype NMV H164 Kott 1973).

The species has been recorded from waters to 92 m deep in sandy habitats.

DESCRIPTION

EXTERNAL APPEARANCE: Sandy, massive, dome-shaped colonies, up to 12 cm in diameter, are formed. The maximum thickness of the colony is about 5 cm. The colony consists of long, cylindrical, crowded zooids, lying parallel to one another between the base and upper surface of the colony, with the largest zooids in the centre. The upper surface is rather loose, the zooids being separate from one another, although adjacent

FIG. 28: *Plurella elongata* (QM GH758) — a, portion of basal part of colony from left side of a zooid showing gut loop, testis and ovary embedded in the test and atrial siphon opening posteriorly; b, posterior rim of internal opening of the atrial aperture showing gonads embedded in the test. (Scales: 1.0 mm).

zooids do adhere to one another and to the sand that is embedded in the test. Posteriorly the zooids are enclosed in tough common test. Posteriorly directed atrial siphons, which form the posterior part of the dorsal surface of each zooid, are usually free of the common test, and interrupt it to open on the undersurface of the colony.

The body wall is orange in living specimens. Traces of the orange pigmentation can be seen in the siphon lining of preserved specimens. The border of the terminal branchial aperture has about 12 lobes; the posteriorly oriented atrial aperture has 6. The test is generally very thin and brittle, with sand embedded throughout. However, it is thicker on the dorsal part of the body between the atrial siphon and the posterior end, where the gonads are embedded in a glassy, tough, well-vascularised transparent inner layer.

INTERNAL STRUCTURE: The body wall is extremely thin. Circular muscles form a sphincter around each aperture, but the remainder of the cylindrical siphons have few muscles and are very delicate. There is a layer of transverse muscle bands down the right side of the body. The body wall is embedded in the test along its dorsal border between the dorsal tubercle and the atrial siphon (enclosing the neural duct); between the testis and the atrial siphon (enclosing the vas deferens); and in an arc around the postero-ventral curve of the body from the vicinity of the testis to about halfway along the ventral surface (enclosing the heart). At the base of the branchial siphon is a ring of about 40 simple branchial tentacles. The prepharyngeal area is wide. The prepharyngeal groove loops to the left across the mid-line in front of the anterior end of the dorsal lamina to create a branchial fold just to its left. Numerous minute, simple, ciliated pits (0.05 mm in diameter) open into the atrial cavity from the duct of the neural gland, which is embedded in the test along the dorsal mid-line. The neural gland and ganglion are also embedded in the test, just anterior to the base of the atrial siphon.

The dorsal lamina and the endostyle are long and straight, the former a double membrane anteriorly. With the exception of the single dorsal fold to the left of the dorsal lamina, the branchial sac is flat and very delicate, with about 50 internal longitudinal vessels on the right side and about 200 rows of short, oval stigmata (1 to 3 per mesh). Papillae are present at the junctions of internal longitudinal and transverse vessels.

The oesophageal opening is almost at the posterior end of the body. The oesophagus extends posteriorly, opening into a rounded stomach in the posterior curve of the simple arc that is formed by the gut. The intestine extends anteriorly in a more or less straight line, then curves over into a very short rectum that terminates near the anterior border of the base of the atrial siphon. The anus is smooth and bilabiate, with its opening directed down into the posteriorly oriented atrial siphon.

The gonads consist of about 5 sac-like ovaries embedded in the thick, transparent test around the posterior and left rim of the base of the atrial siphon. Each opens by a short oviduct into the base of the atrial siphon. The testis is a single, rather irregular, oblong mass of very small, crowded pyriform follicles that is also embedded in the test at the posterior end of the body, just to the left of the mid-dorsal line. A vas deferens from the distal end of the testis divides into branches, one to each ovary. These branches of the vas deferens expand into a seminal vesicle on the ventral side of each ovarian sac as it lies in the test. At the distal end of the ovary, these vesicles narrow to form short ducts that lie on the surface of each oviduct and open with them into the base of the atrial siphon.

REMARKS: Two large colonies collected from different locations in the Philippines (QM GH542, GH829) are specimens of an undescribed species of this genus very similar to *P. elongata*. The Philippine species has anteriorly directed atrial siphons opening on the upper surface of the colony with the branchial apertures, the gut forming a curved loop (rather than a simple arc) and the rectum being directed anteriorly toward the anteriorly placed atrial opening.

The present species is unusual in having posteriorly directed atrial apertures opening at the base of the colony. It seems probable that the excurrent water from the colony irrigates the sediments in which it is embedded.

The species is distinguished from *Microgastra granosa* by its embedded gut that does not form a loop, and its colonial habit and smaller-sized individuals. Openings of the duct of the neural gland are less numerous than in *M. granosa*

Family AGNESIIDAE Huntsman, 1912

Phlebobranch ascidians in which either bifid or undivided papillae on the transverse vessels are all that remains of the longitudinal vessels; even these are sometimes lost altogether.

The test of members of this family is thin and translucent but is often strengthened, and sometimes made rigid, with embedded sand. The body musculature is usually specialised, muscle-bands being reduced in length and adapted to flatten the body laterally and often to pull folds of the body wall and test across the apertures. Circular muscle-bands are present around the siphons, but horizontal muscles rarely encircle the remainder of the body, usually being confined to short bands around its dorsal and ventral borders. The internal lining of the stomach is not folded.

In addition to the loss of entire longitudinal vessels, the branchial sacs of species in this family are further reduced in that the number of branchial papillae (relicts of longitudinal vessels) on each transverse vessel is usually considerably less than the number of internal longitudinal vessels in the Ascidiidae. There are also fewer transverse vessels.

The two subfamilies are distinguished by their stigmata, which are coiled in the Agnesiinae, but straight in the rarely encountered Ciallusiinae. The latter subfamily contains one monotypic genus (*Pterygascidia mirabilis* Sluiter, 1904; see Tokioka 1971) not yet recorded from Australia. The species is known from the Timor Sea and from the Philippine Is (as *Ciallusia longa* Van Name, 1918) from depths of 70 to 216 m.

Agnesiinae is a subfamily that is not diverse. More than half the species are recorded only from deep oceanic basins. The remainder occur in shallow sublittoral waters, and 4 are recorded from Australia.

Subfamily AGNESIINAE Huus, 1937

Species of the family Agnesiidae in which the stigmata spiral.

Usually the branchial tentacles are arranged in 4 concentric circles. The borders of the branchial and atrial apertures are divided, respectively, into 7 and 6 pronounced lobes. The test is usually impregnated with sand, making it stiff and brittle.

Stigmata occur in symmetrical pairs in each row, each pair partner coiling in the opposite direction to the other. The rows of coiled stigmata also occur in pairs, one row being a mirror image of the other in respect of the direction in which the stigmata coil. Primary transverse vessels occur between pairs of rows, and intermediate transverse vessels occur between the rows of the pair. Papillae on the intermediate vessels are often, but not always, smaller than those on the primary vessels and are sometimes absent altogether. Each coil consists of a single stigma, rather than the two that are usually coiled together in the Molgulidae. There usually are radial vessels along the diagonals of the coil.

Species are usually unattached on the open sea floor. Records of the 4 species reported in Australian waters are few. However, *Adagnesia opaca* and *Agnesia glaciata* are present in relatively large populations in Moreton Bay, and *Adagnesia venusta* n.sp., despite its small size, has been taken at several stations in Bass Strait. Both locations, especially the former, have been subjected to systematic surveys for benthic fauna. It is possible that the family may be represented at other locations that have not yet been subjected to the same collecting effort.

Adaptation for sandy sea-floor habitats is evident in the sand-embedded test and flattened body of most species. *Agnesia arnaudi* Monniot and Monniot, 1974b from Kerguelen is known to brood tailed larvae in the right peribranchial cavity. From Australian seas, *Adagnesia opaca* and *A. venusta* n.sp. have oviducts oriented away from the excurrent aperature. The former species has eggs in the peribranchial cavity like *Agnesia glaciata* and *A. atlantica* Millar, 1982b. Although fertilisation may be internal none of these species appear to be incubating larvae.

There are 5 abyssal species recorded from the northern and 3 from the southern Atlantic, and one each from the northern and southern Pacific (Millar 1970, 1982b; Monniot and Monniot 1973, 1976a, 1976b). Only 8 sublittoral species are known: 4 are confined to southern polar seas (*Agnesia arnaudi* Monniot and Monniot, 1974b; *Caenagnesia bockii* Arnback, 1938; *C. schmitti* Kott, 1969a; *Adagnesia antarctica* Kott, 1969a); one has a range from subtemperate to subtropical waters (*Agnesia glaciata* Michaelsen, 1898); one has a subtropical to temperate range (*Adagnesia opaca* Kott, 1963); one occurs in the northern Pacific (*Agnesia septentrionalis* Huntsman, 1912a); and one occurs in South African waters (*Agnesia capensis* Millar, 1955a).

There are not very great differences in the morphology of species of this family. In particular, abyssal species do not display the same loss of stigmata that usually characterises abyssal species of other families. Although abyssal species usually have fewer coils than do littoral species, this could be the result of their small size.

Key to the Genera to Agnesiinae

(* not recorded from Australia)

1. Branchial papillae absent .... *Proagnesia* *
   Branchial papillae present 2
2. Papillae on transverse vessels bifid 3
   Papillae on transverse vessels not bifid .... *Agnesia*
3. Dorsal lamina a plain membrane .... *Caenagnesia* *
   Dorsal lamina with triangular languets......... .... *Adagnesia*

Genus **Agnesia** Michaelsen, 1898

Type species: *Agnesia glaciata* Michaelsen, 1898

Agnesia glaciata is the only species of this genus recorded from Australian waters. The other known species (*A. capensis* from South Africa, *A. septentrionalis* from the northern Pacific and *A. arnaudi* from Kerguelen) are closely related, distinguished principally by features of the body musculature and branchial sac (Kott 1969b, Monniot and Monniot 1976b).

Agnesia glaciata Michaelsen, 1898
(Fig. 29)

Agnesia glaciata Michaelsen, 1898, p.370; 1900, p.76; 1907, p.75. Van Name, 1945, p.200. Millar, 1960b, p.92. Kott, 1969a, p.97; 1969b, p.450; 1972c, p.238. Monniot, 1970a, p 341. Monniot and Monniot, 1974c, p.[illegible]

Agnesia krausei Michaelsen, 1912, p.181.

Agnesia himeboja Oka, 1915a, p.1.

Agnesia sabulosa Oka, 1929, p.152.

Agnesia septentrionalis: Van Name, 1945, p.201 (part, specimens from Newport Harbour, Southern California).

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H373–4 H397, ZMC 30.9.14).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — QM G4914 G5214 G5914–5921 G5922-9 G9643 Kott 1969b, 1972c). Sub-Antarctic (Antarctic Peninsula, South Shetlands, Tierra del Fuego — Michaelsen 1898, Kott 1969a). Patagonian Shelf (Michaelsen 1912, Millar 1960b). Kerguelen Is. (Monniot 1970). California (Van Name 1945). New Zealand (Millar 1960b). Japan (Oka 1915a 1929).

The species is recorded from water down to 95 m in Bass Strait. The sampling stations in Moreton Bay are shallower. Elsewhere, the species has not been taken at depths greater than 115 m.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are usually longer than wide, with both apertures sessile on the upper surface. They are dorso-ventrally or laterally flattened. Individuals up to 4 cm in length have been reported, although specimens from Australian locations are seldom more than 1 cm long. The test is thin and translucent, usually with fine hairs that are especially conspicuous posteriorly. Both test and hairs, however, are obscured by sand that adheres to the hairs and is embedded in the test, which is consequently often rigid. Except for an area around the apertures, the test around the anterior end of the body is thicker than that on the rest of the body. The apertures can be withdrawn into the body where, in larger specimens, they are protected by the surrounding dome of thick test. In laterally flattened specimens, the edge of the thickened test forms folds along each side of the apertures. These meet in the mid-line when the apertures are withdrawn. Kott (1969b) believed that variations in the shape of the body depended on the rigidity of the test, and that dorso-ventral flattening occurred when the test was too rigid to allow lateral flattening.

INTERNAL STRUCTURE: Short, longitudinal muscle-bands radiate from the apertures and extend beneath a fold of the body wall that is associated with the outer perimeter of the thickened test on the anterior end of the body. Most of the longitudinal muscles terminate a short distance down each side, although dorsal and ventral pairs are longer and extend down the dorsal and ventral border respectively. External circular bands are present around each aperture. Horizontal muscles extend across the mid-line at the anterior end of the body between, and dorsal and ventral to, the siphons. They terminate in the fold of the body wall on each side. Short, parallel, horizontal muscles form a band on each side of the dorsal and ventral mid-line. Variation in the number of muscle-bands in specimens from different locations seems to be related to size (Kott 1969b). A single, internal, circular muscle lies at the base of the branchial tentacles. The neural gland is long, lying along the right side of the ganglion, and there is a conspicuous tongue-like projection of the body wall over a large, flattened ciliated pit that opens into the pharynx through a long oblique slit. A plain, flat membrane along the dorsal mid-line of the branchial sac is crossed by primary transverse vessels, each expanded into a large, triangular languet just to the left of the dorsal line.

The branchial sac has 6 double rows of 11 conical infundibula with stigmata coiled 8 to 10 times around each cone. Triangular papillae, smaller than those to the left of the dorsal mid-line, are present on the primary transverse vessels between the infundibula, but are only rarely present on the intermediate transverse vessels.

The gut forms a curved loop to the left of the branchial sac. The gonad, consisting of a tubular ovary and branching male follicles, is present in the primary gut loop. Eggs are sometimes floating free in the peribranchial cavity.

REMARKS: As Van Name (1945) emphasised, *Agnesia septentrionalis* Huntsman is closely related to the present species, but is readily distinguished (Kott 1969b, Monniot & Monniot 1976b). Kott (1969b) suggested that the widely dispersed records of the present species represent populations that are relicts of an ancient, well-

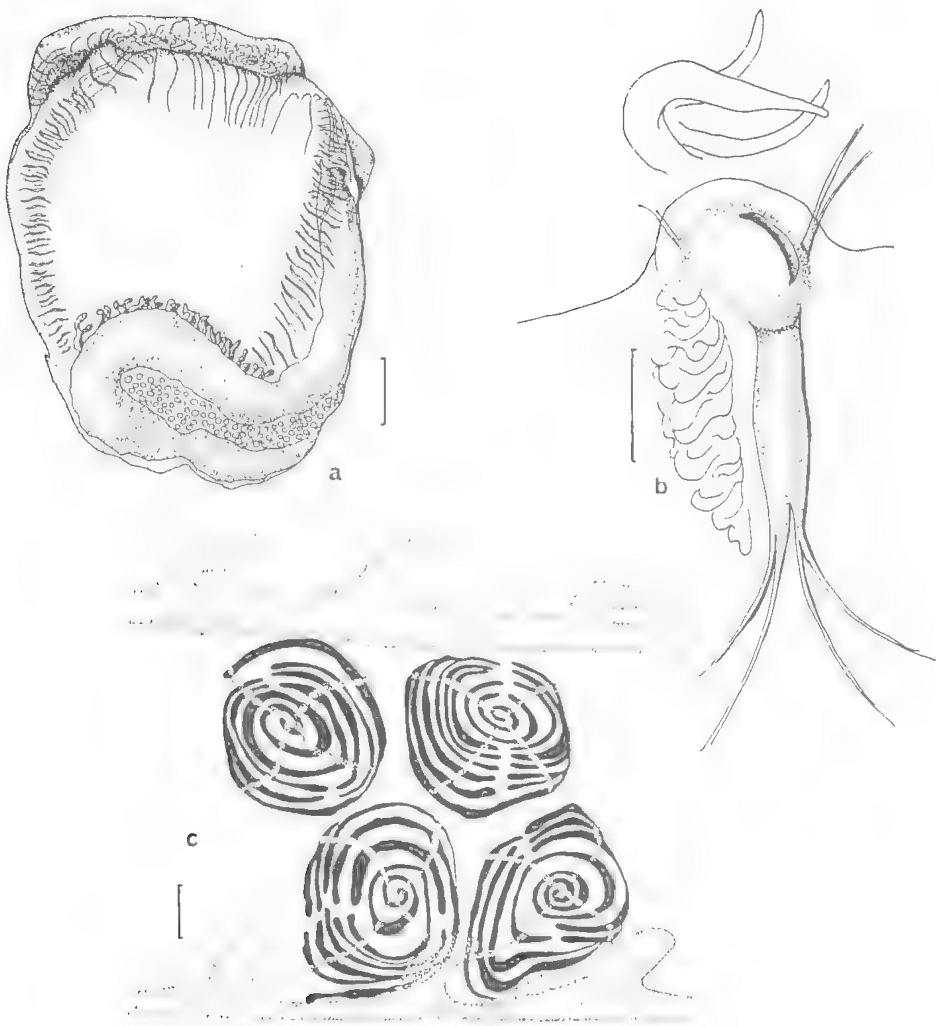


FIG. 29: *Agnesia glaciata* — **a**, body removed from the test, from the left side (ZMC); **b**, neural complex (QM G5924); **c**, portion of the branchial sac (NMV H373). (Scales: **a**, 1.0 mm; **b**, **c**, 0.25 mm).

established species. *Agnesia capensis* Millar, 1955a is distinguished by the absence of radial vessels.

Genus **Adagnesia** Kott, 1963

Type species: *Adagnesia opaca* Kott, 1963b

The genus is characterised by the presence of dorsal languets as in *Agnesia*, but is distinguished by the bifid branchial papillae that resemble those of *Caenagnesia*.

The body musculature of all species is confined to short, transverse bands across the ventral and dorsal borders, especially anteriorly; longitudinal bands radiating only a short distance from the siphons; and circular siphonal muscles. There usually are folds of test that close over sessile apertures. In two of the Australian species clearly related to one another, the gonoducts extend through the gut loop and lateral to its pole, their openings into the atrial cavity being in front of the gut loop and directed anteriorly. This is an unusual adaptation that appears to contribute to retention of gametes of both sexes in the atrial cavity.

Six species of the genus are known, of which 3 are reported only from abyssal basins of either the eastern Pacific, the northern Atlantic or the Argentine Basin (Monniot and Monniot 1976a; Millar, 1970). *Adagnesia antarctica* Kott, 1969a is known from the southern Pacific. The Australian species *A. opaca* and *Adagnesia venusta* n.sp. are known exclusively from shallow sublittoral waters.

Key to the Species of *Adagnesia* Recorded from Australia

1. Gonoducts extend anteriorly, lateral to pole of gut loop 2
   Gonoducts extend parallel to rectum toward atrial aperture .... *A. charcoti*
2. Gut loop confined to posterior end of body .... *A. venusta* n.sp.
   Gut loop not confined to posterior end of body .... *A. opaca* n.sp.

Adagnesia charcoti Monniot and Monniot, 1973 (Fig. 30)

Adagnesia charcoti Monniot and Monniot, 1973, p.424; 1976a, p.635; 1976b, p.666. Millar, 1978, p.104; 1982b, p.168

Distribution

New Records: Victoria (Bass Strait, NMV H779).

Previously Recorded: Atlantic Ocean (Guyana Shelf — Millar 1978; Argentine Basin — Monniot and Monniot 1976a; Surinam Basin — Monniot and Monniot 1976b; Bay of Biscay, Mid-Atlantic and off the Azores — Monniot and Monniot 1973; Rockall Trench — Millar 1982b).

The Australian record is of a single specimen from 22 m depth. However, all previous records in both the northern and southern Atlantic Oceans are from depths of 500 to nearly 5000 m.

Description

External Appearance: The single specimen is 2.5 mm high and more or less top-shaped, rounded at the upper free end and narrowing toward the substrate where it is fixed to small pebbles by two short, papilla-like projections of the test. The atrial aperture is terminal and the branchial aperture halfway down one side. Both apertures are sessile, the border of the branchial aperture with 7 inconspicuous, pointed lobes and the atrial aperture with 6 lobes. The test is naked, smooth and rather firm, gelatinous and transparent.

Internal Structure: The body wall is very delicate. It has a wide band of thin muscles around each aperture and some longitudinal bands radiate from each aperture. Those around the branchial aperture extend a little distance posterior to the circular muscles; however, those radiating from the atrial aperture do not. No other muscles were detected on the body. There are about 16 rather robust, curved, branchial tentacles, but it was not possible to determine whether these are in a single circle or not. There is a very wide prebranchial space. The dorsal tubercle is in the anterior part of the peritubercular V. The dorsal ganglion is just behind the tubercle, about half way down the body. There are 4 large, pointed dorsal languets.

The branchial sac has 6 transverse vessels with bifid papillae. There is a single row of almost circular or irregular perforations of the pharyngeal wall alternating with the transverse vessels. These perforations do not show any sign of coiling.

The gut forms a wide but closed curved loop extending about halfway along the ventral part of the left side of the body. The oesophagus is only of moderate length; the smooth, egg-shaped stomach terminates about one-third of the distance up the ascending limb of the gut loop. The rectum curves around, more or less parallel to the oesophagus to terminate near the atrial opening.

The gonads consist of a very large, sac-like ovary in the wide intestinal part of the gut loop. The testis follicles are long and club-shaped. They curve over the lateral side of the gut wall on both the ascending and descending limbs, the proximal ends of the follicles being evident from the inner surface, closely applied to the outer border of the intestine. Some male follicles also extend out over the mesial surface of the stomach and gut loop. Vasa efferentia join to form a vas deferens near

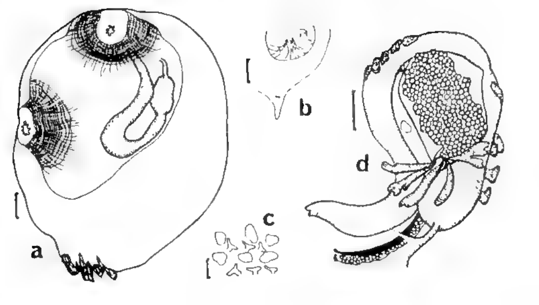


FIG. 30: *Adagnesia charcoti* (NMV H779) — **a**, body *in situ* in the test; **b**, portion of pre-branchial area showing some branchial tentacles and opening of neural gland; **c**, portion of branchial sac showing stigmata and forked branchial papillae; **d**, gut loop and gonads. (Scales: **a**, **b**, 0.25 mm; **c**, 0.1 mm; **d**, 0.2 mm).

the distal end of the ovary. Both ducts extend towards the atrial aperture parallel to the rectum. The distal part of the vas deferens is expanded into a seminal vesicle between the stomach and its opening near the atrial aperture. Both ovary and vas deferens contain mature gametes.

REMARKS: The Australian specimen most closely resembles that described by Millar (1982b) from the Rockall Trench. It has similar muscles, and the large, open stigmata resemble those of Millar's specimen, although in the latter the perforation show some incipient spiralling. The other known specimens (from the Atlantic) have bands of transverse muscles across the dorsal and ventral mid-line, behind the apertures but not between them. Their dorsal tubercle and neural ganglion are in the same positions as in the Australian specimen. The specimen from the Rockall Trench resembles the Australian specimens more closely than it does the other known specimens from the Atlantic. Their separation is not justified. The species is closely related to *Adagnesia bifida* Millar, 1970 from the Guatemala Basin in the eastern Pacific. However, the latter species has more numerous perforations of the branchial wall and better developed musculature than *A. charcoti*.

In view of the widely separated records of this very small species, it is possible that its actual range is great and that the species extends into the southern basins of the Pacific Ocean and even into more shallow waters.

TABLE III — SUMMARY OF CHARACTERS OF SPECIES OF *ADAGNESIA* RECORDED FROM AUSTRALIA

Species	Range Outside Australia	[1]Range in Australian waters	Body	Test	[2]Stigmata	Gonoduct orientation	Proportion of left side occupied by gut
A. opaca	—	Bass Strait - Moreton Bay	laterally flattened, lies on side	sandy	34;30	anteriorly through gut loop	not less than half
A. venusta n.sp.	—	Bass Strait	"	"	14;12	"	less than half
A. charcoti	Atlantic Ocean	"	top-shaped, upright	naked	6;6	posteriorly parallel to gut	not less than half

[1]Range given anti-clockwise around the continent. [2]Number of rows; number per row.

Adagnesia opaca Kott, 1963
(Fig. 31)

Adagnesia opaca Kott, 1963, p.76; 1969b, p.454; 1972c, p.238; 1972d, p.250.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, J1754).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — holotype QM G4907, paratypes G4936 Kott 1963 1969b; QM G5902-5913 Kott 1972c). New South Wales (Port Hacking — Kott 1972d).

The species has been taken on sandy substrates down to about 8 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are almost circular, lens-shaped, and laterally flattened, 4 to 5 cm long and 3 to 4 cm wide. The animal always lies on the bottom on its right side. The test is thin and brittle with embedded sand, and there are some fine test hairs and processes to which sand also adheres. The apertures are sessile and fairly close together on the anterior end of the body. They are obscured by curved folds of test. One from the right side of the atrial aperture folds up over the opening, directing it away from the substrate; the other, from the left side of the branchial aperture, folds down over the opening, directing it down toward the substrate. Sand is absent from a thin strip of test enclosing the apertures along the mid-line anteriorly. The siphonal lining is tough, membranous, white and opaque.

INTERNAL STRUCTURE: Thin folds of the delicate body wall are enclosed in the folds of test that close over the apertures. Short, longitudinal muscle-bands radiate from each side of each aperture beneath the circular sphincter muscles that surround them. Very strong but short transverse bands extending across the mid-line between, and dorsal and ventral to, the apertures are inserted into the base of the protective folds of test on the opposite side of the body. Their contraction appears to shorten the mesial sides of the folds, drawing them across the mid-line to cover the apertures. There is also a continuous series of very short, parallel muscle-bands around the border of the body on each side of the mid-line that probably depress the body and emphasise its lateral flattening. The simple branchial tentacles form 4 concentric circles, the tentacles in adjacent circles alternating with one another. The largest tentacles are in the outer, or most posterior, circle; they become progressively shorter anteriorly. The dorsal tubercle is low, circular and more or less doughnut-shaped with a circular opening in the central depression. The neural gland is large and oval, usually along the right side of the ganglion, but becoming dorsal to it in larger specimens. The wall of the wide, circular, dorso-ventrally flattened, ciliated pit folds inwards to form a broad, flat fold that spirals up to 3 times toward the pharngeal wall. The inner margin of this spiral fold can be seen through the simple circular opening in the centre of the dorsal tubercle. The dorsal lamina is represented by 34 curved languets. There is a plain, unperforated area of pharynx over the rectum to the right of the dorsal languets.

Each side of the body has up to 34 double rows of approximately 30 small, square meshes, each containing a stigma coiled up to 5 times in the opposite direction to those in the adjacent meshes. The bifid papillae are present on the transverse vessels between the paired rows of coiled stigmata. At the posterior end of the branchial sac, the number of rows of coiled stigmata can be seen to be proliferating by horizontal subdivision of each coil. Secondary dorsal languets alternating with longer primary processes are associated with this proliferation.

The gut is voluminous throughout. It forms a dorsal loop in the postero-ventral part of the left side of the body. The rectum extends anteriorly, parallel to the descending limb of the primary loop, to form the deep secondary loop.

The gonad is enclosed in the gut loop. The ovary is a large, curved sac. Anteriorly it overlaps the proximal part of the descending limb of the gut loop, curves around inside its inner curve, and overlaps its ascending limb in the pyloric region. Very small, branched male follicles surround each end and the convex anterior border of the ovary. In mature specimens, 2 distended male ducts from opposite ends of the ovary gather semen from the male follicles and join together halfway along the concave, posterior border of the ovary to form the very large vas deferens lying on top of the oviduct (which also leaves the ovary in the centre of its posterior concave border). The oviduct and the vas deferens pass through the gut loop and then turn anteriorly on the parietal side of the gut to open into the peribranchial cavity just anterior to the pole of the loop. The oviduct crosses over the vas deferens as they cross the parietal side of the gut. The distal end of the vas deferens thus lies on the mesial surface of the oviduct as it opens into the atrial cavity, which is its usual position in most species of the Ascidiacea. Small (0.1 mm diameter) eggs are found free in the peribranchial cavity.

REMARKS: The unusual folds of test that protect the apertures and direct the incurrent and excurrent ciliary streams, together with the highly adapted body musculature and anteriorly directed gonoducts, distinguish the species.

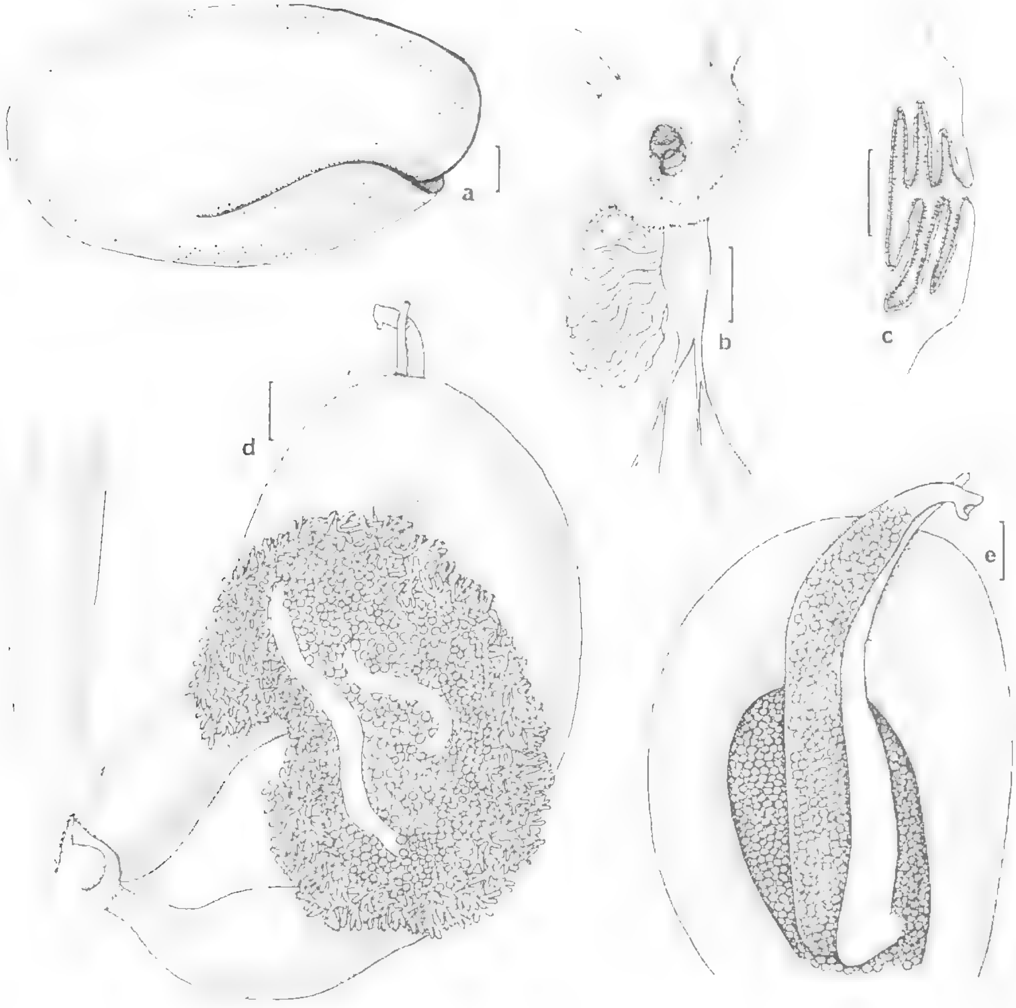


FIG. 31: *Adagnesia opaca* — **a**, external appearance (QM G4907); **b**, neural complex (QM G5907); **c**, cross section through ciliated pit showing opening into pharynx (QM G5907); **d** gut and gonads from mesial surface (QM G4907); **e**, gut loop and gonoducts from outside body wall (QM G4907). (Scales: **a**, 5.0 mm; **b**, **c**, 0.5 mm; **d**, **e**, 2.5 mm).

The ovary with the oviduct extending from halfway along its length may represent 2 enlarged branches from the proximal end of a tubular ovary. As in *Adagnesia venusta* n.sp., the gonoducts appear to have moved around beneath the rectum and the descending limb of the gut loop in order to lie antero-ventral, instead of postero-dorsal, to the rectum.

The orientation of this species on the sea floor, with its left side uppermost, is unusual. Most species of the Ascidiidae lie on their left side.

The large ciliated pit with its spiral fold inside rather than on the surface of the dorsal tubercle is also unusual.

Adagnesia venusta n.sp.
(Fig. 32)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, 39°06.7'S, 143°28.7'E, 92 m, fine sand with abundant sponges, Bass Strait Survey, 31.1.81, holotype H381).

FURTHER RECORDS: Victoria (Bass Strait, NMV F51565, paratypes F51569, H394).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are sandy, laterally flattened, oval and not more than 6 mm long. Both apertures are sessile and depressed into a thin strip of sand-free test around the antero-dorsal border of the body. The test is thin and quite brittle with sand.

INTERNAL STRUCTURE: The body wall is very delicate. Circular muscles are confined to the area immediately around each aperture. Longitudinal muscles from each of the apertures radiate only a short distance over the anterior part of the body. There are short, transverse bands across the dorsal and ventral mid-lines behind and between the apertures. At the posterior end of the mid-ventral line there is a slight, projecting circular fold of the outer layer of the body wall. This encloses a circular area from which a group of small, blind papillae and blood vessels project. The branchial tentacles form 3 circles, made up of about 16 larger tentacles in the outer ring, about the same number of moderate length in the middle circle, and twice the number of smaller tentacles in the inner ring. The neural gland opens into the anterior part of the large peritubercular V with a simple, transversely oriented, curved slit. A long, elliptical neural ganglion, with its associated neural gland, extends posteriorly from the slit-like opening of the gland. There are 7 large, triangular languets, corresponding to each primary transverse branchial vessel, in the dorsal mid-line.

There are 7 paired rows of about 12 rather square meshes each with a single stigma coiled about 3 times. On the transverse vessels, between the paired rows are bifid papillae, with long arms

The gut loop is short and confined to the postero-dorsal curve of the body, the rectum extending anteriorly to open near the atrial aperture in a bilabiate opening.

The female gonad is tubular, curving through the gut loop to pass anteriorly lateral to the pole of the intestinal loop. The anal opening to the atrial cavity is anterior to the pole of the gut loop. Testis follicles spread over the wall of the gut. The vas deferens accompanies the ovary and opens with it anterior to the gut loop.

REMARKS: The species is very closely related to *Adagnesia opaca*, the orientation of the gonads being identical. However, *A. venusta*'s small size, together with the posterior position of its relatively short gut loop and its less specialised musculature readily distinguishes it. Specimens of *A. opaca* that are 1 cm long (QM G5910) are juveniles with immature gonads, a gut loop characteristic of the species reaching about two thirds of the way up the body, and about 30 rows of coiled stigmata that are actively subdividing, especially posteriorly. It is not possible, therefore, that the present species could be confused with juveniles of *A. opaca*.

The function of the papillated organ at the posterior end of the mid-ventral line is not known.

FIG. 32: *Adagnesia venusta* n.sp. (NMV H394) — **a**, body from left side showing gut, gonads, muscles and postero-ventral vascular papillae; **b**, postero-ventral vascular papillae; **c**, portion of branchial sac; **d**, dorsal tubercle with U-shaped opening overlying neural gland and ganglion. (Scales: a, 0.5 mm; b – d, 0.2 mm).

Similar organs are present in *Molgula mollis* and *Hartmeyeria chinensis* Tokioka, 1967a. A vesicular organ reported in the peculiar stalked species, *Adagnesia vesiculiphora* Nishikawa, 1982 from 20 m in the Japan Sea, is also similar.

Family CORELLIDAE Lahille, 1888

Phlebobranch ascidians in which the gut is present on the right side of the branchial sac. After leaving the stomach, the intestine turns posteriorly and dorsally behind the ascending limb of the gut loop. The rectum crosses the oesophagus to reach the atrial aperture. Unlike most phlebobranch families, the stomach wall has numerous parallel longitudinal folds. Species of the family otherwise resemble Ascidiidae, having a translucent gelatinous and usually naked test, and a flat branchial sac, but with coiled (Corellinae) or straight (Rhodosomatinae) stigmata.

Although *Rhodosoma turcicum*, the only known sublittoral species of the subfamily Rhodosomatinae, is found in warmer waters around the world, the subfamily Corellinae is represented mainly by species that are confined to colder waters; and although a few species have been recorded from Japan and Indonesia, the single species (*Corella eumyota*) recorded from Australia has Antarctic rather than tropical affinities.

Subfamily CORELLINAE Herdman, 1882

Corellidae in which single stigmata spiral and sometimes form infundibula in the otherwise flat branchial sac.

The subfamily is not diverse. Although 6 genera are recognised, they are (as are Agnesiinae) mainly found in cold abyssal or polar waters (see Van Name 1945; Kott 1969a). Two genera (*Corynascidia* and *Xenobranchion*) are exclusively abyssal; two are Arctic genera (*Corelloides* and *Corellopsis*). Of these 4 genera only *Corynascidia*, a genus closely related to *Corella*, is not monotypic. *Chelyosoma* and *Corella* are the only two genera that are at all diverse, 4 species being known in each. In each genus, half of the species are Arctic or sub-Arctic. Both also have species known from tropical locations including the western Pacific. However, their ranges do not appear to extend to Australia. In fact, the genus *Chelyosoma* has not been recorded south of tropical latitudes of the eastern Pacific or Indonesia in the western Pacific (see Van Name 1945; Tokioka 1953a). *Corella eumyota*, with a range from the Antarctic continent to the temperate waters of southern Australia, is the only species of the subfamily yet recorded from Australian waters.

Key to the Genera of Corellinae
(* not reported from Australia)

1. Test thickened into plates ...... *Chelyosoma* *
   Test not thickened into plates 2
2. Internal longitudinal vessels interrupted 3
   Internal longitudinal vessels not interrupted 5
3. Stigmata in regular spirals....................... 4
   Stigmata not in regular spirals .... *Xenobranchion* *
4. Branchial papillae project above remnants of longitudinal vessels............. *Corelloides* *
   Branchial papillae do not project above remnants of longitudinal vessels .... *Corellopsis* *
5. Gut forms simple loop in postero-dorsal corner of thorax .... *Corynascidia* *
   Gut forms curved loop across posterior third of body .... *Corella*

Genus **Corella** Alder and Hancock, 1870

Type species: *Ascidia parallelogramma* Mueller, 1776

The genus is characterised by the coiled stigmata in the branchial sac, the presence of internal longitudinal vessels, and a gelatinous test, which is translucent or glassy, seldom with foreign particles adhering and never thickened into the plates that are characteristic of the genus *Chelyosoma*. In addition to *C. eumyota* (discussed below), the following species are known (see Van Name 1945; Tokioka 1953a): *Corella willmeriana* Herdman, from the north-eastern Pacific; *C. borealis* Traustedt from the Artic and northern Atlantic; *C. parallelogramma* Mueller from the nortern-eastern Atlantic and Mediterranean; *Corella minuta* Van Name, a tropical species from the West Indies; and *Corella japonica* Herdman from Japan and the western Pacific.

Corella eumyota Traustedt, 1882
(Fig. 33)

Corella eumyota Traustedt, 1882, p.271; 1885, p.9. Sluiter, 1898a, p.40; 1914, p.26; 1932, p.3. Michaelsen, 1900, p.10; 1907, p.74; 1915, p.423; 1918, p.50; 1922, p.481. Herdman, 1910, p.16; 1923, p.30. Hartmeyer, 1911, p.458; 1920b, p.132. Van Name, 1921, p.397; 1945, p.212. Bovien, 1922, p.45. Arnback, 1929, p.7; 1938, p.40. Brewin, 1946, p.108; 1950a, p.54; 1950b, p.344; 1950c, p.354; 1956, p.122;

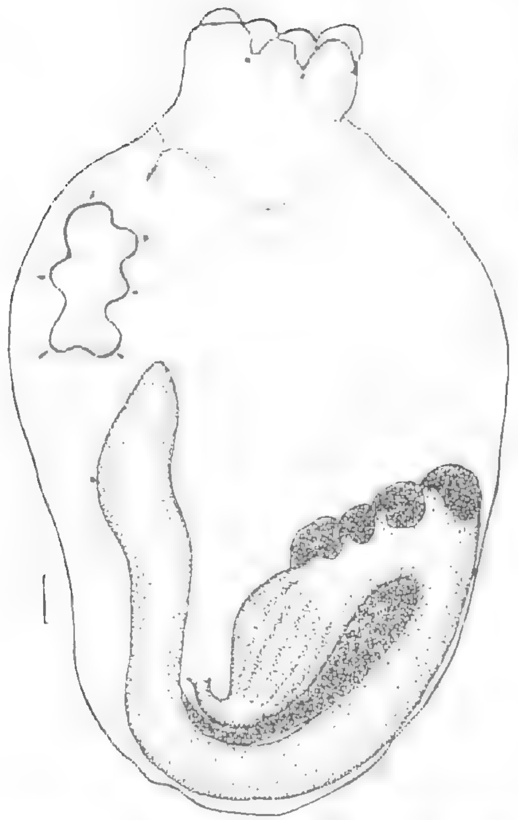


FIG. 33: *Corella eumyota* — body from right side. (Scale: 0.5 mm).

1957, p.577; 1960, p.119. Kott, 1952, p.318; 1954, p.150; 1969a, p.84; 1971, p.20; 1972a, p.23. Millar, 1955a, p.193; 1960b, p.95; 1962a, p.174; 1966, p.366. Vinogradova, 1962, p.200. Monniot and Monniot, 1974c, p.372.

Corella novarae Drasche, 1884, p.382.

Corella japonica; Sluiter, 1900, p.20. (Not Herdman, 1880, p.472).

Corella antarctica Sluiter, 1905b, p.471; 1906, p.31.

Corella benedeni Beneden and Longchamps, 1913, p.9. Arnback, 1938, p.41.

Corella dohrni Beneden and Longchamps, 1913, p.15. Herdman, 1923, p.30. Arnback, 1938, p.41.

DISTRIBUTION

NEW RECORDS: Western Australia (Rockingham, WAM 120.75). Tasmania (Huon Channel, TM D1859; S.E. Tasmania, TM D1865; S.E. Bruny I., TM D1854; Taroona, TM D1808).

PREVIOUSLY RECORDED: Western Australia (Trigg I. — Kott 1952). South Australia (St Vincent Gulf — Kott 1972a). Tasmania (d'Entrecasteaux Channel — Kott 1952). Victoria (Balnarring Beach — Kott 1952; Frankston — Millar 1966). New Zealand (Michaelsen 1922, Brewin 1946 1950a-c 1957 1960). Chatham, Auckland and Macquarie Is (Sluiter 1900b, Herdman 1910, Michaelsen 1922, Bovien 1922, Kott 1954, Brewin 1956). South Africa (Sluiter 1898a, Michaelsen 1915, Millar 1955a 1962a). Chile and Argentina (Traustedt 1882, Hartmeyer 1920b, Arnback 1929).

For records from the Magellanic region, Scotia Ridge, Antarctic Peninsula, Weddell and Ross Seas, and off the Antarctic mainland see Kott (1969a) and Monniot and Monniot (1974c).

The species has been taken at depths to 842 m (off Macquarie I., Kott 1971) but also occurs in shallow sublittoral waters on rocks and jetty piles.

DESCRIPTION

EXTERNAL APPEARANCE: Body ovate to elongate, laterally compressed, sometimes with a short stalk posteriorly, but more often sessile and fixed by part of the right side. Specimens up to 15 cm long and 6 cm wide have been recorded from the Antarctic, but they are more often 1 to 4 cm in length (Kott 1969a). The test is thin and often completely transparent and glassy, although it is thick and firmer in larger specimens. The surface is smooth and there is no sand. The 7- or 8-lobed branchial aperture is terminal, and the 6-lobed atrial aperture is up to half the distance along the dorsal surface. Externally the apertures are on small, wart-like siphons.

INTERNAL STRUCTURE: The body wall is thin, with circular muscles on the short internal siphons. There is a meshwork of irregular transverse and longitudinal muscles on the left side of the body, but the right side of the body, over the gut loop, is free of muscles. The irregular muscles on the left terminate around the dorsal and ventral borders of the body in short parallel bands that cross the mid-line.

There are 50 to 100 long, simple branchial tentacles. The dorsal tubercle is a rounded cushion with a U- to C-shaped slit with the horns turned in. In longer specimens the slit becomes convoluted. Long, triangular languets are present where transverse vessels cross the dorsal mid-line.

The branchial sac has numerous rows of coiled stigmata with rudimentary and accessory coils forming between the primary stigmata. There are up to 60 slender, internal longitudinal vessels on each side of the body, with 2 or 3 vessels crossing each coil. The stigmata spiral up to 4 times.

The gut forms a curved loop across the posterior third of the right side of the body, the descending loop extending postero-dorsally behind the ascending loop, and the rectum crossing the oesophagus (as is usual in this subfamily). The stomach has longitudinal folds. Gonads form a compact mass enclosed by the gut loop.

REMARKS: The western Pacific *C. japonica* Herdman, 1880 (Tokioka 1953a, 1967a; Millar 1975; Kott 1981) has its musculature gathered into wide bands across the mid-dorsal line between the siphons (unlike the diffuse musculature of the present species) and has fewer internal longitudinal vessels. *Corella aequabilis* Sluiter, 1904 from Indonesia is possibly conspecific with *C. japonica*.

Characteristics of *C. eumyota* are its very numerous internal longitudinal vessels, rather irregular branchial sac with accessory coiled stigmata, and the small number of spirals made by each stigma.

Subfamily RHODOSOMATINAE Seeliger, 1893

Corellid genera with straight stigmata. The subfamily contains 3 genera: *Abyssascidia* Herdman, 1880, known only from deep basins of the Southern Ocean and from Indonesia (Kott 1969a); *Rhodosoma*, a pan-tropical to temperate species known from continental shelf locations; and *Dextrogaster* Monniot, 1962b, a small interstitial species from Sweden.

Genus **Rhodosoma** Ehrenberg, 1828

Type species: *Phallusia turcica* Savigny, 1816

Rhodosoma is characterised by the remarkable horizontal fold of the body that is produced anteriorly along a line to the right of the sessile apertures. The fold acts as a lid over the apertures on the upper surface of the upright, elongate body. It is operated by the highly adapted body musculature. The morphology otherwise resembles that of species of the genus *Ascidia*, having internal longitudinal vessels in the branchial sac and the gonad enclosed in the gut loop.

Rhodosoma turcicum (Savigny, 1816)
(Fig. 34)

Phallusia turcica Savigny, 1816, p.102.
Rhodosoma turcicum: Van Name, 1930, p.471; 1945, p.203. Kott 1952, p.317; 1972a, p.23. Tokioka 1952, p.111; 1953a, p.230. Millar, 1975, p.266.
Rhodosoma verecundum Ehrenberg, 1828, p.3.
Schizascus pellucidus Stimpson, 1855a, p.377.
Rhodosoma pellucidum: Van Name, 1918, p.113; 1921, p.392; 1924, p.29.
Schizascus papillosus Stimpson, 1855a, p.377.
Rhodosoma papillosum: Traustedt, 1885, p.9. Herdman, 1891, p.598. Hartmeyer, 1901, p.151; 1906, p.25; 1919, p.95. Sluiter, 1904, p.26. Van Name, 1918, p.113. Oka, 1932a, p.194.
Rhodosoma huxleyi Macdonald, 1862, p.78.
Chevreulius callensis Lacaze-Duthiers, 1865, p.293.
Rhodosoma seminudum Heller, 1878, p. 9. Sluiter, 1898b, p. 10. Hartmeyer, 1901, p. 162
Rhodosoma pyxis Traustedt, 1882, p. 274.
Rhodosoma ceylonicum Herdman, 1906, p. 302.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 114.72 847.83, QM GH2117). South Australia (Nuyts Archipelago, QM GH2287 GH2316). Queensland (Tallebudgera Creek, QM GH2444; Heron I., QM GH3035-8; Abbot Point, QM GH661 GH708; Lizard Is., QM GH3110-1; Mossman, QM GH793).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919). South Australia (St Vincent Gulf — Kott 1952 1972a). Queensland (Kott 1952). Coral Sea (Macdonald 1862). Arafura Sea (Tokioka 1952). Indian Ocean (Sri Lanka — Herdman 1906). Indonesia (Sluiter 1904). Philippines (Van Name 1918). China (Stimpson 1855a). Gulf of Siam (Millar 1975). Japan (Southern Japan — Oka 1932a, Hartmeyer 1906, Tokioka 1953a). Red Sea (Ehrenberg 1828). Mediterranean (Lacaze-Duthiers 1865). California (Van Name 1945). Chile (Traustedt 1882 1885). Atlantic Ocean (Caribbean — Heller 1878, Sluiter 1898b, Hartmeyer 1901, Van Name 1945).

The species has a wide pantropical and temperate range and is known down to 118 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright, oval in section, slightly laterally flattened, and up to 5 cm high and 2 cm wide. They are fixed by the posterior end or part of the right side. There is a deep cleft that penetrates the body from the left side, almost entirely separating the anterior end from the remainder. The apertures, on short siphons, are present in the base of this cleft. Closure of the apertures and withdrawal of the siphons reduces the angle at the base of the cleft and causes the anterior flap to close over the remainder of the body as a lid, concealing the closed apertures. When the muscles relax the cleft opens out, the lid being propped open by the inflated area around the base of the siphons, which project out to the left.

Except in the cleft, where it is thin and flexible, the test is firm, gelatinous and translucent. Pointed papillae are present on the outer surface of the lid and around the anterior end of the body. These become less crowded and smaller posteriorly.

INTERNAL STRUCTURE: Generally the body wall is thin, the musculature being localised in strong bands that extend from the anterior half of both the dorsal and ventral lines, and extend obliquely across the left side of the body to the base of the atrial and branchial siphon, respectively. There they subdivide into branches that extend anteriorly

FIG. 34: *Rhodosoma turcica* (QM GH2444) — a, external appearance; b, body removed from test showing muscles on left side; c, body removed from test, showing right side with gut, gonads, gastric reservoir, heart and posterior ends of muscles. (Scales: a, b, 5.0 mm; c, 2.5 mm).

along the siphons, or that cross over to join the branches from the opposite set of muscles. There are circular muscles around the siphons, but the longitudinal bands stop abruptly at either the dorsal or ventral mid-line and are not present on the right side of the body. The bands at each end of the upper surface near the ends of the hinge-line of the lid are longer and wider. There are about 30 well-spaced branchial tentacles of varying size. The dorsal tubercle is a wide, conspicuous cushion, with a wide U-shaped slit with the right horn turned in. There is a row of wide, triangular languets along the dorsal mid-line.

The branchial sac has numerous rows of straight stigmata. Small, curved papillae supporting slender, internal longitudinal vessels occur on the transverse vessels, separated by 3 or 4 stigmata. The papillae project only slightly above the longitudinal vessels, which are sometimes interrupted and are occasionally represented by bifid papillae.

The oesophagus is short, curved around onto the right side of the body where it opens into a short, longitudinally-folded stomach. A large spherical gastric reservoir is sometimes present, connected to the distal end of the stomach and to the intestine by narrow ducts. The intestine turns posteriorly and dorsally to form a narrow loop, and the rectum crosses the oesophagus to extend up toward the atrial aperture. The anal border has small, inconspicuous lobes.

The gonad is enclosed in the gut loop. It consists of a very branched ovary, with testis follicles surrounding it and spreading over the gut wall.

REMARKS: The asymmetrical lid of this species is unique; no species is known with which it could be confused. Its wide pantropical range is inexplicable, however, except on the basis of relict populations. The species was recorded from the rubble fauna at Heron I. only in September, 1984 (QM GH3035-8). It seems unlikely that it was overlooked in previous occasions and the explanation for its sudden appearance at this location is not known.

The large gastric reservoir was apparently mistaken for a caecum by Kott (1952).

Family PEROPHORIDAE Giard, 1872

Colonies of small, rounded zooids joined by stolons from the postero-ventral part of the body. There are variable and sometimes relatively large (up to 14) numbers of lobes around the borders of the apertures. Very small pigment spots, possibly light sensitive ocelli, are often present between these lobes. The branchial sac is flat, without folds, with internal longitudinal vessels and relatively few rows (up to 25) of numerous (up to 40) stigmata. The gut loop is at the left of the branchial sac. Vegetative zooids are generated from mesenchymal cells of the vascular stolon (Berrill 1935b). Species are usually viviparous, the oviduct forming a brood-pouch across the posterior end of the right side of the peribranchial cavity. The vas deferens extends forwards to open with the gut near the atrial aperture.

The epicardium, which breaks up into excretory vesicles over the gut of solitary phlebobranch species, has not been detected at any stage in the life histories of *Perophora* spp. and *Ecteinascidia* spp. and this, together with their large larvae and colonial habit has caused some doubt about the phlebobranch affinities of the family, despite their morphological resemblance to the Ascidiidae (Berrill 1950). The larvae of the Perophoridae are large, with a large mass of yolk and well developed larval sense organs, as in viviparous larvae of other colonial groups (Polyzoinae, Botryllinae and Aplousobranchia). Although the adhesive organs are unstalked like those of other phlebobranch and stolidobranch families, perophorid larvae also resemble the Aplousobranchia in having the adhesive organs in a median vertical line (rather than a triradial arrangement), and in the presence of an ectodermal cup around each cone of adhesive cells. Adult organs (branchial sac and gut) are also very well developed in these larvae, again resembling the aplousobranch rather than the phlebobranch or stolidobranch condition(see Berrill 1950). However, in addition to the relationship with other phlebobranchs indicated by general morphology, Webb (1939) has demonstrated an affinity between Perophoridae and Ascidiidae on the basis of blood cell type. Similarities between larvae of aplousobranch families and those of Perophoridae are most likely the result of convergence associated with a colonial habit, rather than being indicative of a phylogenetic relationship (Kott 1982). The loss of all trace of the epicardium may be a result of size reduction and simplification associated with vegetative reproduction (see Berrill 1950).

The main blood vessel to the delicate test that surrounds the zooids of this family, originates from the basal stolon and not directly from the subendostylar vessel as it does in the Ascidiidae.

There are only two genera of the Perophoridae, *Ecteinascidia* and *Perophora*. Berrill (1950) regards differences between them to be related to size reduction of the zooids. Although this appears to have directly affected the branchial sac, differences in the male follicles do not seem to be size-related and afford a reliable distinction between the genera.

Both genera are well-represented in Australian waters, although *Ecteinascidia* does not extend into temperate regions.

Key to the Genera of Perophoridae

Gut loop straight and horizontal; rectum shorter than primary loop; male follicles large and few .... *Perophora*

Gut loop curved or oblique; rectum at least as long as primary loop; male follicles small and numerous .... *Ecteinascidia*

Genus **Ecteinascidia** Herdman, 1880

Type species: *Ecteinascidia turbinata* Herdman, 1880

The genus contains the larger species of the two genera of the Perophoridae. They have more than 10 rows of stigmata, with over 20 stigmata in each row. The gut is relatively long, the proximal part forming either an oblique loop that projects back into the postero-ventral corner of the body or a deeply curved loop in the posterior half of the body. The rectum is long and extends anteriorly, but usually does not reach the atrial aperture. Testis follicles are numerous, short, pyriform and often lobed. They are clustered in an arc in the pole of the gut loop proximal to the small ovary.

The longitudinal muscles are usually very reduced, seldom extending posterior to the base of the siphons. Circular muscles are always present around the siphons. Circular muscles on the rest of the body consist of horizontal bands across the dorsum that extend varying distances down the sides of the body. In some species (e.g., *E. sluiteri*), these horizontal muscles are interrupted along a line on each side of the dorsal mid-line, limiting the muscles to 3 longitudinal strips of short, parallel, horizontal bands. The arrangement of the horizontal muscles is also affected by the position of the atrial siphon. When it is on the upper surface of the body near the branchial siphon, the horizontal bands cross the mid-line only behind the atrial aperture. In species where the branchial aperture is terminal and the atrial aperture opens on the dorsal surface, muscle-bands cross the mid-line between the siphons as well as posterior to the atrial aperture. The position of the atrial aperture is also related to the course of the gut. The intestine and rectum are stretched out in a sinuous curve when the atrial aperture is on the anterior surface, but they form a deep secondary loop when the atrial aperture is on the dorsal surface. In species in which the atrial aperture is on the upper surface, the anus is up to one-third of the body length distant from the excurrent aperture. This distance is reduced if the atrial aperture is on the dorsal surface of the body.

In some species, the dorsal lamina is in a primitive condition, with antero-posteriorly flattened languets where the transverse vessels cross the mid-dorsal line. In these species, stigmata between the transverse vessels continue across the mid-line without interruption. In other species, a raised membrane along the dorsal mid-line interrupts the stigmata. The membrane is ribbed, each rib continuous with a laterally flattened languet that projects from the edge of the membrane (Beneden 1887). The neural gland and ganglion are compact in all species, and the neural duct is short, straight and wide, opening directly into the pharynx by a wide opening.

Zooids are joined to basal or axial common stolons by short stolons from the postero-ventral part of the body. The main stolonic vessel emanates from the subendostylar sinus and is an homologue of the main test vessel of solitary phlebobranch ascidians. Perophorid test vessels appear to originate as branches from the stolonic vessels and do not enter the test directly from the subendostylar sinus. The test vessels are conspicuous in *E. imperfecta, E. maxima* n.sp., *E. rubricollis*, and *E. nexa*, although in other species the test does not appear to be vascularised (*E. diaphanis* and *E. sluiteri*). A conspicuous vascular network is usually present and is always conspicuous in the body wall of *E. nexa, E. sluiteri* and *E. imperfecta*.

E. diaphanis (see below), *E. turbinata* (see Berrill 1950; MHN P₂.ECT.17) and *E. maxima* n.sp. have been observed with the distal part of the oviduct curving around into the posterior end of the right peribranchial cavity and distended to form a large, thin-walled brood-pouch anterior to the heart. The opening of the brood-pouch is against the body wall near the endostyle.

Species of this genus often share the same habitat and are found growing together. Despite this, and their usually wide range, *E. nexa, E. rubricollis* and *E. diaphanis* are common at the southern end of the Great Barrier Reef, while *E. sluiteri* is common at Lizard I. No species of this genus has yet been recorded from temperate waters.

Many of the species are known to be viviparous. Nevertheless they have a wide range in the West Pacific and possibly into the Indian Ocean. Although there are many gaps in the recorded ranges of all the species occurring in Australia this is less likely to be evidence of isolation than a consequence of the inconspicuous nature of the colonies, causing them to be overlooked by collectors.

KEY TO THE SPECIES OF *ECTEINASCIDIA* RECORDED FROM AUSTRALIA

1. Both apertures on or near upper anterior end of body; no transverse muscles between apertures; no secondary gut loop 2
   Atrial aperture dorsal, removed from anterior end of body; branchial aperture terminal; transverse muscles between atrial and branchial apertures; gut forms secondary loop 4
2. Transverse muscles in 3 longitudinal bands .... *E. sluiteri*
   Transverse muscles not in 3 longitudinal bands 3
3. Transverse muscles absent from ventral half of body .... *E. diaphanis*
   Transverse muscles absent only from ventral border of body .... *E. thurstoni*
4. Test sandy; meshwork of muscles on right side of body .... *E. imperfecta*
   Test naked; no meshwork of muscles on right side of body..................................... 5
5. Stomach ridged 6
   Stomach smooth.................................. 7
6. With conspicuous siphons... *E. maxima* n.sp.
   No conspicuous siphons ....*E. rubricollis*
7. Zooids rounded; apertures sessile .... *E. flora*
   Zooids long; apertures on conical siphons .... *E. nexa*

The following species have been recorded from the Indian or west Pacific Oceans, but have not yet been recorded from Australia:

Ecteinascidia bandaensis Millar, 1975 from Indonesia is reported to have primarily longitudinal musculature. Only in this species and in *E. flora* does the longitudinal musculature extend posterior to the siphons. The species otherwise resembles *E. rubricollis*

Ecteinascidia diligens Sluiter, 1900b from Laysan (Philippines) has no languets on the dorsal lamina, and only 11 rows of stigmata. The remarkable stolonic structure (which Sluiter believed to have been acting as a brood-pouch) may be developing buds as have been observed in *E. rubricollis* (which it resembles in other ways).

TABLE IV — SUMMARY OF CHARACTERS OF SPECIES OF *ECTEINASCIDIA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Atrial aperture	Test vascular-isation	Colour in life	Origin of stolon	Transverse body muscles	Secondary gut loop	Gonad arrangement	Additional features
E. maxima n.sp.	—	Lord Howe I.	antero-dorsal	conspicu-ous	cream with red markings	posterior	long inter and post-siphonal bands	present	♂scattered ♀central	long siphons; numerous pouches at proximal end of intestine
E. flora	—	Abrolhos	"	"	?	"	"	"	?	axial stolon; long longitudinal muscles
E. imperfecta	WP	Torres Strait	"	"	sandy	postero-ventral	short inter and post-siphonal bands	"	"	mesh of muscles on right
E. rubricollis	WP	Lord Howe I; Hervey Bay - Mackay	"	"	lemon-vermilion	"	"	pro-nounced	♂semicircle ♀distal	apertures sessile
E. nexa	WP	Moreton Bay - Lizard I.	mid-dorsal	"	greenish yellow	ventral	long inter and post-siphonal bands	"	♂circle ♀central	prostrate zooids with accessory connectives; conical siphons
E. diaphanis	WP	NSW - Darwin	sub-terminal	incon-spicuous	pinkish	posterior	short post-siphonal bands	absent	♂semicircle ♀distal	—
E. thurstoni	IWP	Cockburn Sound	"	"	?	postero-ventral	long post-siphonal bands	"	"	—
E. sluiteri	IWP	Lizard I. Deltaic Reef	"	"	yellow	"	post-siphonal bands interrupted each side of dorsum	"	♂arc ♀distal	long irregularly branched male follicles

[1]WP, western Pacific; IWP, Indo-West Pacific. [2]Range given anti-clockwise around the continent.

Ecteinascidia garstangi Sluiter, 1898a, 1900b, from Mozambique (see also Vasseur 1969) and Laysan, has a dorsal atrial aperture well separated from the anterior end of the body. Its gut has a deep secondary loop, horizontal musculature is well developed and red pigment is present anteriorly. On presently recognised characters, the species appears separable from *E. rubricollis* only on the basis of the centrally placed elongate opening of the neural gland.

Ecteinascidia hedwigiae Michaelsen, 1918 from Natal has a sub-terminal atrial aperture very close to the branchial siphon. The gut does not form a secondary loop, and horizontal muscles are present behind the atrial siphon but not between the siphons. The species resembles *E. diaphanis* most closely, but living specimens are an intense violet colour anteriorly, providing the principal distinction between the species.

Ecteinascidia diaphanis Sluiter, 1885
(Fig. 35; Pl IIa,b)

Ecteinascidia diaphanis Sluiter, 1885, p.168; 1904, p.10. Beneden, 1887, p.28.

Ecteinascidia hataii Tokioka, 1950, p.127. Kott, 1964, p.145; 1966, p.292.

DISTRIBUTION

NEW RECORDS: New South Wales (Solitary I., QM G9632). Queensland (Wilson I, QM GH2069; Heron I, QM G9410 GH1348 GH2008 GH2035-7; Swain Reefs, QM G10154; Lizard I., QM GH2038).

PREVIOUSLY RECORDED: Queensland (Heron I. — Kott 1964). Northern Territory (Darwin — Kott 1966). Palau Is (Tokioka 1950). Indonesia (Sluiter 1885).

The species is taken on the undersurface of boulders or under ledges from low tide level to 10 m.

DESCRIPTION

EXTERNAL APPEARANCE: Living specimens are upright and sub-cylindrical, tapering to a stalk posteriorly. The test is very thin, almost glassy and transparent. The zooids are fixed by their short posterior stalk to common basal stolons that are attached to the substrate. Zooids are up to 1 cm high and 0.5 cm in diameter. When contracted, the apertures appear to be sessile, on very low rounded prominences on opposite sides of the upper surface. These extend into very short cylindrical siphons when relaxed. There are 7 branchial lobes and 6 atrial lobes. The posterior vessel leaves the body at the posterior end of the endostyle and traverses the stolon system. There is a fine network of blood vessels, often inconspicuous, in the anterior part of the test. No major test vessels were detected entering the test from the body wall.

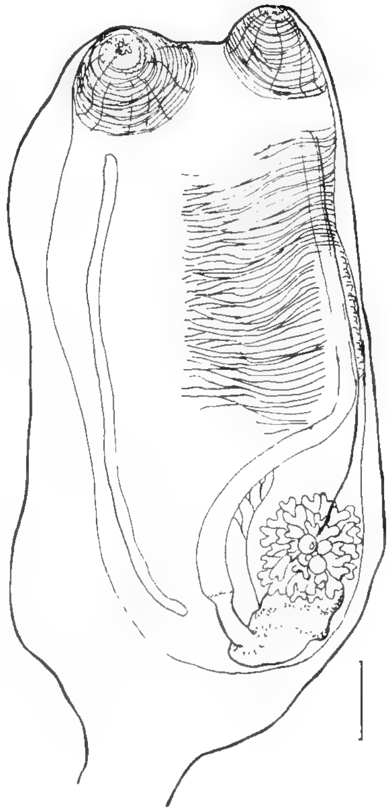


FIG. 35: *Ecteinascia diaphanis* — zooid from left side. (Scale: 1.0 mm).

Living specimens from the Capricorn Group (Heron I, Wistari Reef) are pink anteriorly. The colour, due to pink-orange pigment spots in the body wall around the anterior part of the body, fades in preservative. Although no morphological differences were detected, photographs of living specimens from North Solitary I (QM G9632) and the Swain Reefs (QM G10154) show them to have a red band around the rim of the apertures and the base of the siphons, but no spots are evident and neither spots nor bands of colour are present in preserved specimens.

INTERNAL STRUCTURE: The body wall is thin and transparent, the internal organs being clearly visible from the external surface. A fine network of vessels can sometimes be seen in the anterior part of the body wall where it closely adheres to the test. The delicate longitudinal muscles along each siphon do not extend posterior to its base. Strong circular muscles are present around each siphon. A wide band of about 40 fine, parallel, transverse muscles crosses the dorsal mid-line behind the atrial aperture. The dorsal tubercle has a wide, 2-lipped, more or less trumpet-shaped opening. The dorsal lamina is long and consists of a series of transversely flattened, long, pointed languets without an upright, longitudinal membranous fold between them.

The branchial sac has 16 to 19 rows of up to 50 stigmata. Internal longitudinal vessels cross every second to third stigma, and are supported by short papillae on the transverse vessels. The longitudinal vessels are sometimes interrupted, and are occasionally absent from parts of the branchial sac especially anteriorly.

The oesophageal opening is at the posterior end of the branchial sac. The oesophagus is short. The stomach is roomy and has 5 spiral ridges. A narrow mid-intestine curves anteriorly to abruptly expand into the intestine. The intestine forms a wide curve toward the dorsal border, and the rectum extends anteriorly toward the atrial aperture. There is a gastro-intestinal connective from the distal end of the stomach which breaks up into many branches along the inner curve of the intestine.

The gonads are in the gut loop. Numerous immature pear-shaped follicles are arranged in a semicircle distal to the small ovary. When mature, they become long and clavate, filling a wide, circular area in the curve of the gut loop around the central ovary. Larvae are sometimes present in the left peribranchial cavity. The larval trunk, about 1 mm long, is characteristic of larvae of this family, with its large branchial sac, adhesive organs with epidermal cups around the cone of adhesive cells, and an otolith and ocellus. The tail is wound about three-quarters of the distance around the trunk.

REMARKS: Living material of the present species can be readily identified by the transparent test, posterior position of the stalk, wide band of transverse muscles over the dorsal surface behind the atrial siphon, almost sessile apertures close together on the upper surface, and antero-posteriorly flattened dorsal languets. The present specimens consistently have 18 or 19 rows of stigmata, while Tokioka's specimens from Palau Is. had only 16. Although this may indicate some genetic diversity between the populations it is not a sufficient difference to indicate their complete isolation.

Ecteinascidia hedgwigiae Michaelsen, 1918 from Natal is related and very similar to the present species in most characters. The neural complex described by Michaelsen (1918) for *E. hedgwigiae* is identical with that of *E. diaphanis*. However the zooid is violet anteriorly; this is the only known character distinguishing it from the present species.

Ecteinascidia maxima n.sp. is also closely related and living specimens look almost the same as those of some populations of the present species. However, its siphons are longer, its gut forms a loop, the male follicles are scattered over the body wall (rather than being arranged in a semicircle) its transverse muscles are longer and some cross the dorsal border anterior to the atrial siphon.

The synonymy of *E. hataii* with *E. diaphanis* is based on the shape of the zooids, position of the posterior stalk, very delicate test without test vessels, arrangement of muscles behind the atrial siphon, and absence of an upright membrane between the antero-posteriorly flattened languets of the dorsal lamina.

Ecteinascidia flora Kott, 1952
(Fig. 36)

Ecteinascidia flora Kott, 1952, p.316.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (W of Houtmans Abrolhos — holotype AM U3903, paratype AM U3970 Kott 1952).

The holotype and paratype specimens were taken in a drift net at about 40 m.

DESCRIPTION

EXTERNAL APPEARANCE: The main axial basal stolon of the colony grows along a stalk of weed, the side branches and the growing tip extending out from the weed and not fixed to a substrate. The largest zooids are only about 3 mm long, becoming progressively smaller toward the terminal tip of the main axis and along the side branches. The test is naked and transparent. It is thin over the zooids, but firm on the axial or basal stolons. Zooids are rounded, but narrow toward a very short posterior stalk by which they are joined to the main axis. Each zooid has 2 blood vessels, one from each side of the posterior end of the endostyle. These join before entering the main vessel of the common axial stolon. A second branch from the axial stolon extends up into the test of the zooid and branches there. The apertures are sessile, the branchial aperture terminal, and the atrial aperture one-third of the distance along the dorsal surface. There are 14 small lobes around the branchial aperture and 6 around the atrial aperture.

INTERNAL STRUCTURE: The body wall is especially muscular. Longitudinal bands radiate

FIG. 36: *Ecteinascidia flora* (AM U3970) — a, colony; b, zooid from left side showing muscles. (Scales: a, 2.0 mm; b, 0.25 mm).

from beneath a narrow band of circular muscles around each aperture and extend a short distance over the sides of the body. Transverse bands cross the dorsal mid-line between the apertures and posterior to the atrial siphon. These extend over most of the body wall, being absent only from the ventral border of the body. The branchial tentacles are long and crowded. The dorsal tubercle has a simple opening. There are dorsal languets where the transverse vessels cross the mid-line, but no membrane was seen connecting them.

There are 18 rows of about 38 stigmata. Fine longitudinal vessels extend the length of the branchial sac; there are about 2 stigmata per mesh.

The gut loop extends around the posterior end of the zooid. A deep secondary loop is formed by the rectum extending forward at an acute angle to the descending limb of the primary loop. The stomach is oval and smooth. A gastro-intestinal duct branches over the voluminous intestine.

There are no gonads present in these specimens.

REMARKS: The unusual colony form of these specimens, with zooids progressively developing from the growing tip of an axial stolon, resembles that of *Perophora clavata* n.sp. Although an arborescent growth form appears to be characteristic of the latter species, the narrow algal stem on which the available colonies of *E. flora* are growing would not accommodate the basal mat of tangled stolons that is the usual habit of species of this genus. Consequently, the substrate may have affected the colony form, which may not be characteristic of the species. The muscular body wall and the short longitudinal muscle bands that extend past the circular bands of the sphincter muscle are characteristic of *E. flora*, however.

Ecteinascidia imperfecta Tokioka, 1950
(Fig. 37)

Ecteinascidia imperfecta Tokioka, 1950, p.129; 1967a, p.137.

DISTRIBUTION

NEW RECORDS: Queensland (Deltaic Reef, northern Great Barrier Reef, QM GH303).

PREVIOUSLY RECORDED: Palau Is (Tokioka 1950 1967a).

The species was taken with colonies of *Ecteinascidia sluiteri* from a channel face.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are formed of small (up to 4 mm in diameter), almost spherical, sessile individuals joined by basal stolons. The test is extremely delicate and transparent, with sand grains attached to its surface. The apertures are on conical siphons, the branchial aperture terminal and the atrial about halfway down the dorsal surface. Externally the apertures appear to be sessile. Blood vessels from the stolon branch in the test.

INTERNAL STRUCTURE: The body wall is muscular on the right, but on the left the muscles extend less than halfway down the body. Circular muscles and short longitudinal muscles are present on the siphons, but most of the body musculature consists of transverse bands that cross the dorsum between the siphons and posterior to the atrial siphon. These form an irregular network in the centre of the right side, but form into parallel transverse bands again around the ventral and posterior margin of the body (to the right of the mid-line). There is a conspicuous vascular network in the body wall. The dorsal tubercle has a simple opening. The long, pointed, dorsal languets are antero-posteriorly flattened basally. Their distal half twists around to the right, their anterior (left) margin being continuous with a membranous fold between the languets.

There are 20 rows of short, oval stigmata. Rounded papillae are present on the transverse vessels opposite each stigma. Under high magnification, these papillae were seen to have remnants of internal longitudinal vessels on each side. There were no entire internal longitudinal

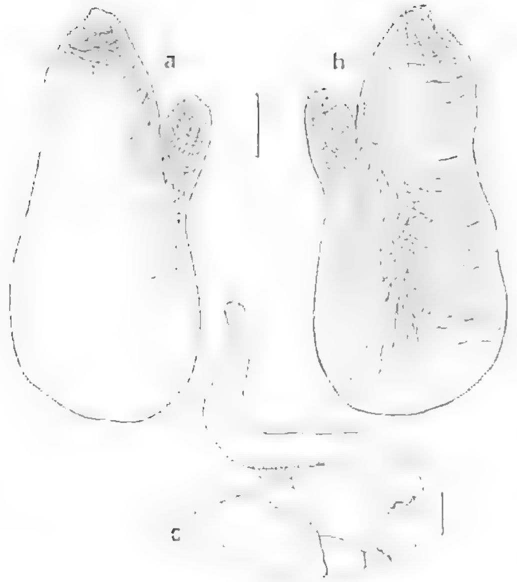


FIG. 37: *Ecteinascidia imperfecta* (QM GH303) — **a**, zooid from left; **b**, zooid from right; **c**, gut loop with gastro-intestinal duct. (Scales: **a**, **b**, 0.5 mm; **c**, 0.2 mm).

vessels in the newly recorded specimens although some were present in the types from the Palau Is.

The gut forms a curved loop around the posterior end of the body, the rectum forming a rather shallow secondary loop with the descending limb of the intestine. The oesophagus is short and curved. The stomach is large, almost spherical and usually smooth, although some spiral folds are occasionally present. There is a duodenal area distal to the stomach, a narrow mid-intestine and an oval posterior-stomach. There are a few slight pouches at the proximal end of the intestine. The gastro-intestinal duct from the distal end of the stomach breaks into tubules that spread over the distal part of the descending limb of the primary gut loop.

The gonads are not known for the species.

REMARKS: The dorsal languets and the position of the atrial muscles and their arrangement over the dorsal mid-line resemble *E. rubricollis*. However, *E. imperfecta* is distinguished by its better development of musculature on the right side of the body, especially the presence of transverse bands around the ventral and posterior part of the right body wall, and the very regular occurrence of branchial papillae between the stigmata. Despite their small zooid size, they have a relatively large number of rows of stigmata.

The 5 zooids known from the Palau Is are fixed by their left sides to the basal stolons as in the Atlantic species *E. tortugensis* Plough and Jones (see Van Name 1945) rather than being upright as are the Australian specimens. The distinctive, sand-covered test of the Australian specimens is also different from the naked test of those from the Palau Is. Possibly the two populations are not conspecific. This cannot be resolved until mature specimens are available from both locations.

Ecteinascidia maxima n.sp.
(Fig. 38; Pl.IIc)

DISTRIBUTION

TYPE LOCALITY: Lord Howe I. (Sugarloaf, reef, 17 m, coll. N. Coleman, 27.12.79, holotype QM GH50).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of a basal mat of branching and anastomosing stolons around a stalk of coral debris. Zooids are large, up to 2 cm high, joined to the basal mat by a very short, narrow stalk from the posterior end of the body. There are also a few short, narrow accessory connectives from the posterior end of the body to the basal stolons, and some blood vessels can be seen in the posterior part of the test. The test is thin and transparent. Apertures are on relatively long cylindrical siphons, the branchial siphon terminal and the atrial siphon antero-dorsal. The border of the atrial aperture has 7 inconspicuous lobes; 8 similar lobes occur around the branchial aperture.

Living specimens have a thin red band around the rim of each aperture and a thicker band around the base of each siphon. They closely resemble living specimens of some populations of *E. diaphanis* but their colour is more intense.

INTERNAL STRUCTURE: The body wall has a continuous and conspicuous layer of circular muscles that is interrupted only across the ventral border. The muscles are less conspicuous around the posterior end of the body. Longitudinal bands extend along each siphon but do not continue posterior to the siphons. They are obscured by an outer layer of circular muscles on each siphon. There are about 5 transverse muscles crossing the dorsal border between the siphons. The branchial tentacles are long and narrow. The dorsal tubercle has a simple opening directed anteriorly. The dorsal lamina is a thin, ribbed membrane, the ribs continuous with languets that project from the edge of the membrane.

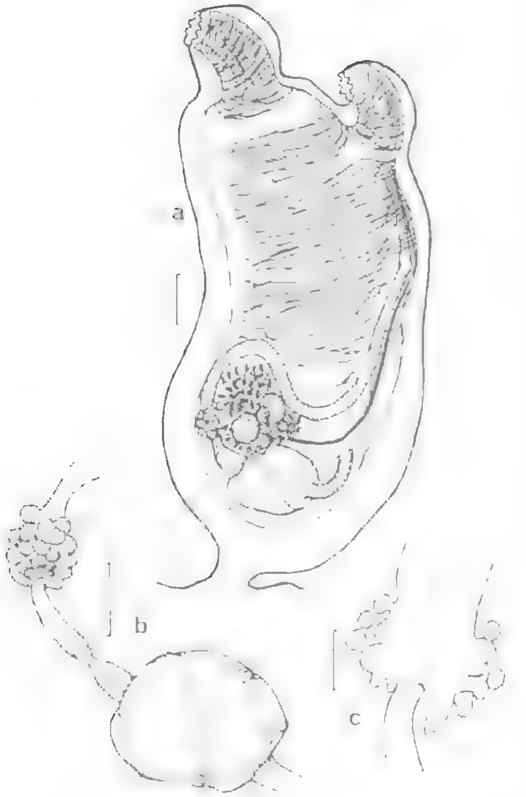


FIG. 38: *Ecteinascidia maxima* (QM GH50) — a, body in test, from left side, showing gut, gonads and muscles; b, stomach and proximal part of intestine with pouches; c, longitudinal section through proximal part of intestine. (Scales: a, 1.0 mm; b, 0.5 mm; c, 0.2 mm).

The branchial sac has 21 rows of about 50 stigmata, and 22 internal longitudinal vessels on each side. The longitudinal vessels are entire and not interrupted. The oesophageal opening is at the posterior end of the branchial sac; the oesophagus curves posteriorly and to the left. The stomach is large and rectangular, with 4 conspicuous ridges. The narrow mid-intestine expands abruptly into the intestine which curves anteriorly, dorsally, and then posteriorly to form an open primary loop. The rectum extends anteriorly and forms a wide secondary loop with the descending limb of the primary loop. A short extent of the thin epithelial wall of the proximal part of the intestine evaginates into rounded pouches, appearing mulberry-like externally. Neither a gastro-intestinal duct nor tubules extending along the intestine were observed.

The gonad is present in the loop of the gut. The testis is diffuse, consisting of small follicles scattered over the body wall in the pole of the gut loop and spreading onto the surface of the stomach. The vasa efferentia join the vas deferens underneath the ovary. The vas deferens accompanies the rectum anteriorly, but the oviduct crosses over into the posterior part of the right peribranchial cavity, where it expands into a brood-pouch, its opening directed ventrally near the endostyle.

REMARKS: In its dorsal lamina, branchial sac and secondary gut loop the present species resembles *E. rubricollis*. Its differences from *E. diaphanis* are discussed above (Remarks, *E. diaphanis*). Unique features that characterise *E. maxima* are the long, cylindrical siphons; the long, parallel transverse muscles including those between the siphons; the scattered male follicles; and the pouches in the proximal part of the intestine. The gastro-intestinal duct and its branches along the intestine were not detected in these specimens, but may be obscured by gonads.

Ecteinascidia nexa Sluiter, 1904
(Fig. 39; Pl.11d-f)

Ecteinascidia nexa Sluiter, 1904, p.11. Kott, 1966, p.292; 1981, p.196.
Perophora hornelli Herdman, 1906, p.298.
Ecteinascidia tokaraensis Tokioka, 1954a, p.255.

DISTRIBUTION

NEW RECORDS: New South Wales (Lord Howe I., QM GH41). Queensland (Hervey Bay, QM GH2025–30; Tannum Sands, QM G4964; Wilson I., QM GH2068; Heron I., QM GH2041–3 GH2059 GH2061–3 GH2065–7 GH2974 GH2980 GH3014 GH3017 GH3024 GH3055–6; Wistari Reef, QM GH1348 GH2058 GH2060; Tryon I., QM GH2064; North West I.; Green I., QM G12502; Lizard I., QM GH2039–40).

PREVIOUSLY RECORDED: Queensland (Hervey Bay — Kott 1966). Indonesia (Sluiter 1904). Fiji (Kott 1981). Sri Lanka (BM 1907.8.30.1 Herdman 1906). Japan (Tokara I. — Tokioka 1954a).

The species is very common under rubble at low tide at Hervey Bay, Heron I. and Green I. It was not common at Lizard I. It has been taken only down to 3 m depth.

DESCRIPTION

EXTERNAL APPEARANCE: Living colonies form extensive mats of small (usually less than 6 mm long) and crowded zooids. They are transparent and pale lemon to rather opaque, olive yellow (Ridgeway 1886). The more transparent, paler zooids have a distinct yellow ring around the rim of the apertures. Several small colonies (QM GH3055) had pale, blue irridescent, transparent zooids with yellow guts. Zooids are prostrate or,

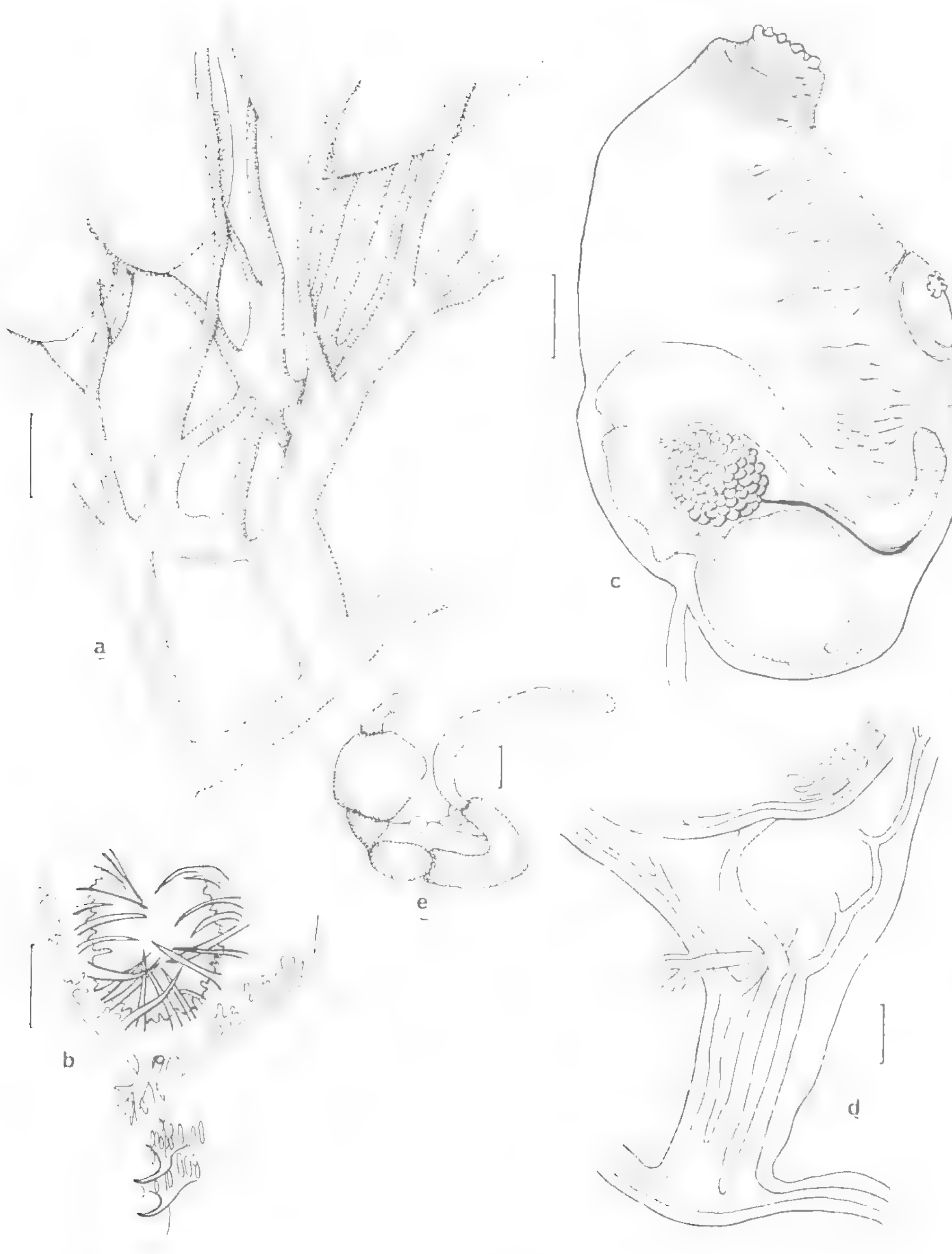


FIG. 39: *Ecteinascidia nexa* — **a**, posterior end of zooids showing accessory connectives to basal stolon (QM GH41); **b**, prebranchial region showing tentacles and branched protruberances on prepharyngeal groove (QM GH41); **c**, zooid removed from test, from left side, showing gut, mature gonad and muscles; **d**, postero-ventral corner of body showing stolonic and test vessels; **e**, gut loop showing gastro-intestinal reservoir and duct. (Scales: 0.5 mm).

in crowded colonies, curved into an upright position. They are fixed to basal stolons by a wide connective from the posterior end of the ventral surface. The stalk is of variable length and is often wide, spreading out along the basal stolon. There are often (but not always) accessory connectives between the basal stolon and the posterior test. Blood vessels from the basal stolon into the test extend through both primary and accessory stalks. These vessels divide into long branches in the test. Zooids are connected to one another along their sides by short test connectives. These colonies cannot be removed entire from the substrate: relatively strong basal stolons branch and extend into the interstices of the calcareous substrate. Apertures are sessile or on conspicuous conical siphons, the branchial aperture terminal and the atrial halfway along the dorsum. When zooids are prostrate, the branchial siphon curves dorsally; and the atrial siphon is directed straight up. In upright zooids, both siphons project vertically when contracted. The branchial aperture is 8-lobed and the atrial aperture 6-lobed.

Preserved zooids are always very flaccid and distorted, losing the well defined outline that is characteristic of the living specimens.

INTERNAL STRUCTURE: The body wall is thin and delicate, but is relatively muscular. It is always cloudy in preservative, with very numerous blood cells and often with a rather conspicuous vascular network. It is often a dark reddish brown in preservative. The muscles consist of circular and longitudinal siphonal muscles and transverse muscles that cross the dorsal surface between the siphons and posterior to the atrial siphon. These extend over most of the right side of the body, but only halfway across the left side. The dorsal tubercle is a simple opening. The dorsal lamina has laterally flattened languets with a membrane between them. The main vessel which enters the vascular stolon originates from the body wall one-third to half of the distance from the posterior end of the body.

There are 13 to 19 rows of stigmata and about 14 internal longitudinal vessels in each row, with about 3 stigmata in each mesh.

The long gut loop occupies most of the posterior half of the body. The rectum forms a deep secondary loop with the descending limb of the intestine. The oesophagus is curved, and the large stomach is almost spherical and always without folds or ridges. A short, narrow duodenal area and a wider mid-intestine are separated from the posterior-stomach by a slight constriction. The intestine expands abruptly almost in the pole of the loop and has a few pouches at its proximal end, although these are not numerous as in *E. maxima* n.sp.

The gonad, enclosed in the gut loop, consists of a circle of pear-shaped male follicles converging toward the centre of the circle, where they join the vas deferens. The small ovary is in the centre of the circle of male follicles on their mesial surface. As the male follicles mature, they become long and fan-shaped. They subdivide along their length to form a tight hemisphere, flat on the mesial surface where the ovary is located, and rounded on the outer or parietal surface where the wider, rounded, proximal ends of the follicles are crowded together. Gonads are rarely present; it is possible that sexual reproduction is a relatively rare occurrence, all available energy being diverted to the prolific vegetative process. Mature male follicles were found only in specimens from Hervey Bay collected in November.

REMARKS: The species is characterised by its small zooids with prostrate habit, the position of the atrial aperture halfway down the dorsum, the large carpet-like colonies with interzooid test connectives, and the cloudy body wall, deep secondary gut loop and large, spherical, smooth stomach.

A deeply curved gut loop and a similar arrangement of musculature occur in *E. rubricollis*. However, *E. rubricollis* is distinguished by its more anteriorly positioned atrial aperture; less regularly arranged and not so crowded male follicles; posterior rather than ventral stolon; less cloudy body wall, and longer and ridged stomach.

The holotype colony of *Perophora hornelli* Herdman, 1906 (BM 1907.8.30.1) has small, prostrate zooids fixed by their ventral surfaces to a basal mat of stolons. They have 13 rows of stigmata, 14 internal longitudinal vessels per side, 2 to 3 stigmata per mesh and a smooth stomach. Lateral test connectives were not detected between the few zooids of this fragile colony, but these may have been lost. It is otherwise identical with the Australian material of this species.

Ecteinascidia rubricollis Sluiter, 1885
(Fig. 40)

Ecteinascidia rubricollis Sluiter, 1885, p.163. Beneden, 1887, p.33. Kott, 1964, p.146.
Sluiteria rubricollis Sluiter, 1900b, p.5.

DISTRIBUTION

NEW RECORDS: Queensland (Hervey Bay, QM GH2046; Wistari Reef, QM GH1366; Heron I., QM GH2279 GH2981 GH3001 GH3026 GH3077).

FIG. 40: *Ecteinascidia rubricollis* (QM GH2046) — a, zooid in test; b, gut loop and gonad with immature male follicles. (Scales: 0.5 mm).

PREVIOUSLY RECORDED: Queensland (Tannum Sands, Sarina — Kott 1964). Indonesia (Sluiter 1885 1900b).

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are upright, up to 1 cm high. The test is thin and transparent. Apertures are on short siphons, the branchial aperture terminal and the atrial aperture antero-dorsal. The borders of the branchial and atrial apertures are divided into 10 and 8 broad, flat lobes respectively. The body is rounded posteriorly, and has a stalk from the postero-ventral corner which attaches the zooid to a mat of branching basal stolons. There are some epibionts or foreign particles on the test, but these are never crowded and do not obscure the zooid. Living zooids are transparent vermilion (Ridgeway 1886). The red colour results from a network of blood vessels containing red cells, in the test.

In some zooids (QM GH2046), buds appear to be developing on the stolons in the stem of the zooid.

INTERNAL STRUCTURE: The body wall is thin. There are transverse muscles across the dorsal surface between the siphons and posterior to them. These muscle-bands break up into branches each side of the mid-line, form wide bands along the middle of each side of the body, and then branch again before they terminate about three-quarters of the way down each side of the body. There are also circular muscles around each siphon. Tentacles are of 3 orders, arranged in close-set concentric rings around the base of the siphons. The deep peritubercular area is bounded by a rounded, fleshy rim along each side. The anteriorly directed circular opening of the neural gland is on the anterior end of the fleshy rim on the right side of the V. Specimens from Lord Howe I. have small, branched protuberances from around the prepharyngeal groove. The dorsal lamina is long, and the long, pointed dorsal languets, primarily flattened antero-posteriorly, bend around to the right. There is a very fine longitudinal membrane between the languets.

There are 12 to 21 rows of about 50 stigmata on each side of the branchial sac, with 25 internal longitudinal vessels per side.

The gut loop is curved; the rectum forms a deep secondary loop as it extends forwards toward the atrial opening. The stomach has 4 regular, spiral folds. A gastro-intestinal duct with a spherical reservoir extends from the distal end of the stomach to the intestine where it breaks into branches over the gut wall.

The gonad enclosed in the gut loop consists of a circle of pear- to club-shaped, often lobed, testis follicles, their vasa efferentia directed toward the centre where they join a common vas deferens beneath the small, circular ovary.

REMARKS: The structure of these zooids agrees in almost every detail with the types redescribed by Beneden (1887). In particular, the shape of the body, the arrangement of its musculature and the position and shape of the opening of the neural gland are identical with those previously described.

The species can be distinguished from *E. nexa* with which it often occurs, by its less conspicuous and closely positioned apertures, its more transparent body wall, the spiral folds in the stomach and less crowded male follicles.

Zooids in specimens from Hervey Bay (QM GH2046), with buds in the stem, resemble those of *E. diligens* Sluiter, 1900 which was reported to have a blood-pouch extending down into the basal stolon. Sluiter may have misinterpreted this structure.

Ecteinascidia sluiteri Herdman, 1906
(Fig. 41)

Ecteinascidia sluiteri Herdman, 1906, p.300. Tokioka, 1950, p.126. Millar, 1975, p.267.

DISTRIBUTION

NEW RECORDS: Queensland (Lizard I., QM GH2031-4; Deltaic Reef, QM GH302).

PREVIOUSLY RECORDED: Sri Lanka (BM 1907.8.30.2 Herdman 1906). Singapore (Millar 1975). Palau Is (Tokioka 1950).

This species has been taken at low tide. It is the common perophorid found on rubble at Lizard I.

DESCRIPTION

EXTERNAL APPEARANCE: Upright zooids (up to 0.6 cm high) are crowded together, attached to a tangled mat of basal stolons either directly or by short stalks from the postero-ventral corner of the body. Younger zooids are sessile, fixed posteriorly to the basal stolons. The branchial aperture is terminal; the atrial aperture is antero-dorsal. Both apertures are on low, conical siphons. There are 8 inconspicuous, triangular lobes around the border of the branchial aperture and 6 around the atrial aperture. Small ocelli on the tip of minute papillae occur between the lobes. The test is glassy, gelatinous and relatively firm and smooth. There are usually few epibionts, although a specimen from Lizard I. was completely overgrown by a botryllid colony that left only the apertures free. In life the zooids are pale yellow, but are quite colourless in preservative.

INTERNAL STRUCTURE: The body wall is delicate and transparent, the most conspicuous feature being a longitudinal row of short, transverse muscles down each side of the body and along the mid-dorsal line posterior to the atrial aperture. The row on the left stops anterior to the gut loop. Delicate, short, longitudinal muscles confined to the siphons are surrounded by circular muscles. There is often a conspicuous vascular network in the body wall. The dorsal tubercle has a simple, round opening. There are up to 50 simple branchial tentacles of varying sizes. The long dorsal lamina is a continuous, ribbed, membrane with each rib produced into a pointed languet projecting from the margin.

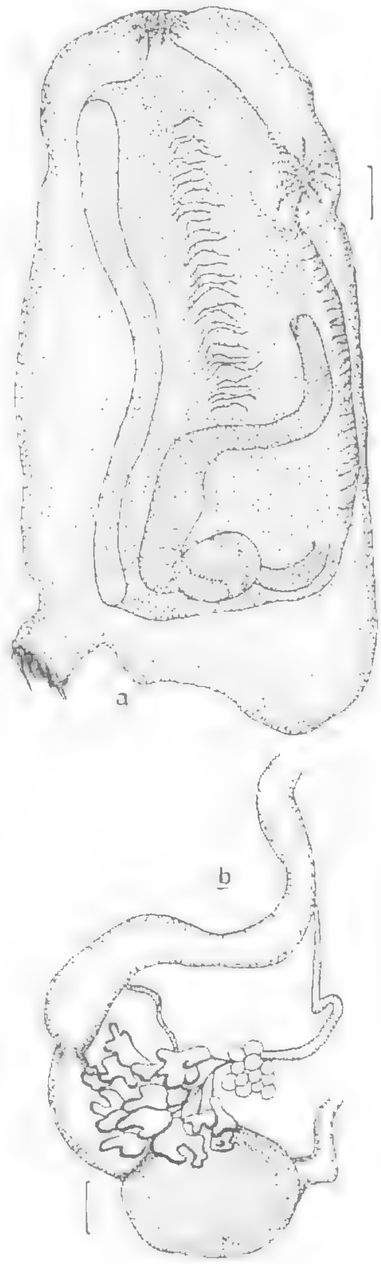


FIG. 41: *Ecteinascidia sluiteri* (QM GH302) — **a**, whole zooid; **b**, gut loop and gonad. (Scales: a, 0.5 mm; b, 0.25 mm).

There are 14 to 22 rows of stigmata, each with 45 to 50 stigmata, and about 2 stigmata between the longitudinal vessels.

A narrow oesophagus opens from the posterior end of the branchial sac. The stomach is large and almost spherical, with 5 oblique ridges. A gastro-intestinal duct from the distal end of the stomach divides into branches over the proximal part of the intestine. This is often obscured by the gonad. A narrow mid-intestine curves anteriorly from the stomach and expands abruptly into the intestine, which curves dorsally to form a wide open loop. The rectum extends anteriorly at never less than a right angle to the descending limb of the intestine.

The gonad is present in the gut loop, in the pole of which are large, lobed male follicles. Their vasa efferentia join the vas deferens ventral to the small, rounded ovary. The male follicles are sometimes spread over the mesial surface of the stomach and mid-intestine.

REMARKS: The species resembles *E. turbinata* Herdman, 1880 (< *E. moorei* Herdman, 1890), which has a wide range in the eastern and western Atlantic, the Mediterranean and the Red Sea (see Van Name 1945). Specimens of *E. turbinata* from West Africa (Sluiter 1905a, MHN Ps.ECT.17) and from the western Atlantic (MHN Ps.ECT.16) have the same bands of short, transverse muscles along the body as has the present species, as well as a ribbed dorsal membrane with languets. However, the male follicles (which are smaller and pyriform) form a semicircle around the ovary rather than being located entirely ventral to it as they are in the present species. The stomach is different, too, in having only 2 partial spiral ridges. Specimens of *E. sluiteri* from Singapore and the Palau Is (Tokioka 1950, Millar 1975) have only 14 rows of stigmata, while the present specimens have 22. As this is the only difference between these populations, they are probably conspecific.

Characteristics of the species are its terminal branchial siphon; longitudinal bands of short muscles; fan of large lobed male follicles proximal to the ovary; spirally ridged stomach; and the membrane between the dorsal languets.

Ecteinascidia thurstoni Herdman, 1890
(Fig. 42)

Ecteinascidia thurstoni Herdman, 1890, p.151; 1906, p.299.

?*Ecteinascidia thurstoni*: Sluiter, 1905a, p.6.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 11.75)

PREVIOUSLY RECORDED: Sri Lanka (Herdman 1906). Gulf of Manaar (Herdman 1890). ? Gulf of Aden (Sluiter 1905a).

DESCRIPTION

EXTERNAL APPEARANCE: Upright zooids 1.2 cm high, they either narrow posteriorly toward a short, posterior ventral stalk that has a constriction where it joins onto the basal stolon or are sessile, fixed by their postero-ventral surface. The test is thin and glassy. The apertures are on low, conical protruberances on the upper surface of the body. Both branchial and atrial apertures are 7-lobed.

INTERNAL STRUCTURE: The body wall is thin and in some parts adheres closely to the test. A layer of circular muscles almost completely surrounds the body, interrupted only over the ventral border and fading out posteriorly. The usual circular muscles and short, longitudinal bands extend from the apertures along the siphons. There are more than 50 branchial tentacles of varying sizes. The dorsal tubercle has a simple, circular opening. The dorsal lamina is a narrow membrane, ribbed on the right side only. The languets are narrow and laterally flattened tongues. Their anterior edge is continuous with the rib, and their posterior edge is continuous with the rim of the membrane.

There are 15 rows of stigmata, 17 internal longitudinal vessels and 3 or 4 stigmata per mesh. Sometimes the internal longitudinal vessels are slightly oblique.

The gut forms an open, sinuous curve, the rectum extending anteriorly toward the atrial aperture. The stomach has 5 spiral folds. A narrow mid-intestine expands abruptly into the rectum at the pole of the gut loop before it curves dorsally.

The gonads are enclosed in the gut loop. Spherical to pyriform and lobed male follicles, are scattered in a semicircle sometimes spreading along the inside of the gut loop. The vasa efferentia join the vas deferens beneath the small, circular ovary in the centre of the semicircle of male follicles. Embryos are present in the right peribranchial cavity.

REMARKS: The constriction between the posterior end of the zooid and the basal stolon has been observed for *E. sluiteri* (Herdman 1906) and may occur throughout this genus at certain growth stages. The almost continuous layer of circular muscles is also present in *E. maxima*, which is distinguished by the form and position of its siphons and its intestinal pouches. *Ecteinascidia thurstoni* resembles *E. diaphanis* in the position of the apertures, form of the siphons, absence of

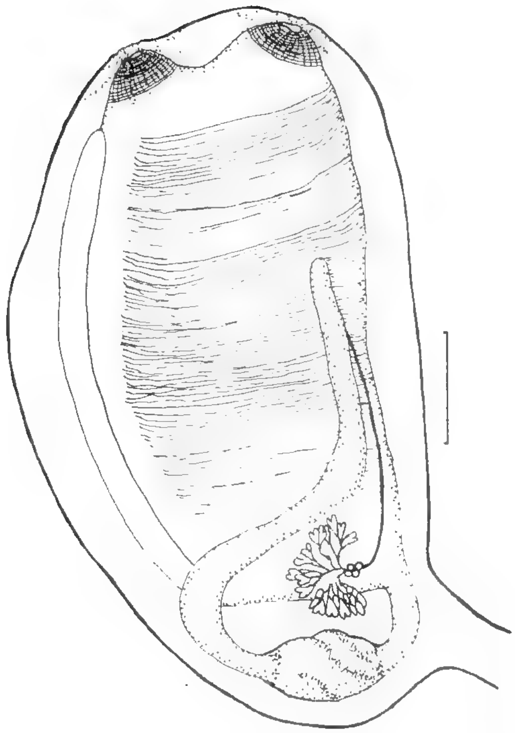


FIG. 42: *Ecteinascidia thurstoni* (WAM 11.75) — zooid. (Scale: 2.0 mm).

transverse muscles between the siphons, and form and arrangement of the male follicles. It is distinguished from it mainly by the absence of pink pigment spots and by its almost complete layer of circular muscles and the membrane between its dorsal languets.

Genus **Perophora** Wiegmann, 1835
Type species: *Perophora listeri* Forbes and Hanly, 1848

Species of the family Perophoridae in which there are never more than 8 rows of stigmata. The relatively short gut forms a short loop across the posterior end of the body. The stomach is invariably smooth. The rectum is very short, and the anal aperture is distant from the atrial opening. The testis is large. It is either undivided or consists of a few follicles with a limited number of deeply divided lobes. There are never the numerous, relatively short pyriform follicles of *Ecteinascidia*.

The zooids of *Perophora* are the smallest known in the Phlebobranchia, usually being less than 5 mm in length. Small size and associated simplification have reduced the morphological diversity of the genus. However, features of the stalk and its vascularisation, and differences in colony form, distinguish the species. The genus contains species in which zooids are supported on short stalks from basal stolons as in *Ecteinascidia*. There are also several species of the genus *Perophora* in which the colonies are vertical and the supporting stalks are relatively long (*P. clavata* n.sp., *P. hutchisoni* and *P. namei*). In the last two species, the colonies have a degree of organisation: each zooid is supported by a long stalk that branches off a central, horny, monaxial stem with the smaller, developing zooids at the top of the stem. As in *Ecteinascidia*, the body musculature is reduced and the test is very delicate.

The genus is most diverse in temperate waters, although species are also present in the tropics. It is well represented in Australian waters.

KEY TO THE SPECIES OF *PEROPHORA* RECORDED FROM AUSTRALIA

1. Zooids encased in sand.......................... 2
   Zooids naked..................................... 3
2. Stalk horny and jointed.......... *P. hutchisoni*
   Stalk not horny and jointed.. *P. clavata* n.sp.
3. Horny vertical axial stalk.............. *P. namei*
   No horny vertical axial stalk.................... 4
4. 4 or 5 rows of stigmata........................... 5
   8 rows of stigmata............ *P. multistigmata*
5. Posterior stolonic extension of body present; 4 rows of stigmata...... *P. modificata* n.sp.
   No posterior stolonic extension of body; 5 rows of stigmata.......... *P. multiclathrata*

The following species recorded from the western Pacific have not been taken in Australian waters:

Perophora euphues (Sluiter, 1895) from Indonesia has 4 or 5 rows of stigmata and gonads that may be similar to those of *P. modificata* n.sp. However the shape of the zooid is different, and the zooids are only about 3 mm long (see appendix, Sluiter 1895).

Perophora jacerens (Tokioka, 1954a) from the Tokara Is is a sessile species, attached by the whole of the ventral side of the body with 7 or 8 rows of stigmata. It has the short rectum of *Perophora* rather than the long rectum of the genus *Ecteinascidia* to which Tokioka had assigned the species. Its gonads are not known.

Perophora japonica Oka, 1927a (see Tokioka 1953a) from Japan also has a prostrate zooids fixed by the ventral surface. It has 4 rows of stigmata and a fan of long, deeply divided male follicles.

TABLE V — SUMMARY OF CHARACTERS OF SPECIES OF *PEROPHORA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Common stolons	Zooids	Terminal aperture	Stigmata: no. of rows (number: row)	Male follicles number; shape	Position of ovary	Additional features
P. multistigmata	—	Moreton Bay	basal mat	naked	branchial	8(16)	several; fan-shaped	distal end ♂	—
P. modificata n.sp.	WP	Swain Reefs – Deltaic Reefs	〃	〃	atrial	4(40)	several; clavate	centre of ♂	vascular mesh in stolonic projection
P. clavata n.sp.	—	Bass Strait	vertical	sandy	branchial	4(18)	several; fan-shaped	distal end ♂	—
P. namei	WP	Coral Sea	〃	naked	atrial	4(35–50)	several; pyriform	〃	horny axial stalk
P. hutchisoni	NZ	Dongara – NSW	〃	sandy	branchial	5(25–35)	single; bean-shaped	near dorsal mid-line	〃
P. multiclathrata	Pan-tr	NSW – Bunbury	basal mat	naked	〃	5(12–20)	〃	distal end ♂	—

[1]WP, Western Pacific; Pan-tr, pan-tropical. [2]Range given anti-clockwise around the continent.

Perophora listeri Tokioka, 1950 and 1952 from the Palau Is and the Arafura Sea resembles *P. multiclathrata* in its habit, but has 4 rows of about 20 stigmata and some of the ventral internal longitudinal vessels are interrupted. The specimens from the Palau Is have a simple, bipartite male gland.

Perophora psammodes (Sluiter, 1895) from Indonesia is a sandy species. The gonad is different from the sandy *P. clavata* n.sp., and the zooid is very much smaller (see appendix, Sluiter 1895).

Perophora sagamiensis Tokioka, 1953a from Sagami Bay, Japan, has a stalked zooid, 4 rows of stigmata and very short musculature, the transverse bands being limited to those between the siphons. It otherwise resembles *P. multiclathrata*, having a similar colony and a large, undivided testis follicle.

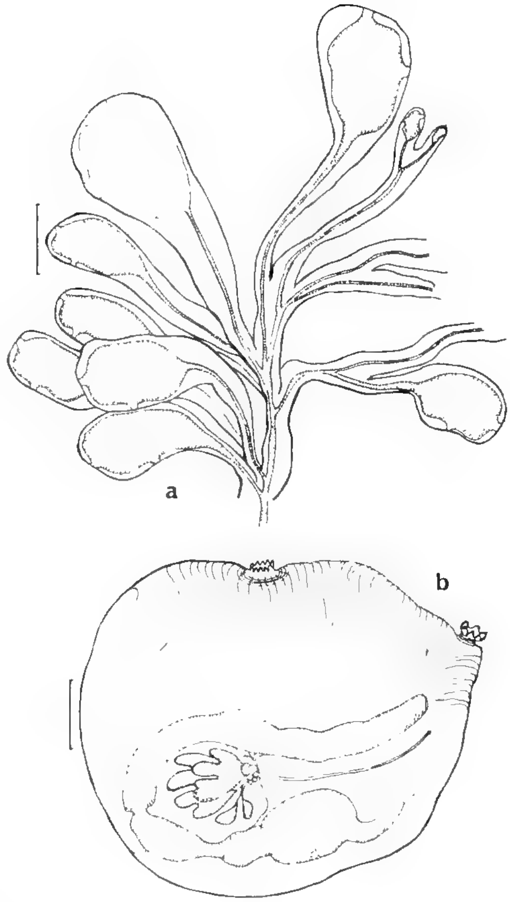


FIG. 43: *Perophora clavata* n.sp. (QM G12732) — **a**, colony; **b**, zooid. (Scales: **a**, 2.0 mm; **b**, 0.5 mm).

Perophora clavata n.sp.
(Fig. 43)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, 2 km off Ninety Mile Beach, 17m, strong currents to 1.5 knots, coll. J.E. Watson, 1977, holotype, QM G12732).

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of delicate, branching stalks, each terminal branch (about 5 mm long) gradually expanding to a zooid about 4 mm in diameter. The branches subdivide many times and the whole colony is long. Fragments up to 4 cm in length comprise the holotype. The diameter of the stalk becomes progressively narrower toward the terminal branches. Weed, hydroids and bryozoans are entangled in the branches, making the colony appear more compact than is actually the case. The test of both stalk and zooids is very delicate and flexible and is covered with sand throughout. The zooids are usually laterally flattened in the preserved material and were probably at least slightly flattened in life. Sessile apertures are in a sand-free median strip of test around the outer border of each zooid. The contracted branchial aperture has about 10 lobes and the atrial aperture has 6.

INTERNAL STRUCTURE: The body wall is extremely delicate. Short, fine muscle-bands extend a short distance down each side of the body from the branchial aperture. However, no longitudinal muscles were detected radiating from the atrial siphon. There are narrow circular sphincter muscles around each aperture. A band of transverse muscles crosses the ventral mid-line between the anterior end of the endostyle and the branchial aperture, with another band crossing the dorsal mid-line behind the atrial aperture. There are also transverse muscles crossing the mid-line between the apertures.

The branchial sac has 5 rows of 18 stigmata, crossed by 12 internal longitudinal vessels. The gut forms an almost horizontal loop across the posterior end of the body, the rectum curving anteriorly only very slightly. The oesophagus is narrow and curves around to the left before opening into a round to oval stomach. The duodenal region is short and wide. A mid-ventral constriction expands to an oval, posterior stomach, narrowing towards its junction with the abruptly expanded intestine. There are inconspicuous pouches in a ring around the proximal part of the intestine. A fine gastro-intestinal duct from the distal end of the stomach branches over the distal part of the intestine before its junction with the rectum.

The gonads consist of large male follicles divided into finger-like lobes that fan out ventrally from a point in the centre of the space enclosed by the gut loop. Vasa efferentia are short and join the vas deferens just dorsal to the distal end of the male follicles. A small (up to 5-egg) ovary is present over the proximal end of the vas deferens. The gonoducts both extend parallel to the gut for most of their length. Only the terminal part of the oviduct separates from the vas deferens, curving over into the right peribranchial cavity.

REMARKS: Superficially, the sandy zooids of this stalked species resemble those of *P. hutchisoni*, as do the colonies. But the present species is distinguished by its sandy and flexible rather than horny and rigid stalk, short and wide stomach, multiple and lobed male follicles, small ovary near the distal end of the male follicles, and transverse muscles each side of the endostyle. Its sandy zooids and five rows of stigmata distinguish it from *P. namei*.

The form of the male follicles suggests a closer relationship to *P. japonica* Oka or the Atlantic *P. viridis* Verrill.

Perophora hutchisoni Macdonald, 1859
(Fig. 44)

Perophora hutchisoni Macdonald, 1859b, p.377. Herdman, 1891, p.602; 1898, p.446. Hartmeyer and Michaelsen, 1928, p.269. Millar, 1966, p.366. (Not: Van Name, 1918, p.121, < *P. namei*).
Perophora boltenina Michaelsen, 1922, p.488. Millar, 1982a, p.16.
? *Tibiana ramosa* Lamarck, 1816, p.149.
? N.gen. n.sp. Bale, 1894, p.96.
? *Sacculina arenosa* Bale, 1919, p.333.
? *Saaba arenosa*: Stechow, 1923, p.92. Bale, 1926, p.13.
? *Saaba scandens* Trebilcock, 1928, p.2.

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, WAM 1252.83). Victoria (Bass Strait, QM G12732; Portland, QM GH94; Port Nepean, QM GH47).

PREVIOUSLY RECORDED: Western Australia (Fremantle, Albany — Macdonald 1859b, Hartmeyer and Michaelsen 1928). Victoria (Port Phillip Bay — Millar 1966). New Zealand (Michaelsen 1922, Millar 1982a).

The species has been recorded from 5 to 20 m on sandy bottoms subject to heavy surge and sand scour.

DESCRIPTION

EXTERNAL APPEARANCE: The preserved colony has a glassy, transparent, sand-encrusted test on the body of the laterally flattened zooids (5.0 mm diameter), which are attached to a central monaxial stalk by short stalks from their postero-ventral corner. The largest zooids are at the base of the colony. The apertures are sessile, the atrial aperture antero-dorsal and the branchial aperture terminal. There are 8 small triangular lobes around the border of the atrial aperture and 10 around the branchial aperture. The test of the central as well as lateral stalks is hard, horny and without sand. The lateral stalks attaching each zooid to the central axis are divided into 1 to 5 articulated nodes by thickened rings that protrude around quite delicate test at the base of each node and at the base of the zooid. These stalks appears to allow some movement of the zooids. The central monaxial stalk and lateral branches are relatively rigid basally, but become less horny toward the apex of the colony, where the number of nodes on the branches decreases. Some colonies have developing buds protruding from the central axial stem as well as at the apex of the colony. Developing zooids toward the base of the colony are supported by horny lateral branches with as many as 5 nodes. Thus, the number of nodes on the lateral branches appears to be related to their position on the central stem, rather than the growth stage of the zooid they support. Their points of origin appear to spiral around the axial stalk. Several colonies may be joined basally where a mass of stolons interwine, and are covered with sand to form a holdfast. The horny stalks resemble those of many hydroids, a feature that appears to be an example of convergent evolution.

INTERNAL STRUCTURE: The body wall is delicate, with fine circular muscles on the siphons. Longitudinal muscles from the siphons radiate from about half to one-third of the distance down each side of the body. Transverse muscles extend across the dorsal surface between the siphons and posterior to the atrial siphon. Bands of quite long transverse muscles are present along each side of the endostyle. A few transverse muscles also cross the mid-line anterior to the endostyle.

There are about 30 tentacles of three different sizes, the shorter ones being about half the length of the next longest group. The dorsal ganglion is long and narrow. The neural gland opens to a simple circular opening facing into the lumen of the pharynx. There is a wide, antero-posteriorly flattened, triangular process projecting back from immediately behind the opening. A pointed dorsal languet is associated with each transverse vessel.

Five rows of 25 to 35 long stigmata are crossed by up to 16 internal longitudinal vessels. There are 1.5 to 2 stigmata per mesh.

FIG. 44: *Perophora hutchisoni* (QM GH94) — a, bases of zooids and central axial stems showing horny jointed test; b, zooid; c, gut loop with mature male gonad. (Scales: a, 1.0 mm; b, 0.5 mm; c, 0.25 mm).

The gut forms a long loop across the posterior end of the body. The relatively short rectum extends anteriorly to form a wide obtuse angle with the descending limb of the intestine. The oesophageal opening is at the posterior end of the branchial sac and the narrow oesophagus curves around to the long, narrow and smooth stomach, which is marked only by a suture line in its posterior border. The stomach occupies up to one half of the ascending limb of the gut loop. There is a wide duodenal area, a short mid-intestine, and an elongate posterior-stomach that gradually narrows distally and expands abruptly into the intestine (before it curves around in the pole of the gut loop). The proximal end of the intestine has a ring of pouches in the gut wall. A gastro-intestinal connective extends from the distal end of the stomach to branch over the central portion of the descending limb of the intestine.

The male and female gonads are separated. The testis is a single, large, kidney-shaped follicle in the pole of the gut loop. The male duct extends from the centre of its postero-dorsal concave border and curves dorsally alongside the rectum. The small, oval ovary has up to 5 eggs. It is located just anterior to the oesophagus, quite close to the dorsal mid-line. Its relatively short duct crosses over into the right peribranchial cavity.

REMARKS: The species is readily distinguished by its sandy zooids, horny, articulated, narrow stalks and its monaxial colony. The large, undivided male follicle and dorsally situated ovary are also distinctive.

Perophora namei is distinguished by its naked zooids, non-jointed stalk, the radial arrangement of its numerous male follicles around the proximal end of the small ovary, and 4 rather than 5 rows of stigmata.

Previously thought to be hydroids, the following may be synonyms of the present species: *Tibiana ramosa* Lamarck, 1816 from New Holland; *Saaba arenosa* (Bale, 1919) from Port Phillip Bay, Victoria; and *Saaba scandens* Trebilcock, 1928 from Bay of Islands, New Zealand.

Perophora modificata n.sp.

(Fig. 45; Pl.IIg)

DISTRIBUTION

TYPE LOCALITY: Queensland (northern Great Barrier Reef, Deltaic Reef, Channel face, coll. E. Lovell, November 1979, holotype QM GH283).

FURTHER RECORDS: Queensland (Lizard I., paratypes QM GH327 GH3115; Deltaic Reef, paratype QM GH264; Lihou Reef, paratype QM GH2083). Philippines (QM GH468 GH441).

The species is taken at 17 to 27 m from channel faces or in lagoons. Photographs of what appear to be this species at the Swain Reefs suggest its range extends further south than the present records indicate.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of a basal mat of tangled stolons with upright, crowded zooids up to 1 cm high. The body of each zooid is more or less quadrate, the atrial aperture terminal at one of the four corners and the branchial aperture halfway along the oblique anterior end.

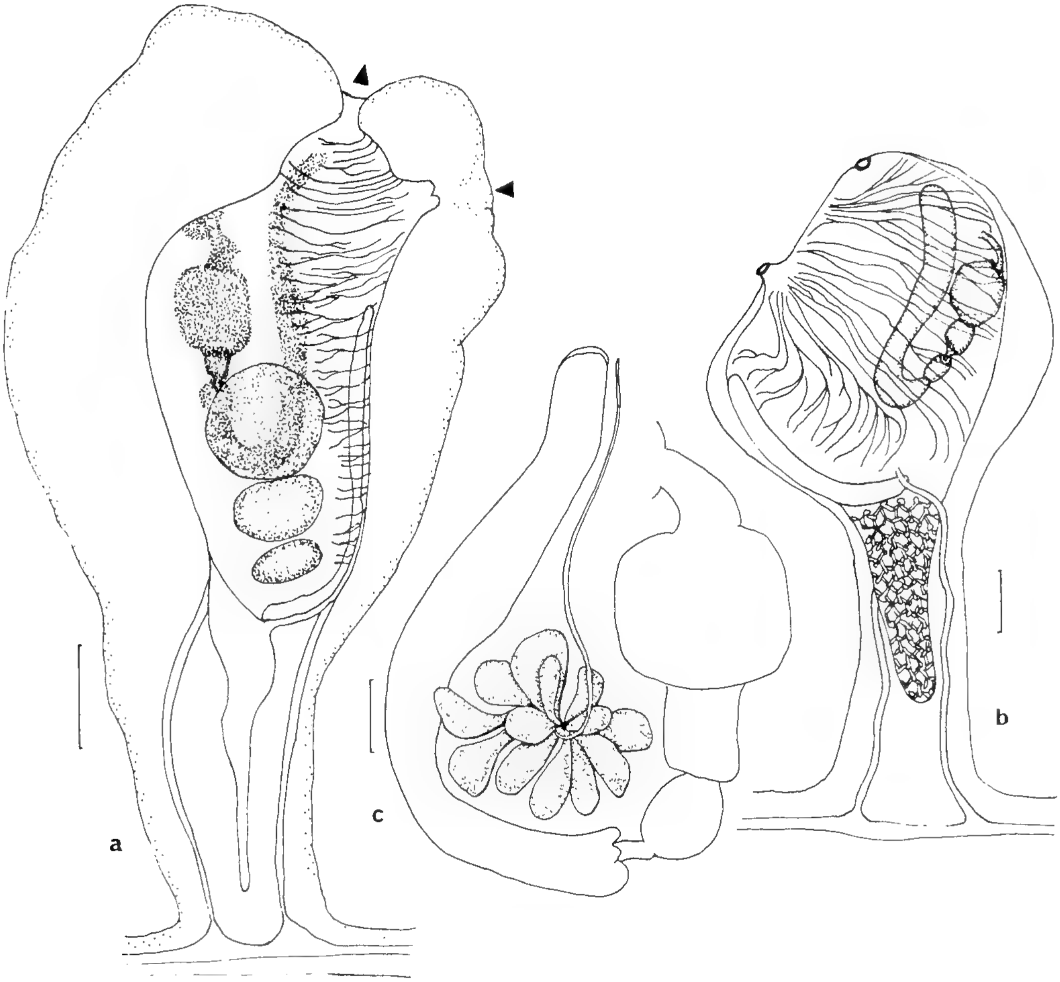


FIG. 45: *Perophora modificata* n.sp. — **a**, contracted zooid in thick test (QM GH283); **b**, zooid with muscle bands relaxed, showing vascular network on posterior extension (QM GH327); **c**, gut loop and testis (QM GH264). (Scales: **a**, **b**, 1.0 mm; **c**, 0.25 mm).

The apertures are sessile. The body narrows toward its postero-ventral corner, where there is a broad stalk about the same length as the rest of the body. The test is soft and completely colourless and transparent, the orange zooids being clearly seen through it. In contracted zooids the atrial aperture is often terminal and the branchial aperture is drawn down onto the side of the zooid. Around the borders of the apertures are strong sphincter muscles. There are 7 small, triangular atrial lobes, and about 10 very inconspicuous branchial lobes.

Living zooids are a clear, opaque yellow colour.

INTERNAL STRUCTURE: The most conspicuous feature of the body is a long, finger-like projection from the postero-ventral corner behind the endostyle down into the stalk. A complex network of vessels along the ventral border of the body continues over this extension. A pair of stolonic vessels from the body wall, one on each side of the central, blind, vascularised, posterior extension of the body, pass down through the stalk into the basal stolon. The body muscles are mainly longitudinal, radiating from the branchial aperture and extending across the median line between the apertures. The more ventral muscles curve obliquely to terminate in branches on each side of the endostyle. Others extend the whole length of the body. Circular muscles are present around the apertures. Contraction of these muscles draws in the antero-ventral and postero-dorsal corners of the body and shortens the antero-posterior axis of the body. The dorsal tubercle is a simple opening. A plain-edged dorsal lamina extends between antero-posteriorly flattened languets at the level of the transverse vessels. There is a long retropharyngeal groove from the oesophageal opening at the postero-dorsal corner of the body to the endostyle at the postero-ventral corner.

There are 4 rows of about 40 long stigmata on each side of the branchial sac. Papillae (12 to 15)on the transverse vessels support longitudinal vessels, although the latter are often interrupted. At the posterior end of the branchial sac, the longitudinal vessels end blindly as short extensions from the last row of papillae.

The gut forms a simple, only slightly curved, loop across the posterior end of the body. In contracted zooids it extends almost vertically, the plain-edged anal opening being just beneath the terminal atrial aperture. The oesophagus is short and narrow, and the stomach smooth and rounded. There is a fairly long duodenal area, a short, narrow mid-intestine, and an oval, posterior-stomach. The proximal part of the intestine forms the pole of the gut loop. A gastro-intestinal duct runs from the distal end of the stomach to the distal end of the intestine before it curves gently into the rectum.

The testis consists of a circle of about 10 long, clavate follicles in the loop of the gut, their narrow ends converging in the centre of the circle. Ovaries were not observed, but embryos are present in the distal end of the oviduct in the posterior end of the right peribranchial cavity of the holotype. They are at an early stage of development, although the tail is formed.

REMARKS: Although it has only 4 rows of stigmata, the species is the largest known member of this genus. The colonial habit is similar to that of *P. multiclathrata*, from which it is clearly distinguished by its size, the large numbers of stigmata in each row, the central vascularised extension of the body and the paired stolonic vessels. The orientation of the zooid on its stalk (with the atrial aperture terminal), its 4 rows of numerous stigmata and fan-shaped cluster of male follicles resemble *P. namei*. However, the latter species lacks the posterior extension of the body; and has long, horny zooid and axial stalks and fewer and finer muscles than *P. modificata*.

Perophora multiclathrata (Sluiter, 1904)
(Fig. 46)

Ecteinascidia multiclathrata Sluiter, 1904, p.12.
Perophora multiclathrata: Nishikawa, 1984, p.123.
Ecteinascidia formosana Oka, 1931, p.173.
Perophora formosana: Tokioka, 1953a, p.218; 1967a, p.136.
Perophora bermudensis Berrill, 1932, p.78; 1935, p.358. Plough and Jones, 1937, p.100; 1940, p.51. Pérès, 1949, p.190. Tokioka, 1950, p.125. Kott, 1952, p.315; 1964, p.147, 1981, p.195. Plante and Vasseur, 1966, p.149. Vasseur, 1969, p.922.
Perophora orientalis Arnback, 1935, p.6.
?*Perophora viridis* Hartmeyer and Michaelsen, 1928, var. hornelli p.273.

DISTRIBUTION

NEW RECORDS: Norfolk I. (QM GH2055). Queensland (Noosa Heads, QM G4986; Hervey Bay; Heron I., QM GH2255 GH3026-7; Wistari Reef, QM GH2243; Northwest Reef, QM GH2244; Green I., QM G12500)

PREVIOUSLY RECORDED: ?Western Australia (Shark Bay, Cockburn Sound, Bunbury — Hartmeyer and Michaelsen 1928). New South Wales (Port Hacking — Kott 1952). Queensland (Moreton Bay — Kott 1964). Palau Is (Tokioka 1950 1967a). Truk I. (Nishikawa 1984). Wake I. (Tokioka 1967a). Japan (Oka 1931, Arnback 1935, Tokioka 1953a). Malagasy (Plante and Vasseur 1966, Vasseur 1969). Tropical eastern Atlantic

(Pérès 1949). Tropical western Atlantic (Berrill 1932 1935, Plough and Jones 1937 1940, Van Name 1945).

Specimens have been taken at shallow depths on rubble and shells, and epizooic on other ascidians including *Ascidia* spp. and *Ecteinascidia* spp.

DESCRIPTION

EXTERNAL APPEARANCE: The species is very small and inconspicuous. Small, upright zooids are attached to fine, creeping basal stolons by very short stalks from the postero-ventral corner of the body. The zooids are spherical to pear-shaped, narrowing toward their stalk. There is a terminal branchial aperture; the atrial aperture is antero-dorsal. The border of each aperture is divided into 7 small lobes. Zooids are seldom more than 3 mm in diameter and the apertures are sessile. The test is very thin indeed and quite transparent, without foreign particles attached. In life, zooids appear as delicate yellow, shining, transparent bubbles.

INTERNAL STRUCTURE: The body wall is very thin, with fine transverse muscle-bands across the dorsal mid-line between the siphons and posterior to the atrial siphon. Circular sphincter muscles surround the apertures. There are short branchial tentacles. The neural gland has a simple, circular opening. Dorsal languets are present in the mid-line between the rows of stigmata.

There are 12 to 20 stigmata in each of 5 rows. Internal longitudinal vessels supported on upright papillae cross the stigmata at intervals of one to one-and-a-half stigmata.

The gut forms a straight loop in the postero-dorsal corner of the body, the short rectum curving anteriorly to form an obtuse angle with it. The narrow oesophagus curves around to open into the long, narrow stomach, which is more than half the length of the gut loop. There is a short, wide duodenal area, a short, narrow mid-intestine and an oval posterior-stomach. The intestine abruptly expands from the narrow end of the posterior-stomach in the pole of the loop.

The testis is a single, compact gland in the gut loop, with a small ovary at its distal end. Initially, the testis is comma-shaped, narrowing to the vas deferens from the posterior side of the ventral half of the gland. The duct curves dorsally and accompanies the rectum toward the base of the atrial siphon. With development, the gland appears to expand backwards into the pole of the gut loop, and the vas deferens originates about one-third of the distance from its dorsal border on its posterior side. The oviduct separates from the male duct to cross into the right peribranchial cavity.

FIG. 46: *Perophora multiclathrata* (QM GH2055) — a, zooid; b, c, gut loop from outside and inside the body respectively, showing different conditions of the testis. (Scales: a, 0.25 mm; b, c, 0.1 mm).

REMARKS: The species is very simplified. Its characteristics are its delicate, transparent body; transverse musculature between the apertures and posterior to the atrial aperture; 5 rows of up to 15 stigmata; compact, undivided male gonad; and colonial habit with zooids on fine, creeping basal stolons. The 5 rows of stigmata and the single testis follicle resemble those of *P. hutchisoni* which, however, has more numerous stigmata in each row, horny jointed stalks and a vertical habit. *Perophora sagamiensis* has similar zooids and habit, but only 4 rows of stigmata.

Hartmeyer and Michaelsen (1928) found variable numbers of rows of stigmata (up to 8) in specimens they assigned to *P. viridis* var. hornelli. The present species differs from *P. viridis* in having a single, undivided male gonad. The gonads of the Western Australian specimens were not observed. In view of the similarity in zooid size, form and colony habit, it is possible that *P. viridis* var. hornelli: Hartmeyer and Michaelsen, 1928 is conspecific with *P. multiclathrata*.

Perophora hornelli Herdman, 1906 and *P. listeri* Tokioka, 1950 (see Tokioka 1952) are also closely related to the present species, but they never have more than 4 rows of stigmata, and their male gland may be different.

Perophora multistigmata Kott, 1952
(Fig. 47a)

Perophora multistigmata Kott, 1952, p.313.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Queensland (Moreton Bay — holotype AM U3905, paratypes AM U3969 Kott 1952).

DESCRIPTION

EXTERNAL APPEARANCE: The zooids are fixed by the posterior end of the body to a tangled mat of basal stolons. They are almost sessile, though the constriction between the body and the basal stolon is not long enough to be termed a stalk. The zooid body is almost spherical, but the apertures are on relatively long, protruding siphons, the branchial siphon terminal and the atrial siphon antero-dorsal. There are approximately 14 small branchial lobes bordering the aperture, and 10 atrial lobes. The test is thin, flexible and completely transparent. It is firm on the basal stolon. A blood vessel from the posterior end of the endostyle joins the main vessel in the basal stolon. An adjacent vessel branches off the main stolonic vessel and enters the test of the zooid.

INTERNAL STRUCTURE: There are longitudinal muscles on the long siphons extending about one-third of the distance down the body wall. External circular muscles extend the length of the siphons. Groups of transverse bands lie across the dorsal mid-line between the siphons and posterior to the atrial siphon and extend about halfway down the body on each side. The dorsal tubercle is a swollen cushion, filling the peritubercular area with an almost circular, ciliated aperture. About 60 crowded branchial tentacles of two principal sizes alternate with rudimentary tentacles.

There are 8 rows of 16 long, oval stigmata and about 12 fine longitudinal vessels on each side.

The gut is voluminous, forming a loop across the posterior half of the body. The short rectum forms a secondary loop with the descending limb of the intestine. The oesophagus is relatively long and narrow, and the stomach is smooth and oval.

The gonad, enclosed in the primary gut loop, consists of a single, long, male follicle subdivided to form a fan of 3 to 5 long, finger-like, male lobes, each rounded proximally (ventrally) and narrowing to the vas deferens distally just beneath a small ovary. Tailed embryos are present in the right peribranchial cavity. They have an ocellus and an otolith, but no other organs were discerned. The larval trunk is 0.5 mm long.

REMARKS: The species is readily distinguished from others by its long siphons, as well as its 8 rows of stigmata. Its gonads resemble those of *P. clavata* and the Atlantic species *P. viridis*.

Perophora namei Hartmeyer and Michaelsen, 1928
(Figs. 47 b,c)

Perophora hutchisoni: Van Name, 1918, p.123.
Perophora namei Hartmeyer and Michaelsen, 1928, p.270. Millar, 1975, p.267.

DISTRIBUTION

NEW RECORDS: Coral Sea (Lihou Reefs, QM GH3425).

PREVIOUSLY RECORDED: Philippines (Van Name 1918, Millar 1975).

The new records are from 26 m, at the base of the dropoff on the front reef, near the sandy bottom. Colonies were quite common growing on vertical surfaces of dead coral.

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are arranged along the distal half of a fine, vertical, horny, central stalk, about 8 cm long and 1 mm diameter. The basal half of the central stalk is free of zooids, and becomes slightly thicker and more horny toward its point of attachment. There are only very faint joints in the horny test of the central stalk, usually where zooid stems branch off it. The stem of each zooid, connecting it to the central stalk, is also horny, changing abruptly into soft thin test where it joins the zooid (at the base of the endostyle). There is a single small terminal zooid on the free end of the central stalk. Zooids gradually increase in size and there is also an increase in the length of their stems toward the base of the colony, so that each colony has a superficial resemblance to a pine-tree. Zooids are laterally flattened and up to 4.0 mm long, excluding the stem, which is up to 5.0 mm long. The zooids are slightly triangular, the posterior border, more or less in line with the stem, forming the long side of the triangle. The atrial aperture is terminal, about halfway along the outer free end of the zooid and directed out and away from the colony. The branchial aperture is always on the lower side of the zooid, directed down toward the substrate. The ventral border of the body slopes in toward the base of the stem to form an acute angle with the posterior border. The apertures are both sessile. They do not appear to be lobed, although the rim is gathered when the aperture is closed. The test on the zooids is very thin and completely transparent. Living specimens are pale yellow.

INTERNAL STRUCTURE: The body wall is very delicate and transparent and the body organs are clearly seen through it. The postero-ventral end of

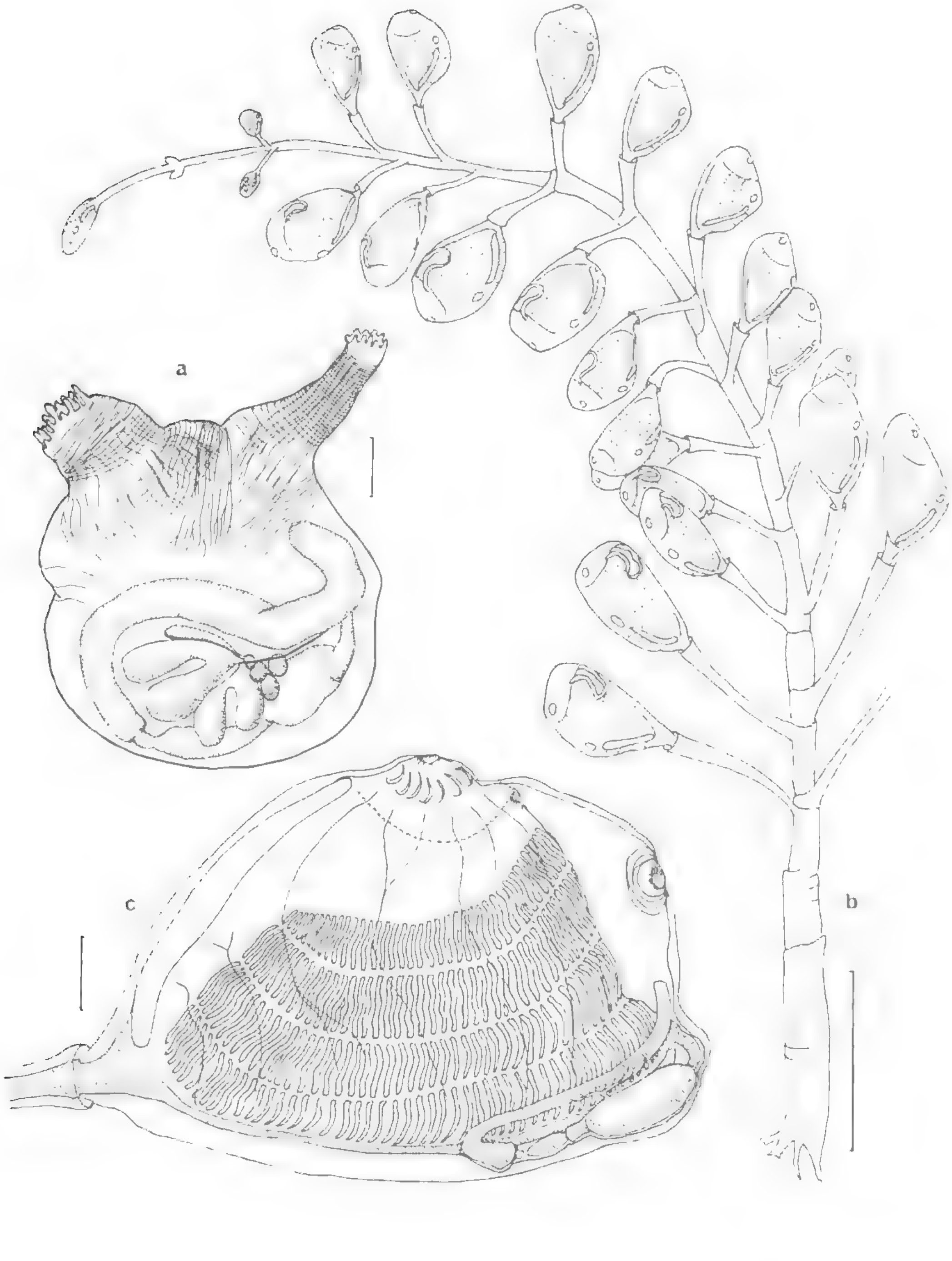


FIG. 47: *Perophora multistigmata* (AM U3969) — a body removed from test. *Perophora namei* (QM GH3425) — b, colony; c, zooid. (Scale: a, 0.2 mm; b, 5.0 mm; c, 0.5 mm).

the body, at the base of the endostyle, projects out into a long vascular stolon that continues through the stem of the zooid and into the axial stalk. There are a few circular muscles around each aperture. Longitudinal muscles are few and very fine: on each side, 2 cross the postero-ventral corner of the body and 5 extend from around the branchial aperture to the level of the gut loop. There are 12 fine branchial tentacles. About one-fifth of the length of pharynx behind a ring of minute papillae (apparently representing the prepharyngeal groove) is unperforated. The dorsal lamina is an inconspicuous fold of tissue, barely interrupting the rows of stigmata.

On each side, there are 4 rows of about 40 long stigmata in the perforated part of the branchial sac and 15 fine internal longitudinal branchial vessels, supported by conspicuous triangular papillae on the transverse vessels. Some short, interstitial stigmata are occasionally wedged between the posterior ends of the stigmata. A long retropharyngeal groove extends across the posterior end of the zooid.

The gut forms a narrow, straight loop that extends only halfway along the posterior end of the body to the left of the retropharyngeal groove. The stomach is long and oval, occupying about half of the ascending limb of the loop. There is a gastro-intestinal duct from the distal third of the stomach, breaking into branches over the distal end of the intestine before it curves up into the very short rectum.

Gonads are not mature in these specimens. Van Name (1918) observed immature pear-shaped testis follices in the gut loop, with vasa efferentia converging to the vas deferens beneath the small ovary.

REMARKS: The species resembles *P. hutchisoni* in its colony form and horny stalks. However, joints in the stalk are not as well developed as in *P. hutchisoni* and the zooids are naked rather than sandy. Further, although both species have large numbers of stigmata in each row, the present species has only 4 rows (*P. hutchisoni* has 5). The naked zooids, and their orientation on their stems, most closely resemble those of *P. modificata* n.sp. However, they are smaller, more delicate and have fewer and finer muscle bands than the zooids of the latter species. *Perophora namei* is further distinguished by its colony form, the single (rather than paired) stolonic vessel that joins with the common vessel in the axial stalk, and the absence of the posterior, vascularised projection of the body that is characteristic of *P. modificata*. Macroscopically, the delicate zooids most resemble those of *P. multiclathrata* but closer examination shows the many characters that separate these species.

Order PLEUROGONA Perrier, 1898

Ascidians in which the atrial cavity develops from a single median dorsal invagination. The pharyngeal wall is usually folded along its length, thus vastly increasing the filtering area over that of enterogonid ascidians. The gonads vary in number, but are always present in the body wall, usually on both sides of the body. Branchial folds are lost and gonads are absent from one or the other side of the body only when size reduction or specialisation results in simplification of the organs (as in colonial Styelidae and in small, solitary interstitial species). On the left side where the gut is located the gonads may be enclosed by its loop or anterior to it, but they are never posterior to the gut.

Suborder STOLIDOBRANCHIA Lahille, 1887

The test is usually tough and often opaque and leathery. Epibionts are frequently present on the surface, and the test often has sand and other foreign particles embedded in or adhering to it. The body is not divided. The heart, gut and gonads are in the body wall at the side of the large branchial sac, which occupies the whole length of the animal. The body wall musculature is well developed. Internal longitudinal branchial vessels are invariably present and usually they are numerous. They arise directly from the branchial wall and are not supported above it by longitudinal papillae as they are in phlebobranch ascidians.

Species are generally large and solitary. However, in two subfamilies of the Styelidae (Polyzoinae and Botryllinae), vegetative reproduction occurs and colonies are formed. The individual zooids in these subfamilies are invariably small, and often simplified.

With the exception of the vegetatively reproducing subfamilies and some *Polycarpa* spp. and *Molgula* spp., which are viviparous, members of this suborder are oviparous, fertilisation being external. Larvae are small and relatively primitive; adult organs are not well developed before metamorphosis. Larval adhesive organs are unstalked and arranged in a triangle at the anterior end of the trunk.

In Australian waters, all families except Hexacrobylidae are well represented. The genera have different biogeographical characteristics: *Polycarpa* and *Cnemidocarpa* (Styelinae), Polyzoinae and *Microcosmus* (Pyuridae) generally having tropical affinities, while *Pyura* (Pyuridae) is usually more closely related to the temperate and Sub-antarctic fauna. The affinities of the Australian molgulid fauna appear to be evenly divided between tropical and temperate waters (see Biogeography).

KEY TO THE FAMILIES OF STOLIDOBRANCHIA
(* not recorded from Australia)

1. Tentacles unbranched (STYELIDAE) 2
   Tentacles branched 4
2. Individuals solitary; 4 distinct branchial folds per side .... STYELINAE
   Individuals colonial; branchial folds often reduced or absent 3
3. Zooids do not form systems ..... POLYZOINAE
   Zooids do form systems .... BOTRYLLINAE
4. Stigmata straight, no kidney .... PYURIDAE
   Stigmata not straight; kidney present 5
5. Stigmata coil .... MOLGULIDAE
   Stigmata absent .... HEXACROBYLIDAE*

Family STYELIDAE Sluiter, 1895

Stolidobranch ascidians with simple branchial tentacles, usually 4 branchial folds, and a simple dorsal lamina not divided into languets. The pyloric region of the gut is expanded into a stomach, the wall of which forms parallel longitudinal folds. There is often a gastric caecum, but no liver diverticulum. The gonads, of which there are usually more than one on each side of the body very considerably in form.

Subfamily STYELINAE Herdman, 1881

Solitary Styelidae that do not reproduce vegetatively. The body wall musculature usually consists of an external coat of circular muscles and inner longitudinal bands extending parallel to one another from the apertures to the posterior end of the body.

Minute curved scales, each overlying an oval granular body, occur in the outer part of the siphon lining of many species of *Styela* and *Cnemidocarpa* (*Styela canopus*, *S. plicata*, *Cnemidocarpa areolata*, *C. floccosa*, *C. lobata*, *C. pedata*, and *C. radicosa*). *Cnemidocarpa intestinata* n.sp. and *Polycarpa olitoria* have sharply pointed, conical spines in the siphon lining. All the genera of this subfamily are closely related. They are separated by differences in the length of the ovarian tube, in the position of the male follicles in relation to it and in the number of gonads. However, there is a wide intrageneric and sometimes intraspecific range in the condition of the gonads. The gonads also vary with the age and maturity of the individual.

Throughout the subfamily, there is progressive loss of the larval ocellus, decreasing the larva's sensitivity to light and associated with open sea-floor habitats and absence of shaded settlement sites (Berrill 1955). Most species are oviparous but in *Polycarpa* there are several viviparous species.

The genera not recorded from Australia are *Pelonaia* Goodsir and Forbes, 1841 (monotypic) and *Dendrodoa* MacLeay, 1925 (polytypic), both from northern temperate and Arctic waters; *Azygocarpa* Oka, 1932b (monotypic) from Japan; *Bathyoncus* Herdman, 1882 (polytypic), *Hemistyela* Millar, 1955b (monotypic) and *Dicarpa* Millar, 1955b (polytypic) from abyssal depths; *Minostyela* Kott, 1969a (monotypic) from the Antarctic; and *Dextrocarpa* Millar, 1955a (monotypic) from South Africa

KEY TO THE GENERA OF STYELINAE
(* not recorded from Australia)

1. Gonads on both sides of body 2
   Gonads only on right side of body 10
2. Pharynx with stigmata 3
   Pharynx without stigmata .... *Bathyoncus* *
3. Testis follicles more than a single pair in each gonad 4
   Testis follicles not more than a single pair in each gonad 9
4. Branchial folds present 5
   Branchial folds not present .... *Pelonaia**
5. Gonoducts open near atrial aperture 6
   Gonoducts open distant from atrial aperture 7
6. Testis lobes projecting away from ovary .... *Styela*
   Testis lobes not projecting away from ovary .... *Cnemidocarpa*
7. Gonads branched .... *Asterocarpa*
   Gonads never branched 8
8. Gonads more than one on each side .... *Polycarpa*
   Gonads not more than one on each side .... *Hemistyela**
9. Gonads more than one on each side .... *Monandrocarpa*
   Gonads never more than one on each side .... *Minostyela**
10. Branchial folds not present .... *Dicarpa* *
    Branchial folds present 11
11. Male and female components of gonad separate .... *Dextrocarpa**

Male and female components of gonad not separate 12
12. One gonad only present 13
More than one gonad present ...*Azygocarpa**
13. Gonad elongate or branched..... *Dendrodoa**
Gonad spherical ....*Podostyela**

Genus **Styela** Fleming, 1822

Type species: *Cynthia canopus* Savigny, 1816

The genus is characterised by the position of the male follicles lying on the body wall around, but not in close association with, the ovarian tube and projecting separately into the atrial cavity. Only occasional male follicles with short vasa efferentia are found closely applied to the sides or the mesial surface of the ovary. However, they never occur beneath the ovary.

The gonads of *Styela*, with an elongate ovarian tube and rather dispersed male follicles separated from the ovary, bear a closer relationship (than those of other genera of the Stolidobranchia) to the gonads found in the Phlebobranchia. A further indication that *Styela* is the least evolved of the styelid genera exists in the tadpole larvae. In *Styela* spp. the ocellus is reduced to a single pigmented cell, while in *Polycarpa* spp. this organ is completely lost (Berrill 1950).

Records from Australia are confined to the pantropical species *Styela canopus* and *S. plicata* and the Japanese *S. clava. Styela clava* is known to have been transported around the world on ships' hulls and to have been introduced to Australia in this way (Holmes 1976). *Styela plicata* is also known to be a common fouling organism. Its records in the Indo-West Pacific are from continental rather than island locations and it may have been dispersed in a similar way. *Styela canopus* is the only one of the three species that is commonly encountered in the Indo-West Pacific. All three demonstrate the variability that is to be expected with species of extensive geographic range. The genus is more diverse in Antarctic, Arctic and cool temperate seas (Kott 1969a; Van Name 1945) than it is in Australia and the Indo-West Pacific.

All species of the genus appear to be oviparous. There are no morphological arrangements for brooding larvae and none have been observed within the body of adult individuals. Oviparity, together with degeneration of the ocellus and probably a consequent reduction in the larval capacity for site selection, may explain why the species occurring in Australia are found in shallow-water, protected habitats, where gametes are not exposed to dispersal and dilution. The mechanisms for gene flow in these wide ranging species are not known. It is possible that Australian populations of introduced species are now isolated from those in the northern hemisphere.

Key to the species to *Styela* Recorded from Australia

1. Gut loop simple and vertical........... *S. clava*
Gut loop deeply curved 2
2. Narrow branchial folds; 2 gonads on the right .... *S. canopus*
Wide branchial folds; 4–6 gonads on the right .... *S. plicata*

In addition to *Styela bicolor* Sluiter (questionably a synonym of *S. canopus*), *S. perforata* Sluiter from Indonesia is the only other species of this genus recorded from the region immediately to the north of Australia and not included in the synonymy of either *S. canopus* or *S. plicata*.

Styela canopus Savigny, 1816
(Fig. 48)

Styela canopus Savigny, 1816, pp.45, 154. Michaelsen, 1898, f. typica p.367; 1919, p.66. Herdman, 1891, p.581. Kott, 1957, p.144. Millar, 1975, p.304. Kott and Goodbody, 1982, p534.
Tethyum canopus: Hartmeyer, 1915b, p.397.
Styela partita Stimpson, 1852, p.231. Van Name, 1945, with synonymy and Atlantic records p.290. Tokioka, 1951b, p.175; 1953a, p.262; 1953b, p.16; 1954a, p.262; 1955a, p.214; 1960, p.213; 1961, p.128; 1962, p.17; 1972, p.398. Tokioka and Nishikawa, 1975, p.335. Millar, 1960b, p.115; 1975, p.302. Vasseur, 1967a, p.117; 1967b, p.139. Rho, 1975, p.139.
Styela orbicularis Sluiter, 1904, p.71. Kott, 1964, p.139.
Styela marquesana Michaelsen, 1918, p.27.
Styela barbaris Kott, 1952, p.224.
Styela rectangularis Kott, 1952, p.224.
?*Styela bicolor* Sluiter, 1887, p.262; 1890, p.333; 1904, p.60. Hartmeyer, 1919, p.32. ?Millar, 1975, p.306.

Distribution

New Records: Western Australia (Broome, WAM 940.83; Cockburn Sound, WAM 980.83). Queensland (Heron I., QM GH2722; Murray I. QM G9830; Lizard I. QM GH559; Cairns (epizooic on *M. helleri*), QM GH800; Townsville Harbour, QM GH2090; Abbot Point, QM GH720; Hervey Bay, QM G9383–5).

Previously Recorded: Western Australia (Fremantle Harbour — Kott 1952). Queensland (Moreton Bay — Kott 1952 1964, Millar 1975). Coral Sea (Millar 1975). New Caledonia (Vasseur 1967b).

The species has also been recorded from shallow tropical and temperate waters in the Atlantic Ocean and in the Mediterranean (see Kott and Goodbody 1982). The most southerly record is from Ascension Island (Millar 1960b). In the northern hemisphere it occurs at Massachusetts Bay, in the Channel Islands and the

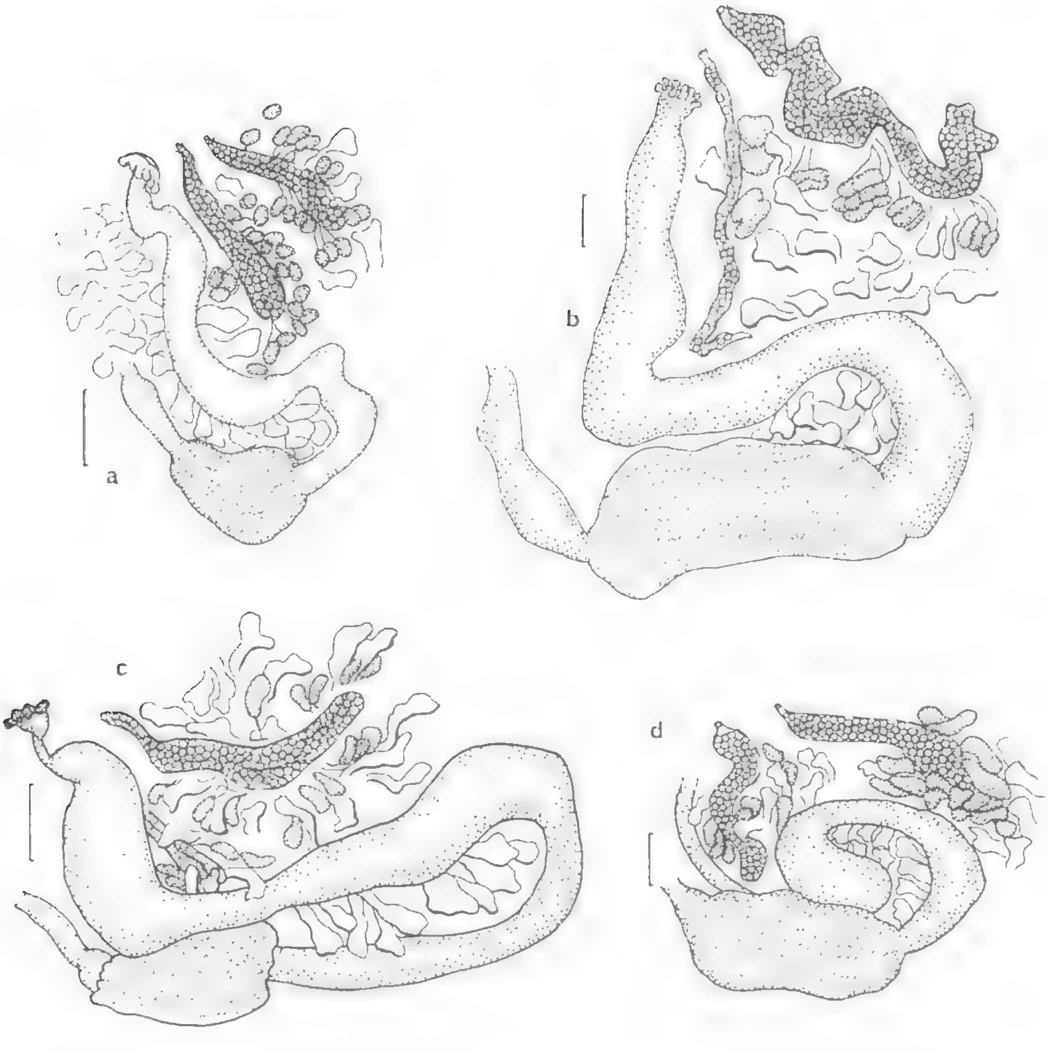


FIG. 48: *Styela canopus* — **a** – **d**, gut and gonads showing variations (QM GH720, G9383, G9830, GH290). (Scales: **a**, **c**, **d**, 2.0 mm; **b**, 1.0 mm).

western coast of France (see Van Name 1945), and from Korea and Sado I. in the Sea of Japan (see Tokioka and Nishikawa 1975). It is the only one of the three species of the genus *Styela* recorded from Australia that appears to be indigenous to the Indo-West Pacific region, having been recorded from Indonesia (Sluiter 1887, 1890, 1904) and the western Indian Ocean (Michaelsen 1918, Vasseur 1967a), and from the Persian Gulf, the Gulf of Siam and the Philippines (Millar 1975) and Hong Kong (Kott and Goodbody 1982).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright and sessile, 1 to 2 cm broad and 1 to 2 cm high. They often occur in aggregates. The test is leathery and pinkish brown. It is usually very tough, although occasionally it is translucent and gelatinous (specimens from Hervey Bay). The colour is darker anteriorly, fading slightly toward the posterior end of the body. In preservative the test fades to a beige-white colour. Sometimes the test is covered with mud and epizoic worm tubes, but at other times is naked. There are transverse wrinkles and tuberculations anteriorly but the test is more regular posteriorly. Sometimes there are root-like extensions and hairs posteriorly to which sand, mud or other particles adhere. The siphons are very short, warty and fairly close together on the upper surface. The lobes around each aperture are thickened to form external rounded ridges. A variable number of white stripes edged with brown run down the external surface of the lobes of both siphons. These very fine stripes are sometimes obscured by irregularities and protruberances of the tough, leathery test that are often present around the apertures. They are more numerous in larger specimens. The siphons are lined with small (up to 0.03 mm long, 0.01 mm wide at the top) fan-shaped, thin, curved scales that continue externally over the striped area of the siphons.

INTERNAL STRUCTURE: The muscles are predominantly longitudinal, extending down the body parallel to one another. They are not crowded and the internal organs are easily seen through the body wall. The dorsal tubercle has a C- or U-shaped opening and is always relatively simple.

The narrow branchial folds are reduced to low ridges as the individuals become older. There are wide interspaces. The internal longitudinal vessels are very crowded, especially on the folds: a 1 cm long individual has up to 12 on the folds and 4 or 5 in the interspace; a specimen of 6 cm from the Red Sea has 14 to 16 between folds and about 20 on the folds. There are only 2 or 3 stigmata per mesh.

The oesophagus is long and extends across the posterior end of the body to an elongate stomach. The gut loop generally lies across the postero-ventral end of the body. The stomach has 18 to 30 distinct internal glandular folds. The primary loop of the gut is very narrow. Its descending limb curves into the long rectum, which lies parallel and close to the oesophagus before extending anteriorly to open in an 8-lobed anus at the base of the atrial siphon. The anal lobes are rounded and shallow. The length and the curve of the gut loop is variable; the stomach may occupy from half to three-quarters of the ascending limb of the primary loop. The secondary loop is rather wide.

There are 2 gonads on the right and 2 on the left side of the body. The ovarian tubes are thick, cylindrical and often curved or undulating. The posterior gonad on the left curves down into the gut loop, while the anterior one extends across the top of the gut loop. The central ovary is thick and cylindrical. Testis follicles are on the body wall, usually confined to the region around the proximal end of the ovary. They are branched, and often broader than their length. Their ducts join into a vas deferens that extends along the mesial surface of the ovary to open with the short oviduct at the base of the atrial siphon. Upright endocarps, enclosed in the gut loop and also present on the body wall between the gonads, are pointed or rounded on their free ends and either cylindrical in section, flattened, or concave on one side.

REMARKS: The flattened siphonal scales are similar to those of other species of the Styelinae. However, their continuation onto the outer surface of the apertures, and the brownish stripes that also extend from around the outside of the apertures and into the siphonal lining, are characteristic of this species. The two gonads on each side of the body and the delicate body musculature confined to longitudinal bands appear to be distinctive characters. The gut loop is generally shorter than that of *S. plicata* and is not so deeply curved. Kott and Goodbody (1982) and Tokioka and Nishikawa (1975) have discussed the variability of the stomach length, number of stomach folds and numbers of branchial vessels in this widely ranging species.

Styela marquesana Michaelsen, 1918 from Mozambique apparently has identical siphonal scales and a similar branchial sac, gut and gonads. The stomach of Michaelsen's specimen is long, occupying almost the whole of the ascending limb of the gut loop, resembling that of specimens of *S. canopus* taken from Queensland

(> *S. rectangularis* Kott, 1952 and specimens from Hervey Bay, QM G9383-5).

Styela bicolor Sluiter resembles the present species in its delicate body musculature, gut, gonads, endocarps and small number of stigmata in branchial meshes in the central interspace. Specimens from Hervey Bay were the same elongate shape as Millar's (1975) specimens in which the anterior, transversely ridged test falls within the range of variability of the present species. The characteristic inconspicuous stripes on the siphons and the siphonal scales may have been overlooked in specimens assigned to *S. bicolor*.

Styela clava Herdman, 1881
(Fig. 49)

Styela clava Herdman, 1881a, p.70; 1882, p.158. Drasche, 1884, p.379. Traustedt, 1885, p.45. Hartmeyer, 1906, p.15. Oka, 1935, p.444. Tokioka, 1951a, p.16; 1951b, p.180; 1953a, p.270; 1953b, p.17; 1954b, p.90; 1955a, p.212; 1959a, p.231; 1959b, p.462; 1967a, p.191. Millar, 1960a, p.509; 1975, p.302. Houghton and Millar, 1960, p.862. Stubbings and Houghton, 1964, p.272. Coughlan, 1969, p.192. Monniot, 1970b, p.152. Guiry and Guiry, 1973, p.127. Holmes, 1976, p.115.
Bostryorchis clava: Redikorzev, 1916, p.219.
Styela mammiculata Carlisle, 1954, p.329.

DISTRIBUTION

NEW RECORDS: Victoria (Station Pier, Port Phillip Bay, QM G10053).

PREVIOUSLY RECORDED: Victoria (Hobsons Bay — Holmes 1976), Japan (Herdman 1881a 1882, Drasche 1884, Traustedt 1885, Hartmeyer 1906, Oka 1935, Tokioka 1951a,b 1953a,b 1954b 1955a 1959a,b, Millar 1975). English Channel (Carlisle 1954, Millar 1960a, Houghton and Millar 1960, Stubbings and Houghton 1964, Monniot 1970, Guiry and Guiry 1973, Holmes 1976). Irish Sea (Loughlan 1969, Guiry and Guiry 1973).

Styela clava is a north-western Pacific species that has apparently readily adapted to protected habitats in European temperate waters and in Port Phillip Bay, Victoria. Although it has not been recorded from tropical waters, populations of the species have been transported on ship's hulls through the tropics from the northern to the southern hemisphere (Holmes 1976). Records in Australia are confined to Port Phillip Bay.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are stalked or sessile. The body is more or less cylindrical, up to 6 cm long, tapering posteriorly to the stalk, which is variable in length, but seldom longer than the body. Both apertures are anterior and are on short siphons. The branchial siphon is slightly more conspicuous than the atrial and may be oriented laterally. The siphons are at the antero-dorsal and antero-ventral corners of the body respectively. The external test has rounded and sometimes conical swellings that are less crowded, or even absent, from the posterior half of the body where there are rounded, longitudinal ridges. The surface of the stalk is creased. The test is leathery and brownish white, yellowish brown or reddish brown.

INTERNAL STRUCTURE: The body wall has moderate to delicate musculature. The dorsal tubercle has a relatively simple U-shaped slit with both horns turned in or out, and sometimes some short branches from the primary slit (Millar 1960a). The 4 branchial folds are curved in the posterior half of the body. There are from 12 to 44 internal longitudinal vessels on the branchial folds and from 4 to 20 in the interspace. The oesophagus opens from the pharynx about halfway down the branchial sac. The gut forms a simple vertical loop. The elliptical stomach, with conspicuous longitudinal folds, occupies most of the ascending limb of the gut loop. The intestine and rectum form the descending (or distal) limb of the loop. The anal border is lobed, and opens at the base of the atrial siphon.

The long gonads, lie parallel to one another and to the gut loop along the length of the body. They consist of a central ovarian tube with crowded testis follicles on the body wall along each side of the ovary. The number of gonads is very variable, from 2 to 4 on the left and from 4 to 8 on the right. Most often the gonads are more numerous on the right than on the left side of the body; however, there are records of populations with 2 (Drasche 1884, Tokioka 1959b) and 3 or 4 (Traustedt 1885) gonads on each side of the body. Small endocarps are crowded on the body wall between the gonads and gut and may also be present on the body wall overlying the rectum.

REMARKS: Tokioka (1959b) has designated specimens from the Inland Sea of Japan with 2 gonads on each side of the body as a separate variety (*S. clava* var. symmetrica). Although this condition of the gonad is apparently a characteristic of this population, it is unlikely that subspecific rank could be justified in view of the variability in the number of gonads that has been observed in the species.

The species is distinguished by its long body, simple vertical gut loop and compact groups of male follicles. The endocarps fringing the intestine are similar to those occurring in *S. plicata*.

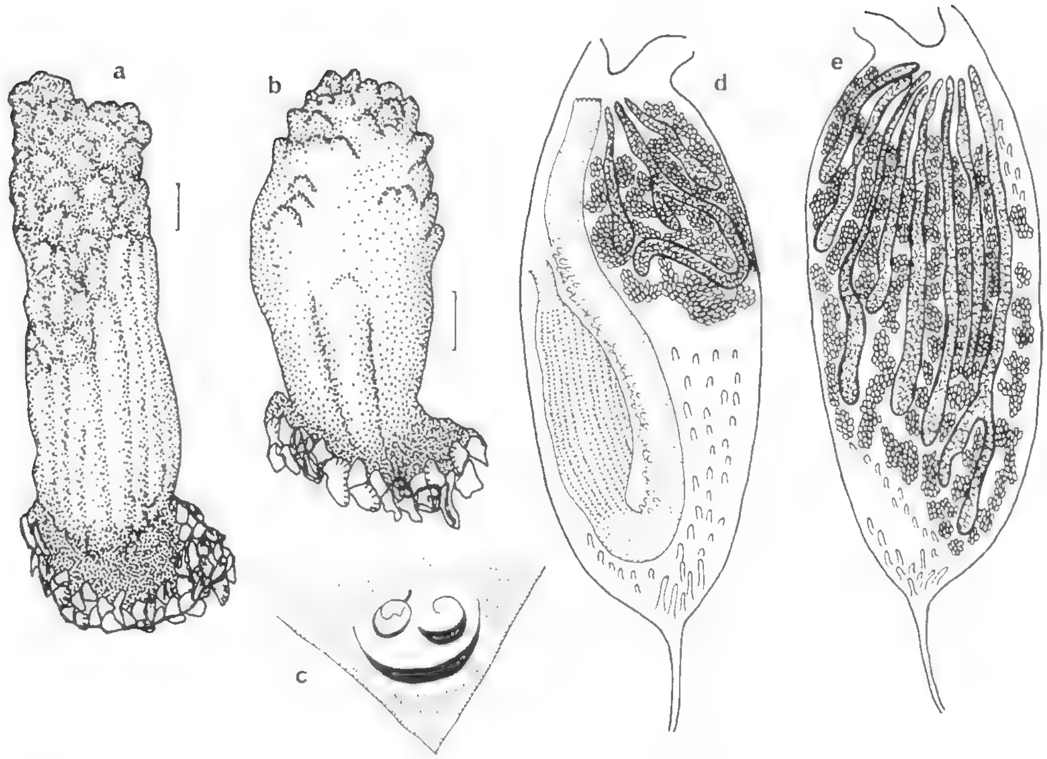


FIG. 49: *Styela clava* (after Tokioka 1953a) — **a, b**, external appearance of 2 individuals; **c**, dorsal tubercle; **d**, left side of body; **e**, right side of body. (Scales: **a, b**, 2.0 mm).

Styela plicata (Lesueur, 1823)
(Figs 50a, 51; Pl.IIh)

Ascidia plicata Lesueur, 1823, p.5. de Kay, 1843, p.259.
Styela plicata: Traustedt, 1883a, p.123; 1883b, p.478; 1885, p.44. Huntsman, 1912a, p.149; 1913, pp.489, 497. Redikorzev, 1916, p.197. Van Name, 1921, p.435; 1930, p.492; 1945, p.295. Michaelsen, 1918, p.36. Harant, 1927a, p.243; 1927b, p.7. Harant and Vernières, 1933, p.31. Kott, 1952, p.216 and synonymy; 1972b, p.185; 1972c, p.239; 1972d, p.254; 1975, p.13. Millar, 1966, p.370. Tokioka, 1960, p.213. Tokioka and Nishikawa, 1975, p.338.
Tethyum plicatum: Hartmeyer, 1909–11, pp.1359, 1630. Van Name, 1912, p.569.
Styela gyrosa Heller, 1877, p.255. Herdman, 1882, p.155.
Styela pinguis Herdman, 1899, p.40.

DISTRIBUTION

NEW RECORDS: Western Australia (Monte Bello Is, WAM 1158.83; Cockburn Sound, WAM 105.72 225.73 23.75 102.75 110.75 1044.83 1157.83 1159–60.83, QM G9646; Swan River, WAM 1156.83; Canning River WAM 106.75; Bunbury, WAM 71.75). South Australia (Spencer Gulf, QM G9613; St Vincent Gulf, QM 9614). Victoria (Port Phillip Bay, NMV H450; Geelong). New South Wales (Port Kembla, QM G10064). Queensland (Moreton Bay, QM G6123-5 GH344; Hervey Bay, QM G9386-7; mouth of Calliope River, QM G12708; Ross Creek, QM GH2565 GH2567).

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound — Hartmeyer and Michaelsen 1928, Kott 1952). South Australia (Great Australian Bight — Kott 1972b; St Vincent Gulf — Kott 1975). Victoria (Port Phillip Bay — Millar 1966). New South Wales (Port Stephens — Herdman 1899; Port Jackson, Port Hacking — Heller 1878, Kott 1952 1972d; Botany Bay — Kott 1952). Queensland (Moreton Bay — Kott 1972c). Hong Kong (Tokioka and Nishikawa 1975, Kott and Goodbody 1982). West Indian Ocean (Michaelsen 1918). Japan (Tokioka 1960). West Indies (Van Name 1921 1930 1945).

Styela plicata is a shallow-water species found in protected habitats in tropical to warm-temperate seas. The species has been recorded from temperate waters of the Atlantic Ocean, and the Mediterranean (Harant 1972a,b, Harant and Vernières 1933, Heller 1877). It has been taken from the eastern (Van Name 1912; Huntsman 1912, 1913) but not from the western coast of North America (Van Name 1945). There are no records from the general Indo-West Pacific region to the north of Australia suggesting that it is not an indigenous species and initially may have been introduced by ships.

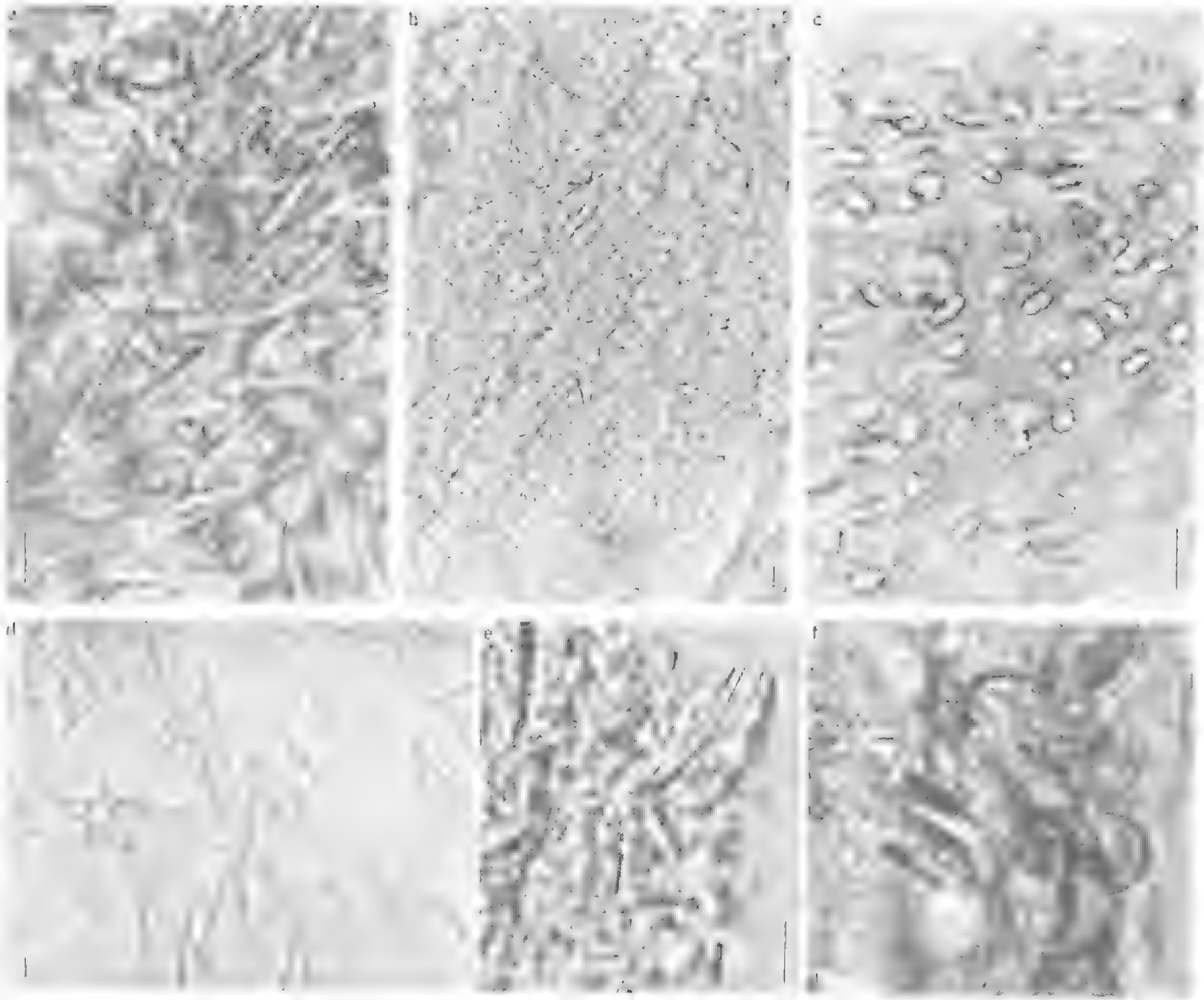


FIG. 50: *Styela plicata* — **a**, siphonal scales seen in profile (top right) and from below. *Cnemidocarpa areolata* — **b**, siphonal scales; **c**, oval bodies embedded in siphon lining. *Cnemidocarpa intestinata* — **d**, siphonal spines. *Cnemidocarpa lobata* — **e**, siphonal scales. *Cnemidocarpa radicosa* — **f**, siphonal scales. (Scales: 0.01 mm).

It appears to accommodate a degree of pollution and is found in brackish waters (Kott 1952, 1972c; Kott and Goodbody 1982). It is this latter capacity that may explain why the species appears to favour habitats in shallow waters around continents or large islands near continents where heavy freshwater run-off reduces salinity. The capacity of the species to withstand pollution and reduction in salinity is especially reflected in records from Audley (Kott 1972d) and the Canning River (WAM 106.75), both locations distant from marine conditions. Specimen QM G10064 is part of an impoverished fauna on wharf piles at Port Kembla (NSW) that is overlaid by a 3 m thick layer of toxic (phenols and cyanide) effluent from steel works (*pers. comm.* J. Watson).

DESCRIPTION

EXTERNAL APPEARANCE: The species does not exhibit any great degree of morphological variation. Individuals are upright, usually fixed by the posterior end of the body. Large specimens are up to 8 cm long. They are sessile and generally do not develop roots or stalks. The test is firm, slightly translucent, and dirty white, with only very occasional epiphytes on the larger specimens. Longitudinal ridges, sometimes subdivided by horizontal creases run parallel to the long axis of the body, which is slightly curved, convex along the ventral border. The branchial aperture is terminal and the atrial aperture antero-dorsal. Both apertures are on short siphons which are seen to be lined with dark brown stripes when extended. In larger specimens, the branchial siphon is slightly curved away from the atrial opening. There are flattened scales in the siphon lining.

INTERNAL STRUCTURE: The dorsal tubercle has a simple, U-shaped slit, directed anteriorly. Both horns of the slit are turned in. The body wall is moderately thick, with an outer layer of circular fibres and internal longitudinal bands radiating from the siphons. The 4 branchial folds are wide, with 15 to 25 internal longitudinal vessels crowded on the folds and 6 to 10 in the interspace. There are 5 to 8 stigmata in each mesh in the interspaces between the folds.

The gut forms a very narrow and deeply curved loop. The long stomach occupies about half of the ascending limb of the primary loop. It has numerous, fine, parallel, longitudinal folds that are conspicuous externally. The rectum runs parallel to the descending limb of the primary loop as it extends anteriorly to the deeply lobed anus at the base of the atrial siphon.

There are usually two gonads on the left and 4 to 6 on the right, all radiating from the atrial aperture. On the left, the anterior gonad extends straight across the top of the gut loop, while the posterior gonad curves down into the secondary gut loop. The gonads consist of a fringe of long, branched testis follicles on the body wall around a central, long tubular ovary. Kott (1952) has described a specimen in which the posterior gonad on the left has an anterior branch that extends anterior to the pole of the gut loop parallel to the anterior gonad. Vasa efferentia are relatively short and the male follicles are close to, sometimes spreading over, the mesial surface of the ovary.

There are crowded endocarps from the body wall along both sides of the intestine, enclosed in the gut loop, and on the body wall between the gonads.

REMARKS: The whitish, almost naked, tough but not leathery test with its rounded swellings and broad brown stripes in the siphons, together with the deeply curved gut, crowded endocarps and relatively long testis follicles distributed along the whole length of the ovary, are characteristic of the species. The deeply curved gut loop, with the descending limb of the primary loop parallel to the long axis of the body and to the rectum, contrasts with its usually more oblique orientation in *S. canopus*.

Genus **Cnemidocarpa** Huntsman, 1912b

Type species: *Styela joannae* Herdman, 1898

In *Cnemidocarpa* the male follicles are usually closely associated with the long ovarian tube, applied along each side or beneath it. The gonoducts open close to the atrial aperture. As male follicles proliferate, they often project up into the ovarian tube and form a rod along the parietal surface of the ovary. The body musculature consists of longitudinal bands internally, surrounded by a layer of sometimes diffuse circular fibres.

The genus appears to be intermediate between *Polycarpa* and *Styela* and there are intermediate species that are difficult to distinguish from one or the other of those genera. In some species the maturing male follicles proliferate out into the body wall, away from the ovary (e.g., *Cnemidocarpa pedata*). They are always completely embedded in the body wall, however, and do not project into the peribranchial cavity separately from the ovary as they do in *Styela*. In other species there are short gonads with ducts opening distant from the atrial apertures that resemble those of *Polycarpa* spp. However, they never occur in more than a single series on each side of the body.

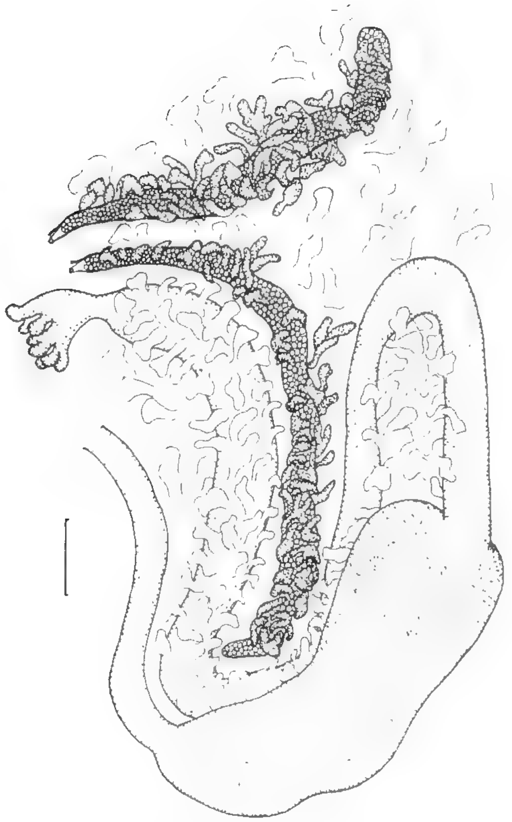


FIG. 51: *Styela plicata* (WAM 71.75) — gut and gonads. (Scale: 2.0 mm).

The genus is common, and several indigenous species occur in both tropical and temperate Australian waters. The range of some species is relatively restricted and, unlike *Styela*, few species have a wide Indo-West Pacific range.

In most species, individuals reach a large size, and very likely have a long reproductive life. As far as is known, the genus is oviparous. There are no provisions for brooding of larvae, and since gonoduct openings are at the base of the atrial siphon, gametes are readily expelled. The larvae of most species are not known, but it seems likely that there is a loss of site-selecting capacity resulting from a tendency to loss of the ocellus (a phenomenon occurring in this family). This suggests that habitat requirements are not stringent, and recruitment and gene flow may be reduced and, cause some isolation of populations and the speciation characteristic of the family in Australian waters.

KEY TO THE SPECIES OF *CNEMIDOCARPA* RECORDED FROM AUSTRALIA

1. Gonads short; male follicles fewer than 10 pairs .... *C. fissa* n.sp.
   Gonads long; male follicles not fewer than 10 pairs 2
2. Gonads parallel to one another and to gut loop; gut loop straight .... *C. floccosa*
   Gonads neither parallel to one another nor to gut loop; gut loop curved..................... 3
3. Gonads up to 10 per side; gonads and gut suspended from body wall by numerous fine ligaments .... *C. completa* n.sp.
   Gonads fewer than 10 per side; gonads and gut not suspended from body wall by numerous fine ligaments 4
4. Gonads with marked undulations 5
   Gonads without marked undulations 7
5. Gut loop very long and narrow, the pole curving back into secondary loop .... *C. lobata*
   Gut loop not very long and narrow, the pole never curving back into secondary loop... 6
6. Stalked ....*C. aculeata* n.sp.
   Not stalked.....................*C. tripartita* n.sp.
7. Gut greatly expanded to occlude space enclosed by primary loop; endocarps not present ....*C. intestinata n.sp.*
   Gut not greatly expanded, space enclosed by primary loop not occluded; endocarps present 8
8. Single gonad on each side ....*C. posthuma*
   More than one gonad on each side 9
9. Gonads deeply embedded 10
   Gonads not deeply embedded 11
10. Gonads branched........................*C. pedata*
    Gonads not branched................*C. radicosa*
11. Stomach occupies most of ascending limb of gut loop...12
    Stomach does not occupy most of ascending limb of gut loop 13
12. Stigmata 9–15/mesh; atrial and branchial siphons close and parallel ....*C. stolonifera*
    Stigmata 3–5/mesh; atrial and branchial siphons not close and parallel *C. personata*
13. Gonads on left more than 3.....*C. oligocarpa*
    Gonads on left fewer than 3 ....*C. areolata*

The following species are recorded from the Indo-west Pacific, but are not yet recorded from Australia:

Cnemidocarpa alentura (Herdman, 1906) has a single divided gonad on each side of the body, a wide gut loop, 14 internal longitudinal

TABLE VI — SUMMARY OF CHARACTERS OF SPECIES OF *CNEMIDOCARPA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	[3]Distance between apertures; body shape	[4]Branchial sac	[5]Stomach length	Curve of gut loop	Gonads: right; left	[6]Endocarps	Additional features
C. areolata	WP	NSW - SW Aust.	1/3; rounded	4-8 (12-20); 4-10	1/4	obtuse - U-shaped	3-5; 2-3	+ ; + +	dark, striped siphon lining
C. personata	—	Tas. - Heron I.	1/3; rounded	3-7 (12-33); 3-5	3/4	obtuse	2-4;2-4	+ + ; +	body fixed ventrally
C. oligocarpa	WP	Bowen	1/3; narrows anteriorly	2-3 (10); 6	1/3	U-shaped	5;5	+ + ; + +	—
C. stolonifera	—	NSW - NE Qld	less than 1/3; upright, stalked	3-6 (7-14); 9-15	3/4	obtuse - acute	3-8;2	+ + ; + + +	gonads branched
C. pedata	WP	S Aust. - Lizard I.	1/2; long axis curved	6-10 (15-26); 5-8	1/2 - 1/3	obtuse - straight	5-8; 3-5	+ ; + +	″
C. posthuma	—	Shark Bay	1/3; cylindrical	10 (15-30); 3-4	1/3	U-shaped	1;1	″	—
C. lobata	—	Cockburn Sd - Townsville	1/3; rounded	2-3 (8-11); 5-6	″	recurved	2-4;1-2	+ + ; + +	gonads lobed, sinuous
C. aculeata n.sp.	—	Bass Strait - Townsville	less than 1/3; upright, stalked	3-4 (20); 2-3	1/3	obtuse	2;2	0; +	″
C. tripartita n.sp.	—	Bass Strait	1/2; small, oval	3 (3);6	1/2	″	2;2-3	1;0	gonads thick
C. fissa n.sp.	—	Cockburn Sound	1/2; long axis curved	4-6 (6-12); 2-4	2/3	″	4-6;4-6	0;0	″
C. completa n.sp.	—	Bass Strait - NSW	1/3; oval	2-3 (13-17); 9-18	″	U-shaped	6-8;8-10	0- + ; +	gonads crowded
C. intestinata n.sp.	—	Gladstone - Darwin	1/3; laterally flattened	2-3 (5-8); 10	1/4	″	2;2	0;0	gut voluminous
C. radicosa	—	Cockburn Sd - NE Qld	1/3; narrows anteriorly	5-8 (10-20); 5-8	1/2	J-shaped	2-4;2	+ ;0	gonads deeply embedded
C. floccosa	WP	Moreton Bay - Bowen	More than 1/2; kidney shaped	4-6 (19-24); 15	1/5	straight	7-9;5-7	+ ; + +	gonads parallel to long axis of body

[1]WP, western Pacific. [2]Range given anti-clockwise around the continent. [3]As a fraction of body length. [4]Internal longitudinal vessels; between folds (on folds); stigmata/mesh. [5]As approximate fraction of ascending limb of gut loop. [6]In gut loop; outside gut loop.

branchial vessels in the interspace and small endocarps over the body wall (BM 1907.8.30.17)

Cnemidocarpa javensis Millar, 1975, a species related to *C. fissa* n.sp., is discussed below.

Cnemidocarpa lapidosa (Herdman, 1906) has a stiff, brittle test with embedded sand to which the delicate body wall adheres very closely, and is reported by Herdman to have a single gonad on each side of the body and narrow branchial folds. The type is in bad condition and details of its structure could not be determined (BM 1907.8.30.15).

Cnemidocarpa quadrata (Herdman, 1882) from the Philippines is known from a single juvenile specimen (BM 1887.2.4.101–3) with a simple gut loop, 2 narrow gonads on the left and 3 on the right, and only 6 rows of unusually long stigmata.

Cnemidocarpa reticulata (Millar, 1975) has a single, long, sinuous gonad on each side of the body as in *C. lapidosa* (Herdman, 1906) from Sri Lanka (see also Michaelsen 1923). Both species are distinguished by that character from all except *C. posthuma* Hartmeyer, 1927 (Hartmeyer and Michaelsen 1928). Their relation to the latter species is discussed below.

Cnemidocarpa sedata (Sluiter, 1904) is laterally flattened and sessile and with sessile apertures. It is 2 cm long and 1.5 cm broad. The test is leathery and tough, glistening internally and wrinkled externally. The body wall has strong muscles. The branchial folds are broad and there are very numerous (25 to 30) internal longitudinal vessels in the interspace and only 1 or 2 stigmata per mesh. The gut forms a double loop and the anus is smooth. Gonads are thin and cylindrical, 2 on each side of the body. The large number of longitudinal branchial vessels in the interspace is diagnostic.

Cnemidocarpa tinkatae (Van Name, 1918) from the Philippines (Millar 1975) has numerous long gonads reminiscent of *C. personata*. Its relation to the latter species is discussed below.

Cnemidocarpa traustedti (Sluiter, 1890) is small (8 mm) and almost spherical, with two distinct siphons of variable length. The thin test has hairs with enmeshed sand. The branchial folds are narrow; there are 7 or 8 stigmata per mesh and 5 vessels in the interspace. The gut forms a wide double loop and there are 2 gonads on each side of the body. The species resembles *C. intestinata* n.sp. in many characters, but is not laterally flattened and the distended gut, so conspicuous in *C. intestinata* apparently has not been observed in Sluiter's species.

Cnemidocarpa aculeata n.sp.
(Fig. 52)

DISTRIBUTION

TYPE LOCALITY: Queensland (Cleveland Bay, 18°42'S, 147°01'E, coll. Arnold and Birtles Sq. 8C. Stn 479, 4.7.79, holotype QM GH1326; paratypes QM GH1327, QM GH1328).

FURTHER RECORDS: Victoria (Bass Strait, NMV H377 H381 H388 H396 F51571). Queensland (Cleveland Bay, QM GH1400 GH3032).

The species has been taken in fine to muddy sand substrates at 20 m to 92 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are club-shaped, 0.4 to 4.0 cm high, the upper free surface up to 0.5 cm in diameter, and the body gradually tapering to a narrow stalk that is narrowest where it attaches to the substrate. This stalk is thread-like in smaller specimens. Sessile apertures are present on each side of the rounded upper free surface of the head. Each aperture is surrounded by 4 rounded lobes, separated by shallow creases. The largest known specimens are from Cleveland Bay. Some specimens from Bass Strait (NMV H377) are very small (head 1.5 mm long). The test is firm, cartilaginous and translucent, with slight horizontal wrinkles. Anteriorly the larger (type) specimens are covered by evenly spaced, short, pointed papillae that are gradually reduced in size toward the middle of the body and disappear on the posterior half of the body. However, these are absent from the smaller Bass Strait specimens, in which the surface test is covered with small slightly protruding vesicles. All the specimens are contracted and it is possible that when fully expanded in life the diameter of the body would be much increased and the wrinkles would not be present.

INTERNAL STRUCTURE: The opaque body wall has an outer layer of strong, circular muscle-bands around an almost continuous layer of longitudinal muscles. These muscles extend down almost the whole length of the tapering stalk. The siphonal lining is slightly iridescent, but no spines were detected. There are only 8 well-spaced and relatively short and stout branchial tentacles. The dorsal tubercle is a protruberant cushion with a C-shaped slit turned to the left. The dorsal lamina is broad with a smooth border.

The branchial sac extends some distance down into the hollow stalk; the peribranchial cavity extends for most of the length of the stalk, its diameter decreasing with the diameter of the stalk. Branchial folds are low and rounded, with very crowded internal longitudinal vessels, 3 or 4 in the interspace and about 20 on each fold. In the small

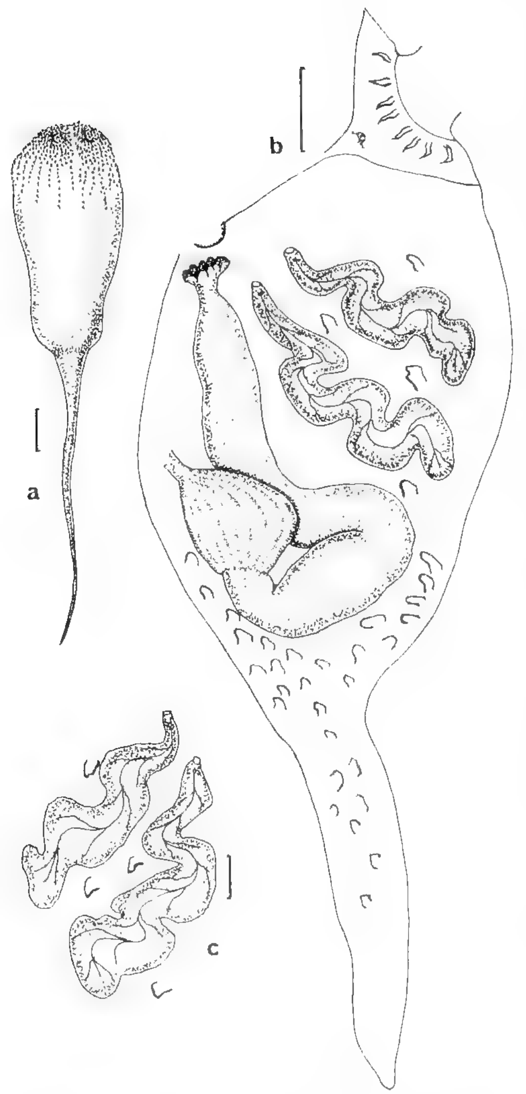


FIG. 52: *Cnemidocarpa aculeata* n.sp. (QM GH1327) — **a**, external appearance; **b**, left side body wall showing gut, gonads and endocarps; **c**, gonads from right side of body. (Scales: **a**, 2.0 mm; **b**, 1.0 mm; **c**, 0.5 mm).

Bass Strait specimens, there are about 18 crowded internal longitudinal vessels on each side of the body, with low, rounded folds being formed only in the dorsal and ventral parts of the branchial sac.

Very numerous ligaments connect the branchial sac to the body wall across the peribranchial cavity. The anterior end of the endostyle undulates from side to side. The oesophageal opening is about one-third of the body length from the posterior end of the pharynx. The oesophagus is short, and the stomach is short and swollen, with conspicuous longitudinal folds. The short, wide, gut loop extends across the postero-ventral end of the body. The rectum is long, extending anteriorly to the atrial aperture. The anal aperture is bordered by 15 rounded lobes.

There are 2 undulating gonads on each side of the body. On the left, they converge toward the atrial aperture, anterior to the rectum. They consist of a double row of lobed male follicles beneath the long ovarian tubes.

A few small endocarps lie between the gonads and gut, but they are more numerous posterior to the gut where the body, including the peribranchial cavity projects down into the stalk.

REMARKS: This is one of the smallest known species of this genus. It has been recorded from only two widely separated locations, and it may have been overlooked elsewhere. Its undulating gonads resemble those of *C. lobata*, from which it is distinguished by the form and length of its short, wide gut loop and its body shape.

The species is characterised by its small size, its long hollow tapering stalk into which the body extends; the conical projecting test papillae; the short stomach and short and wide gut loop; the undulating gonads; and the conspicuous anal lobes. Externally, the species resembles *Hartmeyeria formosa*.

Cnemidocarpa areolata (Heller, 1878)
(Figs 50b,c, 53)

Styela areolata Heller, 1878, p.26. Herdman, 1906, p.316. Van Name, 1918, p.87. Tokioka, 1950, p.145. Kott, 1964, p.138 (part, specimens from Heron I.); 1966, p.297. Vasseur, 1967b, p.139.
Cnemidocarpa areolata: Tokioka, 1953a, p.254; 1953b, p.14; 1954a, p.261; 1954b, p.85; 1959a, p.229; 1961, p.126; 1962, p.17; 1967a, p.181. Kott, 1981, p.201. Kott and Goodbody, 1982, p.537.
Cnemidocarpa valborgi Hartmeyer, 1919, p.35.
Cnemidocarpa hartogi Hartmeyer and Michaelsen, 1928, p.393.
Cnemidocarpa irma Hartmeyer and Michaelsen, 1928, p.388. Hastings, 1931, p.72. Kott, 1952, p.217. Millar, 1963, p.728.
Styela stolonifera: Kott, 1952, p.215 (part, specimens from the Capricorn Group).
Styela etheridgii: Kott, 1952, f. personata p.219 (part, specimens from Long Reef, NSW).
Cnemidocarpa etheridgii: Kott, 1972d, p.253.
Styela pavementis Kott, 1952, p.226.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 174.75 752.82 760.82 1094.83; off Carnarvon, WAM 1093.83; NW Cape, WAM 1090.83; Port Hedland, WAM 972.83; Cockburn Sound, WAM

110.72 224.73 90.75 168.75 866.75 217.82 221.82 749.82 1091-2.83, QM G9611). South Australia (Upper Spencer Gulf, QM GH2727). Victoria (Bass Strait, NMV H396). New South Wales (Shell Harbour). Queensland (Moreton I., QM GH373; Caloundra, QM G10132; Heron I., QM G9378 G9382 G10097-8 GH1392 GH1424-30; Wistari Reef, GH2719; Abbot Point, QM GH654-7 GH719 GH1374-5; Townsville).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Shark Bay, Cockburn Sound, Albany — Hartmeyer and Michaelsen 1928, Kott 1952, Millar 1963). New South Wales (Port Hacking — Kott 1972d; Long Reef — Kott 1952). Queensland (Moreton Bay — Kott 1964; Capricorn Group — Kott 1952; Low Isles — AM G13507-8 Hastings 1931). Northern Australia (Darwin — Kott 1966). Sri Lanka (Heller 1878, Herdman 1906). Noumea, Palau Is (Tokioka 1950 1961, Vasseur 1967b). Philippines (Van Name 1918). Marianas Is (Tokioka 1967a). Japan (Tokioka 1953a,b 1954a,b 1959a, 1962). Fiji (Kott 1982). Hong Kong (Kott and Goodbody 1982).

The species has a wide range in the Indo-West Pacific. It extends into temperate waters off Japan and Australia. It is the most commonly occuring stolidobranch ascidian in the rubble zone near the reef crest at Heron Island. It is found in fairly shallow water down to 70 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are rather irregular, laterally flattened and either upright and oval or squat. The branchial aperture is terminal or near the anterior end of the upper surface; the atrial aperture is from one-third to half of the distance down the dorsal surface. The apertures are usually almost sessile, on short, wart-like siphons that are lined with yellow and red stripes. These stripes of the siphonal lining become black and white in preservative and eventually fade completely, although usually some black pigment is retained in the body wall in the vicinity of the apertures. The test is firm, tough and cartilaginous to leathery and hard. It is moderately thick, with longitudinal furrows and creases that are transversely divided into rounded swellings, especially anteriorly. In smaller specimens, the test is slightly translucent. In life, the test is hazel, orpiment orange, vinaceous rufus, pinkish vinaceous, salmon buff or scarlet vermilion (Ridgeway 1886), but in preservative the outer cuticle is invariably dirty beige to white. Sometimes the test is heavily encrusted with shell and other foreign particles (Hastings 1931, AM G13507-8).

The outer part of the siphon lining where it joins the external test is lined with minute (0.02 mm), overlapping, curved scales, which are identical with those lining the siphons of many species of

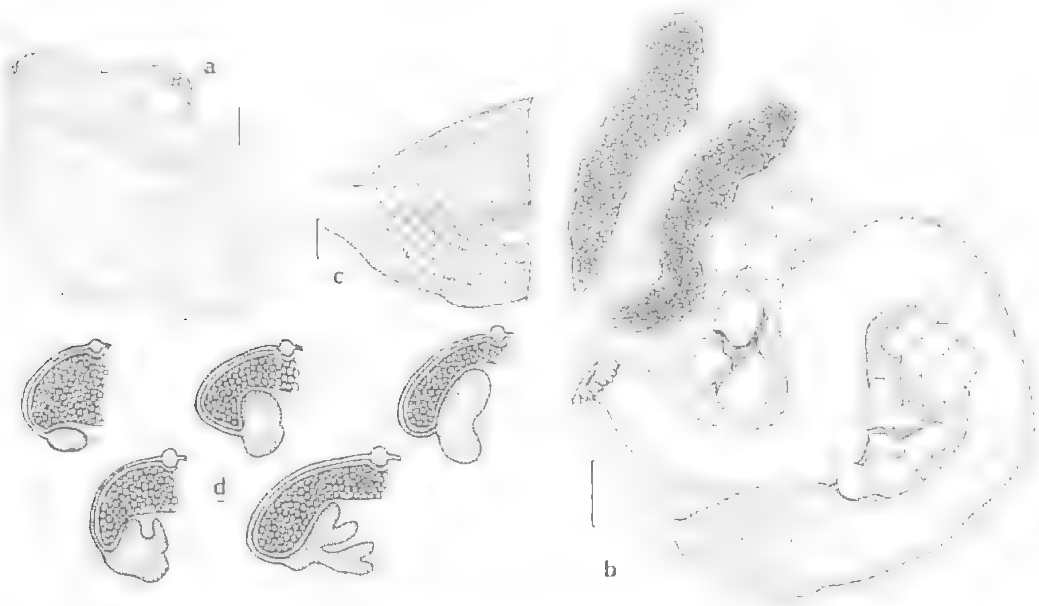


FIG. 53: *Cnemidocarpa areolata* — a, external appearance (WAM 90.75); b, left side of body showing gut loop, gonads and endocarps (QM GH654); c, proximal end of stomach showing folds in relation to suture line (QM GH10098); d, cross section of gonads showing changing relationship of ovary and testis follicles with maturation (diagrammatic). (Scales: a, 1.0 cm; b, 2.5 mm; c, 2.0 mm).

the Styelinae. Each scale overlies an oval granular body.

INTERNAL STRUCTURE: The body wall has a layer of diffuse circular muscles underlaid with well-spaced longitudinal bands. It is relatively thin and sometimes adheres closely to the test. In preservative, the body wall often has some black pigmentation, especially around the siphons. In freshly preserved specimens there are stripes of black pigment in the siphons as well as in the lining. The branchial tentacles are robust, moderately long and not crowded. They often contain black pigment. The dorsal tubercle is a rounded cushion with a U- or S- shaped slit, with the horns turned in or out. In large specimens (5 cm) from Dampier Archipelago (WAM 174.75) and Abbot Point (QM GH656–7), the dorsal tubercle has a convoluted slit. The dorsal lamina is moderately long. The oesophagus opens at least two-thirds of the way down the branchial sac.

In many specimens, the branchial folds are low and well separated, and the internal longitudinal vessels on the folds are crowded. In a few specimens, however, wider folds cover the interspace, and the vessels on the folds are not crowded (QM GH373). This variation appears to be due to contraction of the branchial folds. The largest folds have 10 to 20 vessels and there are 4 to 8 in the interspace. There are 4 to 10 stigmata per mesh, with meshes of variable size. Moderate-sized specimens of 3 cm and 2 cm respectively have internal longitudinal vessels with the following arrangement: E8(10)8(12)6(8)7(9)3DL (WAM 174.75); E4(8)3(10)3(10)4(10)0DL4(10) (AM G13591).

The gut loop is fairly short and extends across the posterior or postero-ventral corner of the body. It is often curved to form a secondary loop of variable depth. Usually the two limbs of the primary loop are almost parallel, but often the pole is more open, accentuating the curve of the secondary gut loop. The oesophagus is short and expands abruptly into the stomach. Externally, the pyloric end of the stomach is not demarcated from the intestine. The stomach is short, and has about 25 short, parallel, longitudinal folds, which are often inconspicuous on the outer surface. Proximally, the folds on both sides of the suture line terminate obliquely against it and do not extend parallel to it. The anal border is fringed by 10 to 20 rounded lobes.

Gonads are long, cylindrical, and extend across the sides of the body converging toward the atrial aperture. They sometimes branch, but seldom more than once. There are 2 gonads on the left, the most posterior extending around the pole of the gut loop and curving into the concavity of the secondary gut loop before terminating at the base of the atrial aperture. Sometimes a branch of this posterior gonad extends down into the secondary loop. On the right side of the body, 3 to 5 gonads converge toward the atrial aperture. When immature, the testes follicles are simple, pear-shaped bodies in two rows beneath the ovary. With maturity, they grow larger and branch, extending up into the centre of the ovarian tube. In specimens from Abbot Point (QM GH656–7), there are occasional male follicles on the sides and mesial surface of the gonad, joined by shorter than usual vasa efferentia to the median vas deferens. Gonads are narrow, long, and slightly sinuous when immature, but become thick and more club-shaped when mature.

Endocarps are moderately tall, narrow and flat-topped. They are present in the pole of the gut loop and in a row along its length; between the gonads; and sometimes on the surface of the gut itself (QM G9661).

REMARKS: This is a variable species, which can be readily confused externally with *Cnemidocarpa personata* and *C. radicosa*. However, the thin, often 'papery' test and gonads of *C. radicosa* distinguish it from the present species. In comparison with *C. areolata, C. personata* has less conspicuous apertures, often (but not always) more numerous gonads, and less numerous endocarps. In *C. personata*, the folds of the long stomach extend parallel to the suture line on its posterior side rather than terminating obliquely against it on both sides as in *C. areolata*. The latter character especially is a consistent and reliable distinction.

Internal organs resemble those of *C. stolonifera*, which, however has a longer stomach and close, parallel siphons that distinguish it from the present species.

Cnemidocarpa completa n.sp.
(Fig. 54)

DISTRIBUTION

TYPE LOCALITY: Victoria (Little Squally Cove, Deal I., 10 m, coll. J.E. Watson, 3.5.74, holotype NMV H634)

FURTHER RECORDS: Victoria (Bass Strait, paratype NMV F51461). New South Wales (Arrawarra, paratype QM GH2216).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are oval, sandy and up to 3 cm long. The branchial aperture is terminal; the atrial aperture is one-third of the body length along the dorsal surface. They are on

FIG. 54: *Cnemidocarpa completa* n.sp. (NMV H634) — gut, gonads and endocarps on left side of the body wall. (Scale: 2.0 mm).

short siphons projecting anteriorly. The test is rather hard, with very fine wrinkles, and is often brittle with embedded sand.

INTERNAL STRUCTURE: There is no siphonal armature. About 40 branchial tentacles of moderate length are crowded at the base of the branchial siphon. There is a shallow, V-shaped peritubercular area, with a relatively large tubercle. The slit spirals one and a half times in a clockwise direction from the centre or it is a conspicuous U or almost circular slit.

The branchial sac is delicate, although the internal longitudinal vessels are broad and protruding. There are 2 or 3 vessels in the interspace and up to 17 on the folds, arranged according to the following formula: E2(3)2(17)2(14)3(16)1DL. Smaller specimens (up to 2 cm) have 9 stigmata per mesh; larger specimens (3 cm) have 16 to 18 stigmata. The stigmata are crossed by parastigmatic vessels. The longitudinal vessels are crowded only on the edges of the folds. Posteriorly, the branchial folds join a retropharyngeal groove posterior to the oesophagus.

The long, narrow gut loop, curves around the posterior half of the body. The oesophagus is short and the stomach long and cylindrical, occupying two-thirds of the ascending limb of the gut loop. It is lined with fine and very regular parallel folds. The anal border has 14 rather irregular lobes and is lower on one side.

The gonads are large, crowded, undulating cylinders, radiating toward the atrial aperture on each side of the body, 6 to 8 on the right and 6 to 10 on the left. They consist of large tubular ovaries with double rows of testis follicles along their parietal surfaces. Both gut and gonads are attached to the body wall only by very fine ligaments and are readily detached. These ligaments allow for a flexibile arrangement of the organs crowded into the peribranchial cavity, and enable the gonads to overlie one another to some extent. One small specimen (1 cm) from Arrawarra has only a single fully developed gonad on the left and two on the right.

A few small endocarps are scattered on the body wall, mostly anterior to the gonads and ventral to the gut loop. There are sometimes a few small endocarps in the gut loop.

REMARKS: *Cnemidocarpa tinkatae* (Van Name, 1918) from the Philippines and Indonesia (Millar 1975) is distinguished from the present species by its branched gonads, short and irregularly pleated stomach, and only 5 to 7 stigmata per mesh. *Cnemidocarpa fertilis* (Hartmeyer, 1909) from Japan (see Tokioka 1953a) resembles the present species in its number of gonads, internal longitudinal vessels and stigmata, but its gut loop is very much longer, and it has a plain anal border. Another Japanese species, *Cnemidocarpa macrogastra* (Oka, 1935), has a long stomach, but it is distinguished from the present species by its fewer stigmata per mesh (6), more internal longitudinal vessels in the interspace, numerous endocarps in the gut loop, and its plain anal border (Tokioka 1953a).

Cnemidocarpa completa is distinguished from other Australian species primarily by its numerous and crowded cylindrical gonads which, with the gut, are suspended in the atrial cavity by ligaments, and not even partly embedded in the body wall. Its large number of stigmata per mesh is also distinctive.

Cnemidocarpa fissa n.sp.
(Fig. 55)

DISTRIBUTION

TYPE LOCALITY: Western Australia (Cockburn Sound, E side, 32° 10.85'S, 115° 45.2'E, 9–10 m, coll. L. Marsh on M.V. Flinders, scallop dredge, 27.9.73, holotype WAM 223.73).

DESCRIPTION

EXTERNAL APPEARANCE: The present specimen is about 2 cm long. The body is narrow, the posterior half curved dorsally, almost at a right angle to the anterior part. The branchial aperture is terminal, on a relatively long, stout siphon that is nearly as wide as the body. The atrial siphon extends from the upper surface of the expanded, posterior end of the body. It is directed upwards, parallel to the anterior half of the body. Both siphons have 4 longitudinal furrows down their length. The test is brittle, with embedded sand that is less dense on the siphons.

The usual minute (0.20 mm) overlapping scales line the outer part of the siphons.

INTERNAL STRUCTURE: The body wall is extremely thin and transparent, with a diffuse network of very fine muscles. It adheres closely to the test. The branchial sac is long, curved and delicate, with narrow folds and wide interspaces. Internal longitudinal vessels are arranged according to the following formula: 5DL 2(6) 6(12) 5(10) 4(4) 6E. There are 2 to 4 long stigmata in each mesh in the interspace.

The slightly curved gut loop is in the posterior two-thirds of the body. The rectum, fringed with rounded lobes, bends upwards into the base of the atrial siphon. The stomach is long and cylindrical, occupying about two-thirds of the ascending limb of the loop. The glandular folds are deep, but they are not clearly evident from the outside of the stomach.

There is a single row of up to 5 sausage-shaped gonads down the middle of the body wall on the left. There may be more on the right, but the specimen is damaged and the number could not be determined. The gonads are unusual in having only 5 pairs of pear-shaped male follicles beneath each ovary.

There are no endocarps on gut or gonads.

REMARKS: The species is closely related to *Cnemidocarpa javensis* Millar, 1975 from Bali. Millar's species is distinguished by its short stomach with very distinct longitudinal folds and very long caecum, small gut loop, sessile apertures, and test fibrils that enmesh sand to form an external casing around the animal. Millar (1975) has drawn attention to similarities between *C. javensis* and *Polycarpa incubita* Sluiter, 1904. The present species resembles *P. incubita* only in the arrangement of its gonads. *Cnemidocarpa fissa* also resembles *Polycarpa manaarensis* Herdman, 1906 from Sri Lanka, but is distinguished from that species by its long, cylindrical stomach.

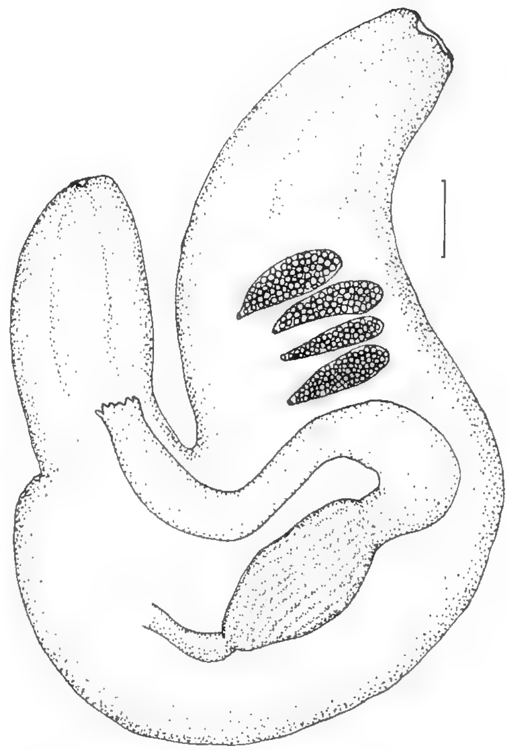


FIG. 55: *Cnemidicarpa fissa* n.sp. (WAM 223.73) — gut and gonads shown through body wall. (Scale: 2.0 mm).

The short gonads with relatively few male follicles resemble those of the genus *Polycarpa*, and this, together with the brittle test, can result in confusion with *Polycarpa procera*. Overlapping siphonal scales that have not, so far, been observed in *Polycarpa*, as well as the presence of only a single row of gonads on each side of the body, support its status as a species of the genus *Cnemidocarpa*.

Cnemidocarpa floccosa (Sluiter, 1904)
(Fig. 56)

Styela floccosa Sluiter, 1904, p.64.
Cnemidocarpa floccosa: Kott, 1972c, p.239.

DISTRIBUTION

NEW RECORDS: Queensland (Moreton Bay, QM G5955–60 G6086 G8581 G9491 G9504 G9606–7, Brisbane River, QM G9958–61; Fraser I., QM G10073; Gladstone Harbour, QM G9676–7 G9679 G9685 G9722 G9797 G10056; Calliope River, QM G11887–92 G12704; Abbot Point, QM GH663; Townsville, QM GH711; Cairns, QM GH788).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1972c). Arafura Sea (Sluiter 1904).

The species is found on sand, coral, and muddy substrates. Its heavy coating of sand makes it inconspicuous and it may, in fact, have a wider range than its present records suggest.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are from 1 to 4 cm long. The body is kidney-shaped and rounded, slightly convex ventrally and with a dorsal concavity. The shape of the body is obscured by the thick coating of foreign particles that adhere to the long, rather irregular, fibrous extensions of the test. Individuals are often found in aggregates, adhering to one another by the mixture of sand and test extensions. The apertures are on siphons that project through the thick layer of sand. The branchial siphon is terminal and is directed obliquely away from the body. The atrial siphon, which is about one-third the length of the branchial siphon, is at the posterior end of the dorsal surface and is directed straight upwards. Internally, the test is pearly white.

INTERNAL STRUCTURE: The body musculature is moderately strong, with an external layer of circular muscles and internal longitudinal bands. The dorsal tubercle is large, completely filling the base of the deep peritubercular area. It has a C- or U-shaped slit with the horns turned in. The branchial tentacles are crowded, but not long.

There are 4 rather narrow, flat, well-separated folds on each side of the body. Up to 25 internal longitudinal vessels are crowded on the folds, but only 3 to 5 well-spaced vessels are in the interspace. Longitudinal vessels have the following arrangement in specimens 3 cm and 4 cm long respectively: DL3(19)5(18)4(19)3(20)3E; DL3(15)6(24)5(20)4(12)3E. There are about 15 stigmata per mesh in the interspace, each mesh crossed by a parastigmatic vessel. The dorsal lamina is very long and the oesophageal opening is at the posterior end of the pharynx.

The gut loop is long and simple, extending in a very slight curve around the postero-ventral part of the left side. The parallel limbs of the loop enclose a single, long, curved endocarp. The stomach and the oesophagus are both very short indeed. The stomach, which is about the same width as the intestine, has longitudinal folds that are not visible externally. These terminate abruptly where a very large typhlosole develops from the gut wall and all but fills the intestine, dividing it into two chambers. In these specimens, the gut is filled with mud. The anal border is not lobed.

The gonads are long and extend parallel to one another along the length of the body, their ducts directed to the posterior atrial opening. There are usually 6 to 8 gonads on the left side of the body and 8 on the right. In addition to the long endocarp enclosed in the gut loop, there are single rows of small, flat-topped endocarps between the gonads.

REMARKS: The species is found in muddy habitats with *Ascidia sydneiensis* and *Cnemidocarpa intestinata*. As in those species, its

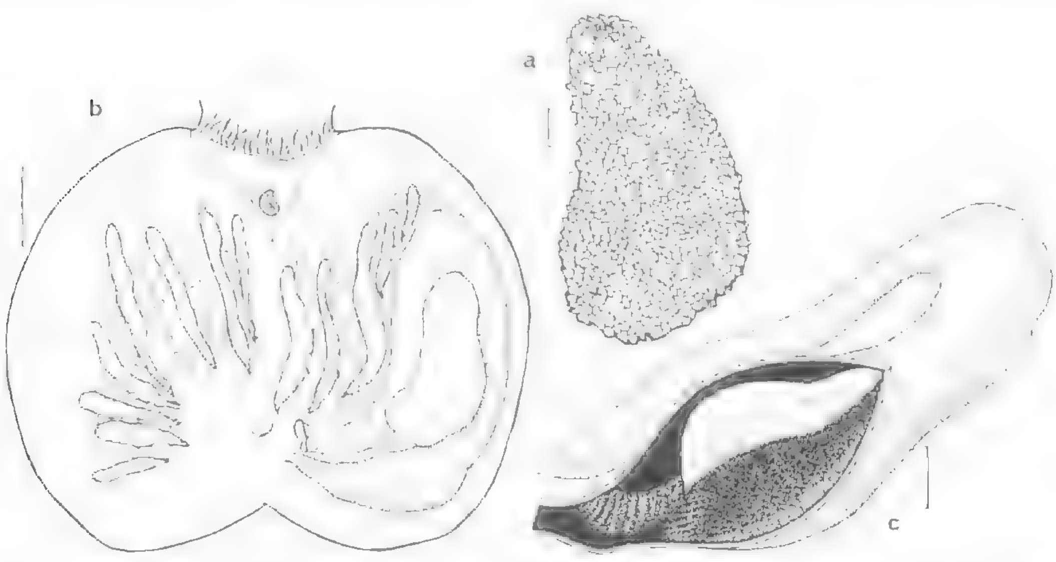


FIG. 56: *Cnemidocarpa floccosa* (QM G8581): a, external appearance; b, internal structure; c, proximal part of intestine, opened to show large typhlosole. (Scales: a, b, 5.0 mm; c, 2.0 mm).

intestine's capacity to accommodate large quantities of sediment may be an adaptative advantage. Its covering of sand and foreign particles has obvious advantages in concealing the individual from predators and increasing the effectiveness of the protective test.

In the large number of long gonads, this species resembles the Japanese *C. fertilis* (Hartmeyer, 1906) and the Philippine *C. tinkatae* (Van Name, 1918). However it is readily distinguished by the great separation of its apertures and by its short stomach, simple gut loop, typhlosolar fold and longitudinal orientation of the gonads. The long gonads of *C. floccosa* never extend beneath the gut loop as they do in *C. tinkatae*, and the gonads of *C. fertilis* are usually even more numerous.

Herdman (1906) has noted a resemblance between *Polycarpa palkensis* and *C. floccosa*, but the gonads of the former are shorter (ovate) and more numerous. The type specimen of Herdman's species was not located.

Cnemidocarpa intestinata n.sp.
(Figs 50d, 57)

Styela etheridgii: Kott, 1952, f. personata p.220 (part, specimens from Rat I., Port Curtis).

DISTRIBUTION

TYPE LOCALITY: Queensland (Gladstone Harbour, 24° 48′39″S,151° 13′9″E,9 m, coll. P. Saenger Stn 21, July 1976, holotype QM G9681).

NEW RECORDS: Queensland (Hervey Bay, QM G9381 GH2211; Gladstone Harbour, paratypes QM G9680 G9716 G9785 G9804 G10062, AM Y1698; Calliope River, GH2162; Heron I., QM GH2971; Abbot Point, paratypes QM GH722 GH828). Northern Territory (Darwin, AM Y1736).

PREVIOUSLY RECORDED: Queensland (Port Curtis — Kott 1952).

The species has been taken from mud and coarse sand with mud substrates and on concrete blocks, at about 10 m. Its records are from a relatively restricted range from the central Queensland coast to Darwin. It is possible that its environmental requirements are stringent, although there is an abundance of similar habitats in its recorded range.

DESCRIPTION

EXTERNAL APPEARANCE: The body is more or less circular and laterally flattened, from 1 to 3 cm in diameter. The test is white, opaque and tough, but usually very thin and flaccid. Two specimens from Hervey Bay (QM G9381, GH2211) have a firm and slightly translucent test. There are some furrows, creases and low swellings on the surface, but they are usually obscured by foreign particles adhering to the test. The apertures are almost sessile and one-third of the body length distant from one another.

There are hollow, conical, sharply pointed, overlapping siphonal spines, 0.05 mm long, on the terminal half of the siphon lining. The siphonal spines have a wide, circular base that contains a single large spherical cell. They narrow abruptly and curve forward. The siphon lining has broad purple stripes in the preserved specimens.

INTERNAL STRUCTURE: The body wall has a very diffuse network of muscles and is delicate, thin and transparent. Longitudinal muscle-bands radiate from the siphons to about one-third of the distance down the body. The dorsal tubercle is a rounded cushion with a U- or C-shaped slit, directed anteriorly. The horns of the slit may be curved in or out and, in one specimen, are irregularly convoluted. The branchial tentacles are long and laterally flattened. The wide dorsal lamina extends most of the length of the pharynx. The branchial folds are broad, but do not overlap.

The internal longitudinal vessels are not crowded and there are up to 8 on the folds and 2 to 5 in the interspace. These vessels are rather thick and solid. In a specimen of 2 cm (QM G9681) they are arranged according to the following formula: E3(8)2(8)2(8)2(6)2 DL. There are 10 to 15 long, rectangular stigmata per mesh in the interspaces.

The gut is voluminous and, in all except the specimen from Hervey Bay, is filled with mud. The oesophagus is short. The narrow stomach, swollen at the cardiac end, and narrowing to the diameter of the intestine at the pyloric end, is about half of the length of the ascending limb of the gut loop. Longitudinal stomach folds are not visible from the outside of the stomach. Where the intestine bends at the pole of the gut loop, it swells to twice its diameter. The proximal part of the rectum is also distended, while the distal part is narrow and terminates in a 12-lobed anus at the base of the atrial siphon. Anal lobes are wide and shallow and are obscured when the anus is distended. A very deep typhlosolar fold along the inner curve of the intestine almost completely bisects the lumen, curves around into the swollen part of the rectum and terminates blindly about halfway along its length. The distended gut is rather fragile. The space enclosed by the primary loop is completely occluded by the gut, although in one juvenile specimen there is a very thin endocarp. The secondary loop is deep and open.

There are two broad, sausage-shaped gonads on each side of the body. On the left, the posterior gonad projects down into the secondary gut loop.

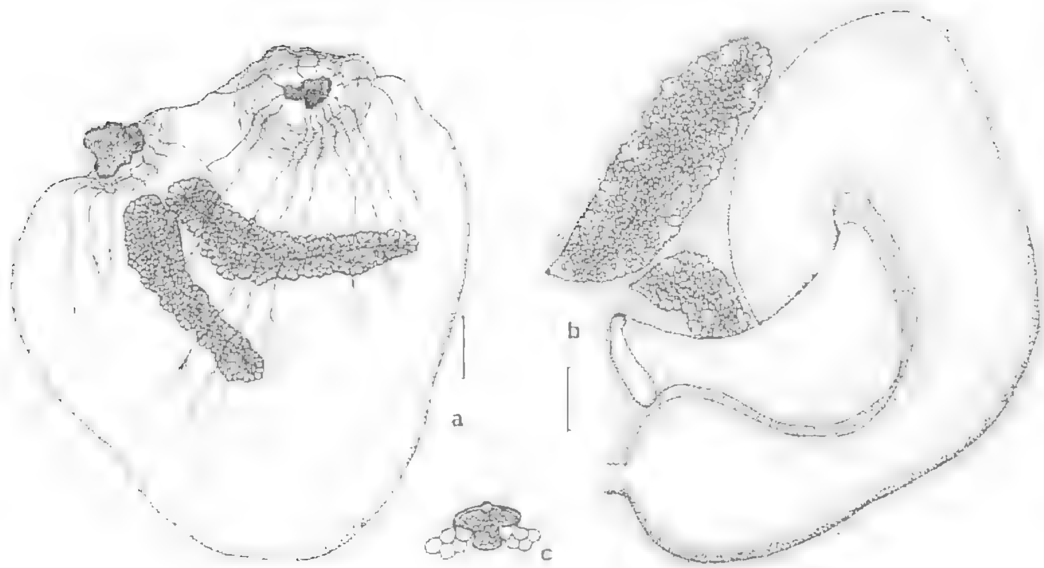


FIG. 57: *Cnemidocarpa intestinata* n.sp. — a, body removed from test, from right (QM G9681); b, gut and gonads (QM G9785); c, cross section through gonad. (Scales: a, 2.0 mm; b, 1.0 mm).

The male follicles are along the sides of the ovarian tube. With maturity, they proliferate and constrict the ovarian tube from the sides at regularly spaced intervals, so that the ovary appears to be segmented, each segment consisting of ovary where it protrudes between the constricting groups of testis follicles.

Usually there are no endocarps either in the gut loop or on other parts of the atrial lining.

REMARKS: The species appears to be specialised for a muddy habitat and is often found in association with *Cnemidocarpa floccosa* and *Ascidia sydneiensis*.

The test and the gonads to some extent resemble those of *C. areolata*, but the present species is readily distinguished by the absence of endocarps, the very delicate and transparent body wall, the specialised gut, the long meshes of the branchial sac with large numbers of stigmata, and the sharply pointed, conical siphonal spines (quite unlike the rounded scales that are usually found in this genus). These spines resemble those of *Polycarpa olitoria*.

Cnemidocarpa lobata (Kott, 1952)
(Figs 50e, 58)

Styela lobata Kott, 1952, p.222.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 218.73; Esperance, WAM 138.75). Victoria (off Ninety Mile Beach, QM G11856; Bass Strait, NMV H396). Tasmania (Hobart, TM D1807; St Patrick's Head, TM D1849; S.E. Bruny I., TM D1855). Queensland (Gladstone Harbour, QM G9801; Calliope River, QM GH2159; Townsville, QM GH718 GH1387 GH1389).

PREVIOUSLY RECORDED: South Australia (Port Noarlunga — Kott 1952). Tasmania (d'Entrecasteaux Channel — Kott 1952). New South Wales (Cronulla — Kott 1952).

The species has been taken from wharf piles and on muddy or sandy substrates. Each record represents no more than one or two specimens. The species apparently has a range in temperate waters across the southern coast of Australia, extending into the tropics along the eastern coast to Townsville.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals range from 1 cm to 5 cm. The body is almost hemispherical, fixed by a wide, flat base that occupies the ventral and left sides; or it is oval, completely encased in sand, and possibly lying free on a sandy substrate. In larger specimens, the apertures are on short siphons projecting from the upper surface, the branchial aperture terminal (and sometimes turned ventrally) and the atrial aperture antero-dorsal and obliquely oriented. In smaller specimens and in sand-encased, possibly free, individuals, the apertures are sessile. The test is thin. When densely encrusted with sand, it is brittle (QM G11856), but when the sand is absent

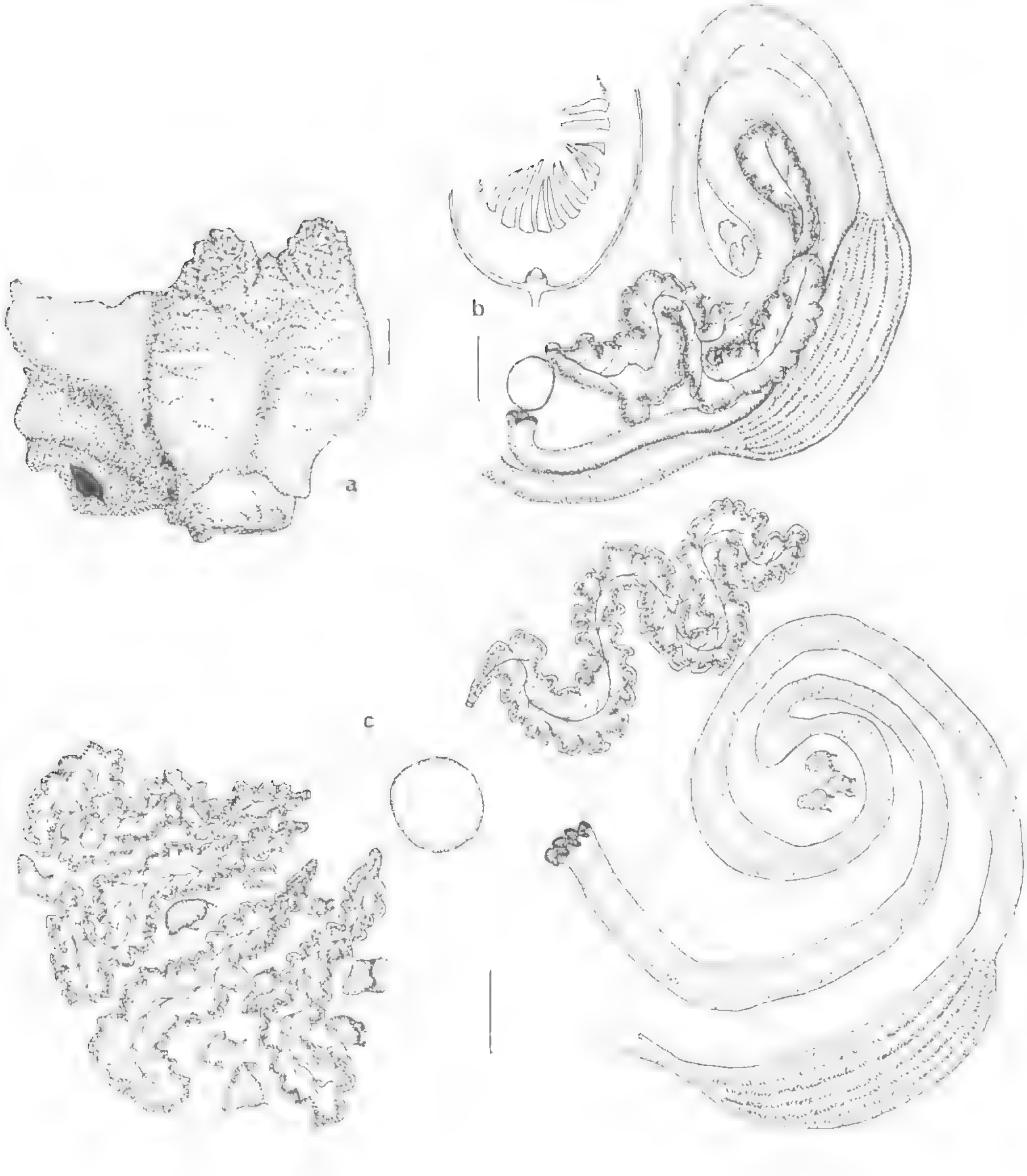


FIG. 58: *Cnemidocarpa lobata* — **a**, external appearance (WAM 138.75); **b**, left side of body (TM D1807); **c**, gut and gonads (QM GH1367). (Scales: **a**, 5.0 mm; **b**, **c**, 2.0 mm).

(WAM 138.75), the test is leathery, rough and tough. Pointed papillae are sometimes present around the apertures.

INTERNAL STRUCTURE: The body wall is very thin and adheres very closely to the test. The musculature is strong on the siphons, but fades out on the remainder of the thin, delicate posterior part of the body (as in other species of this genus). The dorsal tubercle, which protrudes into the lumen of the pharynx, has a simple, C-shaped slit with the opening directed anteriorly. The centre of the tubercle surrounded by the opening is sometimes produced forwards as a rounded papilla.

The branchial sac is delicate. The folds are of variable width, sometimes being little more than raised ridges, but in larger specimens forming flat folds. They never overlap. The internal longitudinal vessels are well-spaced and ribbon-like. They have the following arrangement: E2(9)3(9)2(11)2(10)DL (QM GI1856, 1.5 cm); E8(16)8(19)9(16)6(10)4DL (TM D1849, 4 cm). In larger specimens the number of vessels increases markedly. There are 5 or 6 stigmata per mesh in the interspace.

The gut loop is very long and narrow, the pole of the loop bending back to form a very deep secondary loop. The oesophagus is long. The stomach, which is narrow and elliptical, with longitudinal folds, occupies about one-third of the ascending limb of the gut loop. The rectum is short in relation to the rest of the gut loop, and the anal border has only a few, rather irregular, lobes.

The gonads are long and undulating. There are rounded swellings along each side of the ovary. Vasa efferentia, from a double row of lobed male follicles beneath the ovary, pass around it (usually between the swellings), joining a median vas deferens on its mesial surface. There are 1 or 2 gonads on the left. They extend across the body anterior to the gut loop; or the proximal end of the most posterior of 2, or of the single gonad, is enclosed in the secondary gut loop. Occasionally gonads are absent from the left side of the body. On the right, 3 or 4 gonads converge toward the atrial aperture.

There are a few small endocarps enclosed in the gut loop and scattered on the body wall between the gonads.

REMARKS: *Cnemidocarpa lobata* is distinguished by the narrow and deeply curved gut loop, narrow stomach, the undulating and irregularly lobed gonads, and the thin body wall adhering closely to the test. *Cnemidocarpa clara* Hartmeyer, 1906 and *C. macrogastra* (Oka, 1935) from Japan have similar gonads, but lack the deeply curved gut loop of the present species.

Cnemidocarpa oligocarpa (Sluiter, 1885)
(Fig. 59)

Styela oligocarpa Sluiter, 1885, p.187; 1890, p.332.

DISTRIBUTION

NEW RECORDS: Queensland (Abbot Point, specimen lost).

PREVIOUSLY RECORDED: Indonesia (Sluiter 1885, 1890).

DESCRIPTION

EXTERNAL APPEARANCE: The body is upright (up to 2 cm) with a terminal branchial aperture and an atrial aperture one-third of the distance down the dorsal surface. The body may narrow to a short stalk posteriorly, or be rounded and sessile. The test is thin and leathery, with longitudinal furrows, creases and rounded swellings.

INTERNAL STRUCTURE: The body wall is thin. The outer circular layer of muscles forms an almost continuous thin coat overlying internal longitudinal bands. The dorsal tubercle is in a very wide, shallow peritubercular area. The slit is a shallow U-shape, sometimes with the left horn turned in.

The branchial sac is delicate, with very low, rounded folds. Up to 10 internal longitudinal vessels are crowded on the folds and 2 or 3 in the interspace, as in the following formula: E2(9)3(10)2(10)3(8)1DL. The vessels in the interspace are quite far apart, and there are 4 to 6 stigmata per mesh.

The gut forms a tight, deeply curved loop. The stomach is short and pyriform, with internal pleats. It is wider at the pyloric than at the cardiac end, and narrows abruptly to the intestine. There are 2 or 3 endocarps in the gut loop. The rectum turns anteriorly to the atrial aperture. The anal border has rounded lobes.

There are up to 4 long, thin gonads on each side of the body, radiating in toward the atrial opening. On the left, the anterior gonads extend across the top of the pole of the gut loop and the 3 posterior gonads project down into the curve of the gut loop. Small, rounded endocarps are scattered over the body wall between the gonads.

REMARKS: The type specimen (ZMA V.TU1033) from Billiton closely resembles the Queensland specimen. The species is distinguished by its very low branchial folds and relatively numerous and narrow gonads. *Cnemidocarpa margaritifera* Michaelsen, 1919, from the Red Sea has similar gonads and endocarps, but very much better developed branchial folds.

FIG. 59: *Cnemidocarpa oligocarpa* — gut and gonads. (Scale: 1.0 mm).

Cnemidocarpa pedata (Herdman, 1881)
(Fig. 60; Pl.11la)

Polycarpa pedata Herdman, 1881a, p.71; 1882, p.180. Traustedt, 1885, p.48. Pizon, 1908, p.218. Hastings, 1931, p.74. Harant and Tuzet, 1932, p.5. Tokioka, 1958, p.322. Kott, 1964, p.137

Pandocia pedata: Van Name, 1918, p.97.

Styela pedata: Kott, 1972b, p.185; 1975, p.13.

Styela whiteleggii Herdman, 1899, p.40. Kott, 1952, p.212

Tethyum whiteleggii: Hartmeyer, 1909, p.1364.

DISTRIBUTION

NEW RECORDS: South Australia (Cape Northumberland, QM G11895). Victoria (South Gabo I., QM G11849; Bass Strait, Marlin Oil Rig, QM G9057–8 G9510–11 G9645 G9649 G9731; Iron Prince Reef, NMV F51592). New South Wales (Shell Harbour; Solitary Is, QM G9609–10; Port Kembla; Jervis Bay, QM G10085; off Crookhaven River, AM Y12221; Arrawarra, QM GH1398). Queensland (Moreton Bay, QM G4911; Heron I., QM GH1417; Swain Reefs, QM GH1413; Cairns QM GH763; Lizard I., QM G9731)

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1972b 1975). New South Wales (Port Stephens, Port Jackson — Herdman 1899). Queensland (Townsville — Kott 1964; Port Curtis — Kott 1952; Low Is — Hastings 1931). Indonesia (Harant and Tuzet 1932). Philippines (Herdman 1882, Van Name 1918). Japan (Honshu — Tokioka 1958).

The species has not been recorded from Western Australia or Indonesia, which, in view of its occurrence in the Philippines and Japan, is surprising. The absence of records from these intermediate locations may be the result of lack of collecting at the depths at which the species has been recorded: from 10 to 60 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are robust, from 3 to 20 cm long. The body is swollen and rounded posteriorly. Anterior to the atrial aperture the body narrows to only half the diameter of the posterior end. Both apertures are on distinct, sometimes long, siphons. The terminal branchial siphon usually curves ventrally or to the left. The atrial siphon usually extends forwards from the anterior part of the postero-dorsal swelling, and curves dorsally away from the branchial opening. In younger specimens, the posterior part of the ventral border gradually curves dorsally. As the posterior end of the body swells, the ventral line of the body extends straight from the branchial aperture to meet the posterior border almost at right angles.

Living specimens are orange. In preservative, the larger specimens fade to dark or light grey, while smaller specimens are whitish in colour. Occasionally there is some epiphytic weed on the test, but it is not heavily encrusted. Several of the specimens from more temperate locations are completely enveloped in purple, orange or green sponge.

In specimens from 2 to 5 cm, the external test has longitudinal creases on the anterior half of the body; the surface between the creases may be raised into rounded swellings. However, in larger animals the surface test is smooth, with only very occasional creases. The test is always quite hard and very tough. There are 4 conspicuous, round swellings around each aperture. There is often a short, thick extension of the test from the ventral border supporting the long, curved antero-posterior axis of the body horizontally; or individuals may be upright, with a short stalk postero-ventrally and accessory prop-like extensions of the test postero-dorsally. Some of the specimens from Lizard I. have distinct leathery stalks that are almost as long as the body.

Minute, overlapping scales are present in the outer part of the siphonal lining.

INTERNAL STRUCTURE: The body of preserved specimens is usually dark. It sometimes, though not always, adheres to the test. The musculature is strong but not very thick. Longitudinal and circular muscles branch and anastomose to form an irregular mesh. The body wall is thick and opaque in the larger specimens, but in smaller specimens the internal organs can be seen through the musculature.

The branchial tentacles are not crowded and in large specimens are often rather thick and stumpy.

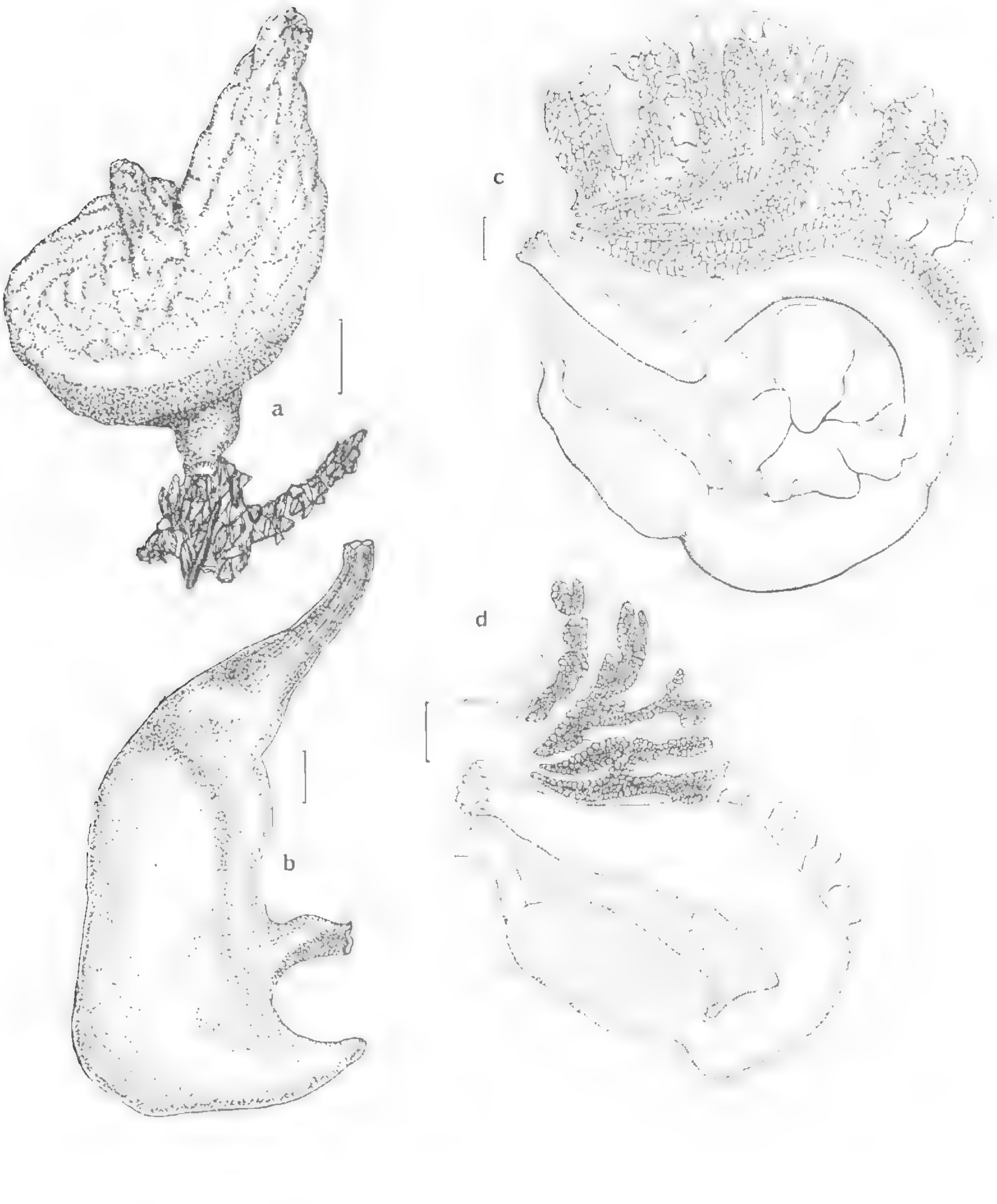


FIG. 60: *Cnemidocarpa pedata* — **a**, external appearance, small specimen from northern Queensland (QM GH763); **b**, body removed from test; **c**, **d**, gut, gonads and endocarps (QM G11849, G9731). (Scales: **a**, **d**, 5.0 mm; **b**, **c**, 2.0 mm).

The dorsal tubercle varies from a simple, rounded cushion with a C-shaped slit (QM G11895) to an expanded cushion with separate, crowded punctate openings or a convoluted slit that completely fills the peritubercular area.

The branchial folds are deeply curved, wide and usually overlapping. They are sometimes so voluminous that there is a secondary pleat in each fold either at the base of the fold or forming a double fold. Branchial formulae from different specimens are: DL8(13)6(15)5(12)5(9)5E (QM G11895); DL18(26)9(26)8(24)8(23)8E (QM G9731); DL35(12;30)12(20;20)15(5;20)15(5;15) 10(9)3E (QM GH1417 with accessory folds and an extra fold).

In the largest specimens, often more than 50 internal longitudinal vessels lie between the dorsal lamina and the first fold, but only about 10 vessels are in the interspaces. There are never more than 5 to 8 stigmata per mesh. The number of vessels between the dorsal lamina and the first fold increases toward the posterior end of the body as its diameter increases, and the vessels, instead of extending parallel to the dorsal lamina, terminate at an angle to it.

The gut loop is relatively short and simple. It is primarily an oblique, simple loop across the postero-dorsal corner of the body, projecting backward from the oesophagus. The stomach is pear-shaped to elliptical, expanding slightly toward the pyloric end. It occupies about half of the ascending limb of the gut loop. The internal, longitudinal and oblique pleats are usually visible externally. The intestine curves through 180° to extend in a straight line parallel to the ascending limb. It terminates in a lobed anus that often bends into the atrial siphon. The 12 to 15 anal lobes are long and conspicuous. As the posterior swelling of the body increases, the proximal part of the descending limb of the loop describes a wide, open curve. The rectum bends antero-dorsally to the atrial aperture. Thus, although the descending limb of the gut loop is often curved, the loop itself is not.

There are up to 8 gonads on the right side of the body and 3 to 5 on the left. They are often so deeply embedded in the body wall that their number can only be recognised by the ducts that project around the atrial opening. They are usually very much branched. When immature, the simple, pear-shaped male follicles are seen to be evenly spaced and tightly applied along each side of the narrow branching ovarian tubes. As they mature, the male follicles, become lobed and proliferate, and are found in patches beneath the ovary as well as forming a wide band along each side. They sometimes overlap onto the mesial surface of the ovary. The proliferation of the male follicles in the body wall around the ovaries causes the gonads to appear confluent. Gonads are developed in specimens from 2 cm long (QM G9131). Endocarps are numerous in the gut loop and also occur profusely between the gonads and their branches.

REMARKS: This is one of the largest and most robust of the species occurring in Australian waters.

Van Name (1918) has discussed the similarity of body shape in this species and *Polycarpa aurata*. However, in the latter species the longitudinal axis of the body is more curved and the atrial siphon projects from deep in the dorsal concavity. In the present species, the body is thicker and the atrial siphon rises from the anterior border of the posterior expansion of the body. The species are more readily distinguished by the position of openings of the gonoducts: around the atrial aperture in the present species; scattered over the body wall in *Polycarpa aurata*.

The species is more closely related to *C. stolonifera*, from which it is distinguished by its shorter stomach, less numerous stigmata in each mesh, and more complex opening of the neural gland.

The rounded, posteriorly expanded body without lateral flattening; the wide branchial folds with numerous internal longitudinal vessels on and between the folds; the short, straight or open gut loop with its conspicuous anal lobes; the pear-shaped stomach broader at the pyloric end than at the cardiac end; and the proliferation of testis follicles around the ovary, are characteristic.

Cnemidocarpa personata (Herdman, 1899)
(Fig. 61)

Styela personata Herdman, 1899, p.41. Tokioka, 1967a, p.184.

Tethyum (Styela) godeffroyi Michaelsen, 1912, p.125.

Styela etheridgii: Kott, 1952, f. personata p.220 (part, specimens from Port Jackson and Long Reef); 1964, p.139 (part, specimens from Moreton Bay).

Styela stolonifera: Kott 1952, p.215 (part, specimens from Tasmania).

DISTRIBUTION

NEW RECORDS: Tasmania (Strahan, AM G2622-3). Queensland (Hervey Bay, QM G9379; Heron I., QM G10097-8).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1964). New South Wales (Port Jackson — Herdman 1899, Michaelsen 1912, Kott 1952, Tokioka 1967a; Long Reef — Kott 1952)

FIG. 61: *Cnemidocarpa personata* — a, gut, gonads and endocarps (QM G10098); b, proximal end of stomach showing relationship of folds to suture line (QM G9379). (Scales: a, 1.0 mm; b, 0.5 mm).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are up to 5 cm in length. They are usually hemispherical or dorso-ventrally flattened, attached posteriorly or along the ventral side, or by the ventro-lateral aspect of the right side of the body. Both apertures are on the dorsal or upper surface; the branchial aperture towards the anterior end; the atrial aperture about halfway along. Both apertures are almost sessile. The test is firm tough and opaque, but usually rather thin. It has irregular creases on the surface. The external lobes of the apertures are small and inconspicuous.

INTERNAL STRUCTURE: The body wall is rather transparent, the internal organs being visible from outside. The muscles are moderately well developed, with conspicuous radiating, internal, longitudinal bands and an outer coat of diffuse, circular fibres. The dorsal tubercle is a large cushion that fills, or sometimes protrudes anteriorly from, the V-shaped peritubercular area. The slit is U- or C-shaped, with the horns turned in or out.

The branchial sac is delicate, with wide, ribbon-like, internal longitudinal vessels, which are usually crinkled. The folds are rounded rather than flat. The branchial vessels are well-spaced, almost the same distance apart on the folds as in the interspace. Specimens from Moreton Bay (QM G4912) have up to 13 vessels on the folds and 4 in the interspace. Tokioka's (1967a) specimens from Port Jackson have more branchial vessels both on the folds and in the interspace, although another specimen from Port Jackson (AM G13591) has the following arrangement of branchial vessels: E3(8)4(10)6(11)6(12)0DL0. The meshes are rather long, with about 10 stigmata.

The gut loop is narrow, but not very long. Although it extends along the whole of the ventral curve of the left side of the body, it may be almost straight or only gently curved. The oesophagus is of moderate length. The stomach is long and cylindrical, occupying most of the ascending limb. It is constricted from the intestine at the pyloric end. There are about 30 long gastric folds, many extending antero-ventrally from the cardiac end of the stomach to the suture line along the greater part of its length. The folds posterior to the suture line extend parallel to it from the cardiac to the pyloric end of the stomach, and only some very short folds at the pyloric end of the stomach meet the suture line. The rectum is short and forms a slight angle with the descending limb of the primary loop. The anal border is irregularly lobed.

The gonads, of variable length and thickness, are usually rather sinuous. There are 2 to 4 on the left, extending across the body wall anterior to the gut loop. On the right, 2 to 4 gonads radiate toward the atrial aperture. They consist of cylindrical, sometimes branched, ovarian tubes with male follicles beneath, and projecting up into the ovary. The male follicles are primarily pear-shaped, and become lobed and branched as they mature.

Small endocarps are present on the body wall between the gonads. There are usually only one or two rather cylindrical, flat-topped endocarps in the pole of the gut loop.

REMARKS: The species is distinguished from *C. areolata* principally by its shorter gut loop and the course of the stomach folds. The large number of gonads that are often found on the right side of the body resemble the condition found in *C. oligocarpa* Sluiter, 1885, *C. tinkatue* (Van Name, 1918) and *C. madagascariensis* Hartmeyer, 1916. Of these, only *C. tinkatae* has a similar range of internal longitudinal branchial vessels and a fairly long stomach, but is distinguished by its greater number of gonads. Only two specimens of *C. madagascariensis* have been recorded (Vasseur 1967a) and its stomach has not been described. It is probably a distinct species, having only 2 or 3 branchial vessels in the interspace, fewer than in the present species. *Cnemidocarpa oligocarpa* is distinguished by its short, pear-shaped stomach, narrow at the cardiac end.

Cnemidocarpa posthuma Hartmeyer, 1927

Cnemidocarpa posthuma Hartmeyer, 1927, p.169. Hartmeyer and Michaelsen, 1928, p.385.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Michaelsen and Hartmeyer 1928).

DESCRIPTION (after Hartmeyer and Michaelsen 1928)

EXTERNAL APPEARANCE: Only a single specimen 1.6 cm long and 1.1 cm wide is known. The body is upright and almost cylindrical. Foreign particles adhere to the base. External siphons are small and wart-like, the branchial aperture terminal and the atrial aperture one-third of the distance down the dorsal surface. The outer surface is smooth on the right side, but has creases on the left. The test is rather thick, tough and leathery.

INTERNAL STRUCTURE: The body wall is moderately strong, but slightly transparent. The muscles are not particularly well developed, however, and the longitudinal bands are more conspicuous than the outer circular layer. The dorsal tubercle is an irregular quadrilateral cushion with a horseshoe-shaped, almost circular slit, the opening turned to the left. The dorsal lamina is moderately high and smooth-rimmed.

The branchial sac has 4 distinct folds, unequal in size, with the dorsal fold the broadest. The inner longitudinal vessels are arranged according to the following formula: E5(8–9)10–12(15)10–12(15)10–12(20)9DL4(30)10–12 (15)10–12(15)10–12(8–9)5E.

The gut loop is deeply curved and extends into the anterior part of the body. The oesophagus is moderately long, and the stomach rather long and spindle-shaped, with distinct longitudinal folds. The primary loop is moderately long, wide at the pole and closed. The secondary loop is wide open. The anal border has 10 to 12 rounded lobes.

The gonads are not mature. There is a single gonad on each side. Numerous endocarps are distributed over the body wall and in the gut loop.

REMARKS: The only other species of *Cnemidocarpa* with a single undivided gonad on each side that are known from the Indo-West Pacific are *C. lapidosa* (Herdman, 1906) and *C. reticulata* Millar, 1975. The latter species is wider than it is long, has both apertures on the rounded upper surface, and resembles *C. posthuma* in the relative size of its branchial folds (with the dorsal fold the largest). However, its branchial formula is: DL5(16)4(5)4(6)6(5)4E. It is distinguished from *C. posthuma* by its shape and by the relatively fewer internal longitudinal vessels in the pharynx. Herdman's species from Sri Lanka has a similar branchial sac to *C. posthuma*, but the test is brittle and impregnated with sand. The type specimen of *C. lapidosa* (BM 1907.8.30.15) is not in good condition and, although the body wall is seen to be very thin and closely adherent to the stiff brittle test, no other details of its structure could be discerned.

Cnemidocarpa radicosa (Herdman, 1882)
(Fig. 50F, 62)

Styela radicosa Herdman, 1882, p.163.

Styela etheridgii Herdman, 1899, p.38. Millar, 1966, p.370.

Cnemidocarpa etheridgii Hartmeyer, 1927, p.170. Kott, 1952, *C. etheridgii* p.219; 1972a, p.31; 1975, p.14; 1976a, p.76; (not: 1972d, p.253, < *C. areolata*).

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, 69.72). South Australia (Port Lincoln, QM G9612; Port Noarlunga, QM G9326). Tasmania (Bruny I., NMV 72/13; Roche's Beach, TM D1839 D1843 D1868; off NW coast, TM D982; Schouten Passage, TM D719; d'Entrecasteaux Channel, QM G995; Port Davey, QM GH2041). Victoria (Lake's Entrance, NMV H261 H923 H983; Bass Strait, NMV H768, QM G9509 G9647–8 G11851 GH2676; Port Phillip Bay, NMV September 1881). New South Wales (Port Kembla, AM G10063; Glass and Bottle Reef, QM G8585; Solitary Is, QM G9611). Queensland (Tallebudgera, QM GH2451).

PREVIOUSLY RECORDED: Western Australia (Triggs I. — Kott 1952). South Australia (Great Australian Bight — Kott 1975; St Vincent Gulf — Kott 1952 1972a; Spencer Gulf — Kott 1952). Tasmania (d'Entrecasteaux Channel — Kott 1952). Victoria (Bass Strait — BM1887.2.4.86 Herdman 1882; Phillip I. — Kott 1952; Cape Grant, Cape Nelson, Portland — Kott 1976a; Port Phillip Bay — Millar 1966, Kott 1976a). New South Wales (Port Jackson — Herdman 1899).

The species has been recorded down to about 50 m, in caves, *Macrocystis* beds and on sandy and rocky substrates. It is an indigenous Australian species and has

FIG. 62: *Cnemidocarpa radicosa* — **a**, **b**, external appearance (WAM 69.72, NMV 72.13); **c**, gut, gonads and endocarp. (Scales: **a**, **b**, 1.0 cm; **c**, 2.0 mm).

not been recorded from adjacent areas. Records are confined to temperate waters, south of Port Jackson on the eastern coast and of Cockburn Sound on the western coast. It is common in Tasmanian waters.

DESCRIPTION

EXTERNAL APPEARANCE: The species is large and robust, up to 10 cm in length and rather flaccid. The external test is marked with longitudinal furrows. The body narrows to the short, terminal branchial siphon, which is sometimes turned to the right. The atrial aperture is also short and is always located one-third of the distance down the sloping dorsal surface. The atrial siphon may be turned to the left, or posteriorly. In smaller specimens, the atrial aperture is sessile, with four swellings of the test corresponding to the external lobes. There is sometimes a thick, posterior extension of the test by which the animal is fixed. More often it is sessile, fixed by a large part of the posterior or postero-ventral surface, or by the posterior half of the right side. The test is tough and leathery but relatively thin (which accounts for the lack of rigidity). It is usually thicker anteriorly, where it is also strengthened by creases and furrows, but is paper-thin posteriorly. Generally the test is white in preservative. However, sometimes the posterior, smooth part of the test is brown, possibly from being partly buried in the substrate (QM G11851). Living specimens are pale cream to bright yellow (Kott 1972a).

The outer part of the siphonal lining has thin, curved and overlapping scales with rounded, free borders.

INTERNAL STRUCTURE: The body wall is closely adherent to the test and is fleshy and thick. It has a well-developed external layer of circular fibres, with inner longitudinal bands radiating from the apertures.

The branchial tentacles are rather long and crowded. The dorsal tubercle is large, almost completely filling the peritubercular area. It has a U-, C- or S-shaped slit with horns turned in or out, and is often even more complex (Kott 1952).

The dorsal lamina is a plain, wide membrane. The branchial folds are wide. The internal longitudinal vessels are evenly spaced on the folds and in the interspaces. The folds are well separated and do not overlap. The branchial formula for a moderately sized individual is: DL7(19)5(9)6(14)6(17)E. There are up to 20 longitudinal vessels on each fold and 7 or 8 in an interspace. There are 5 to 8 stigmata per mesh.

The gut loop occupies the posterior end of the body. It is deeply embedded in the body wall. The stomach is about half the length of the ascending limb of the loop. It has internal longitudinal folds and is more or less cylindrical, being about the same diameter as the intestine. However it occasionally narrows to the intestine and appears more spindle-shaped. The anal border is smooth and bilabiate.

There are 4 or 5 sausage-shaped gonads embedded in the body wall on the right side of the body. Their ducts open around the atrial opening. On the left side of the body, the posterior gonad is round rather than sausage-shaped and is embedded in a thickening of the body wall in the rather shallow secondary gut loop. The second gonad on the left is elongate and extends across the body wall anterior to the pole of the gut loop. Gonads consist of a tubular ovary and pear-shaped follicles that occur beneath and around the sides of the ovary and obscure its shape. The male follicles are not very branched.

There are one or two endocarp-like thickenings of the body wall in the gut loop. These may extend posteriorly over the proximal part of the gut loop and be continuous with the thickened body wall behind the branchial sac.

REMARKS: The thin, flaccid, even papery, test of this species is reminiscent of some smaller specimens assigned to the species *C. areolata* and *C. personata*: the shape of the body, without marked curvature (such as is found in *C. pedata*) and with anterior furrows and creases, is reminiscent of larger specimens of *C. areolata*; the long stomach resembles that of *C. personata*.

Specimens from 3 to 10 cm long have been examined and the characteristic branched gonads, the thick body wall with deeply embedded organs, and the smooth-rimmed anus are always present. None had separate endocarps. The type specimen (BM 1887.2.4.86) conforms with the specimens formerly assigned to *C. etheridgii* in all respects.

Cnemidocarpa stolonifera (Herdman, 1899)
(Fig. 63; Pl.IIIb)

Styela stolonifera Herdman, 1899, p.42. Kott, 1952, p.215 (part, not specimen from Tasmania, < *C. personata*); 1966, p.298. Millar, 1963, p.728.

DISTRIBUTION

NEW RECORDS: New South Wales (Coffs Harbour, QM G11848; Solitary Is., QM G9617; Byron Bay, QM G11847). Queensland (Moreton Bay, QM G10071 G10074 G10007 G4901 G4935 G6140–6144 GH365 GH343 GH1422 G1058; Mooloolaba, QM G10109–11; Hervey Bay, QM G9615–6 G9380; Heron I., QM G10177 GH1421; Wistari Reef, QM G9368; Swain Reefs, QM GH1409; Mackay, QM G9979; Abbot Point, QM GH620–4 GH626–31 GH710; Lindeman I., AM Y1706; Innisfail, QM GH801; Lizard I., QM GH326 G9728; Townsville, QM GH714; Cape Tribulation, QM GH789).

PREVIOUSLY RECORDED: New South Wales (Port Jackson — Herdman 1899, Millar 1963). Queensland (Moreton Bay — Herdman 1899, Kott 1952 1966; Hervey Bay — Kott 1966).

The species is one of the few indigenous Australian species that occurs principally in tropical waters. Kott (1952) records the species from Rottnest I. This record could not be confirmed and the species appears to be confined to the eastern coast, its southern limit being at Port Jackson. The species is recorded from sandy substrates down to 33 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals have a spherical to oval body (up to 6 cm long), usually with a posterior stalk of variable length that breaks up into short, root-like processes basally. Occasionally there is no stalk, and root-like processes develop from the basal test to anchor the individuals. The apertures are on siphons close together on the upper, free surface of the body. The siphons may diverge from one another, or they may project forwards almost parallel to one another. The siphons are of variable length, but the atrial siphon is invariably longer than the branchial siphon; thus the excurrent and incurrent streams of water are separated. Minute overlapping, curved scales are present on the siphonal linings, and in fresh material these are pale blue and slightly iridescent.

The test is tough and leathery but not thick. Rounded swellings extend in 4 regular, longitudinal rows along each of the siphons. Although these swellings tend to be arranged in longitudinal rows on the anterior part of the test, they are not as conspicuously regular as on the siphons. There is always a single, median, dorsal swelling between the bases of the siphons. The posterior part of the body is smooth and is continuous with the stalk. It is usually discoloured and buried in the substrate, with only the anterior half of the body protruding. The stalk is hollow for most of its length, the body wall extending down into it. Living specimens are buff, grey-white, and often have indistinct markings that become brick-red when the animal is removed from the water. This brick red colour is particularly conspicuous between the rounded swellings of the test.

INTERNAL STRUCTURE: The body wall is muscular and closely adherent to the test. About 12 stout, but fairly long, branchial tentacles alternate with minute rudimentary ones. The prebranchial area is very narrow. The dorsal tubercle is in a very shallow peritubercular area. The ciliated aperture on the rounded, conspicuous tubercle is a simple S- or U-shape, the opening

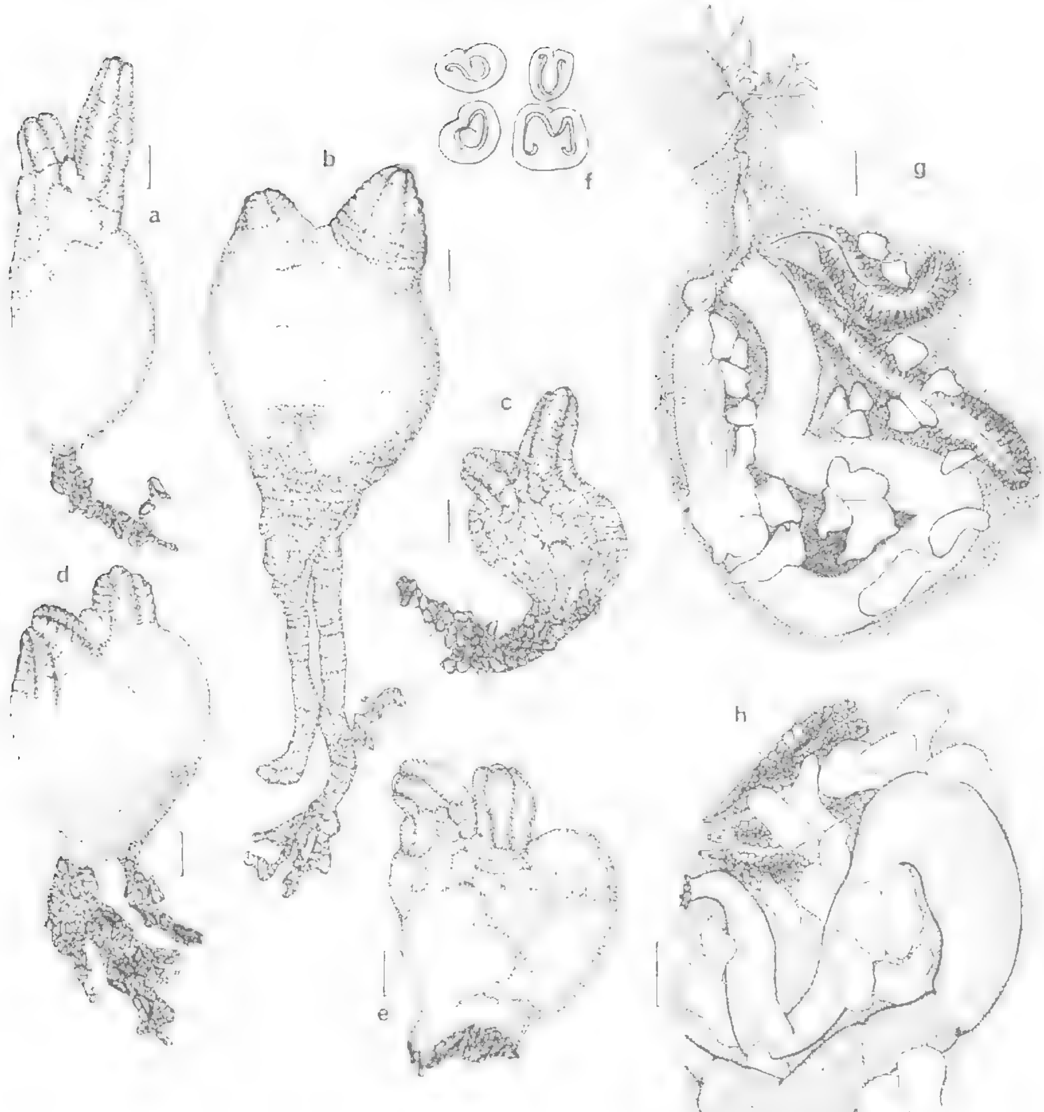


FIG. 63: *Cnemidocarpa stolonifera* — **a – e**, external appearance (QM G9728, G5029, GH326, G1068, G10110); **f**, variation in the dorsal tubercle; **g**, **h**, gut, gonads and endocarps (QM GH326, G9368). (Scales: **a – e**, 1.0 cm; **g**, 1.0 mm; **h**, 2.5 mm).

usually directed forwards with one or both horns turned in or out. Only very rarely is the slit interrupted along its length. The dorsal lamina is a very short, wide membrane and the oesophagus opens from about halfway down the pharynx.

The branchial folds are tall, but not overlapping, and deeply curved. There are from 7 to 14 rather thick, flat, internal longitudinal vessels on the folds and 3 to 6 between the folds. The most dorsal fold on the right often flattens out posteriorly. There are 9 to 15 stigmata per mesh between the folds, in the centre of the branchial sac. No longitudinal vessels run between the dorsal fold and dorsal lamina on the left. Longitudinal vessels are often slightly crinkled along their length. The number of internal longitudinal vessels increases slightly relative to the size of the body.

The gut forms a simple, postero-ventrally oriented, oblique loop when the body is elongate, but when it is wide posteriorly the gut loop is bent up to form a deep secondary loop. The oesophagus is long; the stomach is also long and narrow, being of only slightly greater diameter than the intestine. The cardiac chamber of the stomach has regular, parallel folds. It is separated by a valve from a distal pyloric chamber where the folds are irregular and there are irregular pouches. The oesophagus and stomach together form the greatest part of the ascending limb of the gut loop. The fine, longitudinal ridges of the stomach are not always conspicuous externally. The rectum extends forwards to an anus that is bordered by about 15 slightly irregular lobes. The rectum often contains a large amount of fine, homogenous mud.

Gonads consist of long ovarian tubes with the male follicles in 2 rows beneath the ovary in the typical cnemidocarp arrangement. There are 4 or 5 elongate gonads on the right radiating toward the atrial siphon. On the left, two long gonads or (less often) a single, branched gonad extend parallel to the gut loop. When the gut loop is bent, the gonads extend across the secondary loop to its pole. The gonads are often, but not always, slightly undulating. There is seldom more than primary branching.

The pole of the gut loop encloses about 6 tall, narrow endocarps. Numerous endocarps are also present between the gonads.

REMARKS: This species has sometimes been confused with *C. areolata*, and Millar (1963) suggested that they might be conspecific. However, the strongly curved branchial sac and short dorsal lamina, the long stomach, the thick and absolutely opaque test, the wide branchial folds and thick longitudinal vessels, the long conspicuously ridged siphons and the large number of stigmata in each mesh distinguish the present species. Some larger individuals also resemble *Cnemidocarpa pedata* in external appearance and in the posteriorly oriented, straight gut loop. They can be distinguished from *C. pedata* by their less deeply embedded and usually less branched gonads, longer stomach and rectum, greater number of stigmata in the branchial meshes and undivided slit on the dorsal tubercle.

Cnemidocarpa tripartita n.sp.
(Fig. 64)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, Bass Strait Survey Stn 132, cruise 81.HK.1, 40° 10.8'S,145° 44.2'E, mud with sponges, 76 m, trawl, 3.2.81, holotype NMV H728; Stn 133, 40°33.07'S, 145° 44.7'E, mud with sponges, 68 m, paratypes NMV H725).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are oval or almost spherical, up to 7 mm long and about 5 mm high. The apertures are 4-lobed and sessile, the branchial aperture near the anterior end of the upper surface and the atrial aperture more or less in the centre. The surface is smooth and without wrinkles; sand grains are sparsely embedded in the rather thin, white, translucent test.

INTERNAL STRUCTURE: The body wall is thin, with a layer of circular muscles and internal longitudinal bands. There are about 30 rather short branchial tentacles. The small dorsal tubercle with a U-shaped opening is in a V-shaped peritubercular area.

The branchial sac has only 3 very low folds on each side, formed by internal longitudinal folds crowded together. There are wide interspaces between the folds. The internal longitudinal vessels of the holotype are arranged according to the following formula: E3(3)3(2)2(3)0DL0(2)3(3)3(2)4E. The 6 long stigmata in each mesh are crossed by parastigmatic vessels.

The gut loop is very large, occupying about two-thirds of the ventral half of the body. It consists of a rather short oesophagus, opening at the posterior end of the branchial sac. The longitudinally folded stomach is very large, wide, and more or less elliptical, extending almost two-thirds of the length of the ascending limb of the gut loop. The pole of the loop encloses a small, egg-shaped endocarp. The descending limb of the gut loop forms a shallow curve toward the proximal end of the stomach before the short, narrow rectum bends up toward the atrial

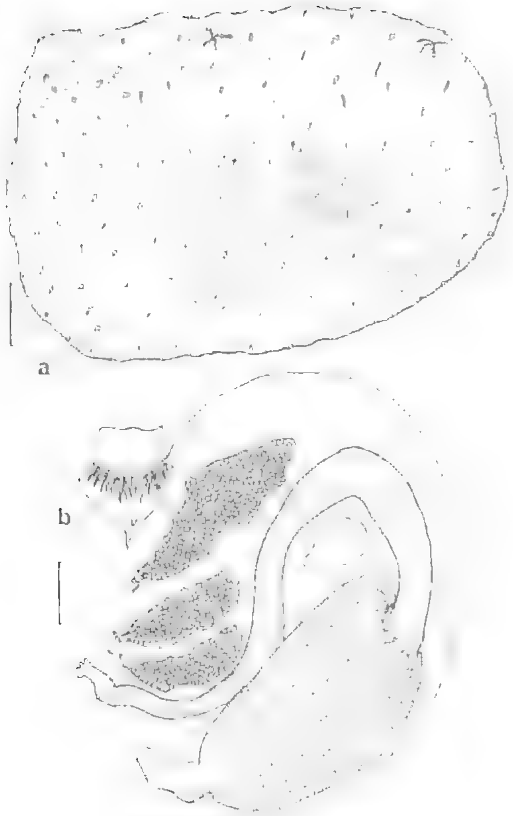


FIG. 64: *Cnemidocarpa tripartita* n.sp. (NMV H728) — a, external appearance from right side of body; b, internal structure. (Scale: 1.0 mm).

aperture. The anal border is divided into 6 well-defined lobes.

There are 2 or 3 gonads on the left and 2 on the right. They are large, thick and slightly undulating, with irregular borders. There are paired rows of slightly lobed testis follicles beneath each large ovary. The gonads are only lightly attached to the body wall.

There are no endocarps on the body wall apart from the one enclosed in the gut loop.

REMARKS: This small species is distinguished from others by its 3 small branchial folds and large gut loop, particularly the large stomach.

Externally, the species resembles *Styela exiqua* Herdman, 1882 (BMNH 1887.2.4.79) from Port Jackson, although the latter species has a short stalk and gathered, rather than lobed, sessile apertures. Herdman has not described the gonads (and they are not present in the holotype, although other internal organs are). The branchial sac of *S. exiqua* has 4 low folds on each side and the branchial formula is: E1(5)1(8)1(9)0(6)DL. There are up to 4 stigmata on the ventral side of the internal longitudinal vessel in the interspace and 2 on the dorsal side. Although *S. exiqua* has a single small endocarp enclosed in the gut loop, its longitudinally folded stomach is not as roomy as that of the present species. It is possible that if further specimens of *S. exiqua* are found, it will prove to be a species of the present genus; it does not, however, appear to be conspecific with *Cnemidocarpa tripartita* n.sp.

The gonads of the present species undulate like those of *Cnemidocarpa aculeata* n.sp., but are much thicker, and more closely resemble those of *C. lobata*. However, the very deeply curved gut loop of the latter species clearly distinguishes it.

Genus **Asterocarpa** Brewin, 1946

Type species: *Styela cerea* Sluiter, 1900

The genus is related to *Cnemidocarpa*. It is distinguished by the position of the gonads, by their more or less radical branching, and by the position and orientation of the gonoducts. Unlike the gonads of *Cnemidocarpa*, those of *Asterocarpa* are confined to a single row along each side of the endostyle. The gonoducts are short; their openings are distant from the atrial aperture and directed away from it.

The genus is monotypic, known from a wide range in the temperate waters of the Indian and Pacific Oceans.

Asterocarpa humilis (Heller, 1878)
(Fig. 65)

Styela humilis Heller, 1878, p.26. Herdman 1891, p.580.
Cnemidocarpa humilis: Michaelsen and Hartmeyer, 1927, p.173.
Styela cerea Sluiter, 1900b, p.24.
Cnemidocarpa cerea: Michaelsen and Hartmeyer, 1927, p.173.
Asterocarpa cerea: Brewin, 1946, p.124; 1950b, p.344; 1950c, p.354; 1952b, p.187. Kott, 1952, p.227. Millar, 1982a, p.78.
Dendrodoa gregaria Kesteven, 1909, p.291.
Pandocia gregaria: Hartmeyer, 1909, p.1484.
Cnemidocarpa gregaria: Michaelsen and Hartmeyer, 1927, p.173.
Tethyum asymmetron Hartmeyer, 1912, p.253.
Cnemidocarpa asymmetra: Michaelsen and Hartmeyer, 1927, p.173.
Cnemidocarpa robinsoni Hartmeyer, 1916, p.224; 1920b, p.131. Van Name, 1945, p.271.

DISTRIBUTION

NEW RECORDS: Western Australia (Albany, WAM 1212.83). Tasmania (S.E. Bruny I., TM D1853; Spring

Bay, QM GH2010). Victoria (Hobson's Bay, QM G11865).

PREVIOUSLY RECORDED: South Australia (Kott 1952). Tasmania (Heller 1878, Kesteven 1909). New Zealand (Sluiter 1900b, Brewin 1946 1950b,c 1952b, Millar 1982a). South Africa (Hartmeyer 1912). Eastern Pacific (Juan Fernandez I. — Hartmeyer 1916 1920, Van Name 1945).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are up to 4 cm in diameter and sometimes occur in aggregates. Apertures are on short siphons, close together on the upper surface and directed obliquely away from one another.

Over most of the body the test is thin, white to beige coloured, smooth, and almost completely opaque and rather flaccid. It is thicker and more irregular around the apertures, where there are small papillae with small, pointed processes.

There are minute overlapping scales in the siphon lining.

INTERNAL STRUCTURE: The body wall is muscular and adheres fairly closely to the test. About 15 larger tentacles alternate with smaller ones; minute rudimentary tentacles occur between them. The dorsal tubercle is large, completely filling the peritubercular area. The slit on the dorsal tubercle is U-shaped, with both horns turned out. The dorsal lamina is long, the oesophageal opening being at the posterior end of the branchial sac.

There are up to 12 internal longitudinal vessels on the relatively narrow branchial folds, but only up to 3 between them. There are 12 to 15 stigmata in each mesh. In a typical specimen the longitudinal branchial vessels are arranged according to the formula: E3(8)3(8)2(10)2(7)0DL.

The gut is narrow and curved around the postero-ventral part of the left side. The pole of the loop is about one quarter of the body length from the prepharyngeal groove. The stomach, which is about half the length of the ascending limb of the gut loop, is broad, internally pleated and tapering at each end. The anal border is bilabiate.

Gonads are present around the ventral curve of the body, on each side of the endostyle. There are 3 or 4 on the right and 2 or 3 on the left, anterior to the gut loop. The irregularly branched ovarian tubes have a double row of male follicles beneath. The branching occurs from about halfway along ovarian tube. Gonoducts are directed ventrally.

Two large flat-topped endocarps are enclosed in the pole of the gut loop. Others are present in the proximal part of the loop between the short oesophagus and the rectum, along the outside of the descending limb of the gut loop and in its curve, as well as along the ventral mid-line between the gonads.

REMARKS: Many authors have discussed the relationships of the synonyms set out above; there seems to be no morphological justification for any one of these to be regarded as distinct species. Although the number and orientation of the gonads and their branches vary, the gut, branchial

FIG. 65: *Asterocarpa humilis* (QM GH2010) — a, external appearance; b, internal structure. (Scales: 0.5 cm)

sac, endocarps and external appearance of individuals of this species are remarkably stable.

Genus **Polycarpa** Heller, 1877

Type species: *Cynthia pomaria* Savigny, 1816

The principal characteristics of *Polycarpa* are the shape and multiplicity of the gonads, which are short with very short ducts opening some distance away from the excurrent aperture. The male follicles lie alongside or beneath the ovary, the ducts joining with a vas deferens on the mesial surface of the ovary. In this they resemble the cnemidocarp condition. Most often the gonads are either arranged in rows or randomly scattered over the body wall. Only very occasionally are they restricted to a single row on each side of the body. They may be entirely embedded in the body wall, or stand on it, projecting partly or completely into the peribranchial cavity. They tend to become more deeply embedded in the body wall with age. The apertures are often sessile; the siphons, when present, are usually only short.

Larvae are small and the larval ocellus is generally lost. Several species are known to be viviparous (*P. argentata*, a western Pacific species; *P. tinctor*, *P. tinctorella* n.sp. and *P. intonata* n.sp. in Australia; and the New Zealand species, *P. pegasis* Michaelsen, 1922 and *P. zeteta* Millar, 1982a). In *P. tinctor* and *P. tinctorella* n.sp. the larval phase is lost altogether and development is direct. This is the only genus of solitary ascidians outside the Agnesiidae and Molgulidae in which these phenomena occur.

Polycarpa, like the Molgulidae, appears to be well adapted to open sea-floor habits, where the necessity for light sensitive larvae to seek shaded settlement sites is removed; and where larval vulnerability to dispersal is reduced by viviparity and direct development. Species denied a capacity for site selection are adapted for open-sea floor habitats when strategies to maintain populations are available (Berrill 1955).

Adaptions in *Polycarpa* that seem to favour a longer retention of eggs and internal fertilisation are: the short gonads and oviducts that usually open into the peribranchial cavity some distance from the atrial aperture; and the tall, crowded endocarps (amongst which the gonads are scattered), which have sometimes been observed to be particularly long around the atrial aperture (see *Polycarpa chinensis*). The arrangement of gonads in the ventral half of the body, or even along the ventral border in so many of the species (as in all the species known to be viviparous), is a further adaptation favouring a viviparous habit.

Other adaptions for a sea-floor habitat that commonly occur in Australian species of *Polycarpa* are a thin test in which strength and often rigidity is derived from embedded sand, test hairs to which sand also adheres; and large or numerous gonads producing large numbers of gametes that complement strategies for population maintenance by maximising opportunities for fertilisation.

An appreciable proportion of the Australian *Polycarpa* spp. display some of the adaptations for the open sea floor (*P. lucilla* n.sp., *P. chinensis*, *P. rigida*, *P. procera*, *P. tinctor*, *P. tinctorella* n.sp., *P. aurita*, *P. intonata* n.sp., and *P. molguloides*).

The species of *Polycarpa* occurring in Australia appear to fall into the following natural groups:

1. *Papillata* group, in which the gut forms a loop and the crowded, narrow, upright endocarps are both enclosed by, and outside, the gut loop. The gut loop is particularly voluminous, with a large typhlosolar fold in the intestine. It has a tendency to be ejected when the animals are collected. One species, *P. intonata*, n.sp. is known to be viviparous.
   The group contains *Polycarpa papillata*, *P. longiformis*, *P. clavata*, *P. aurata*, *P. aurita*, *P. intonata* n.sp., *P. nota* n.sp., *P. olitoria*.

2. *Procera* group, in which the gut forms a simple arc, not a loop, between a posterior oesophageal opening and an anterior atrial opening. The test is thin and rigid with embedded sand. Gonads are usually confined to the margins of each side of the body. The endocarps, which are sometimes especially long around the atrial opening, may restrict the liberation of sexual products. There are two viviparous Australian species (*P. tinctor* and *P. tinctorella* n.sp.) in this group (which also includes the New Zealand species, *P. pegasis* and *P. zeteta*).
   The group contains: *Polycarpa procera*, *P. chinensis*, *P. rigida*, *P. tinctor* and *P. tinctorella* n.sp.

3. *Pedunculata* group, in which the gonads are usually deeply embedded in the body wall. There are always 1 or 2 flat-topped endocarps contained in the gut loop, but none outside it. The internal longitudinal vessels are thick and conspicuous. In some species, testis follicles surround the ovary rather than lie beneath it. Gonads are often especially numerous. *P. argentata* appears to be viviparous, larvae having been found in the peribranchial cavity.

The group contains: *Polycarpa pedunculata, P. ovata, P. molguloides, P. viridis, P. obscura, P. stirpes* n.sp., *P. nigricans, P. flava* n.sp., *P. argentata, P. decipiens*.

Polycarpa contecta may also belong to this group, although its gonads are not embedded. Several attempts have been made to resolve the taxonomy of this group of species (Michaelsen 1905, Hartmeyer and Michaelsen 1928, and Kott 1972a). Differences based on number of polycarps are unreliable, since there is great intraspecific variability in this character with age and maturity. Similarly, the orientation of the gut and the length of the rectum tend to vary with body shape and size. The reliable specific characters appear to be: differences in the size and number of anal lobes; the shape of the testis follicles; other special features such as transparent and pigmented spherical vesicles embedded in the body wall; white fibres in the blood vessels (*P. obscura*); and the colour of the living specimens. However, the colour of the preserved material varies in several of the species. In particular, both the test and body wall of *P. pigmentata, P. argentata* and *P. viridis* range, when in preservative, from beige or pale mauve or greenish cream to dark brown. *Polycarpa obscura, P. flava* n.sp., *P. nigricans, P. stirpes* n.sp. and *P. molguloides* are always black. *Polycarpa ovata* and *P. pedunculata* are never black.

4. *Fungiformis* group, in which gonads are upright and elliptical, projecting vertically into the atrial cavity. There is a simple, flat-topped endocarp in the gut loop, but no other endocarps at all on the body wall.

   The group contains *Polycarpa fungiformis, P. reniformis, P. biforis*.

5. *Thelypanes* group, in which the gonads are long, lightly attached and sausage-shaped. The test is thin and rigid, and the gut usually forms a straight or open loop. The group may be related to the *procera* group, but endocarps are either few or absent altogether.

   The group contains *Polycarpa thelypanes, P. lucilla* n.sp., *P. papyra* n.sp.

Species that do not fall into these groups are *Polycarpa sobria* (which has no endocarps and is unusual in having a conspicuous caecum) and *Polycarpa plenovata* n.sp. (a very small species with special characters).

The genus *Polycarpa* does not occur south of the Subtropical Convergence. It is diverse in Australian tropical waters owing to the occurrence of a larger number of tropical western Pacific species. The number of temperate indigenous species is also relatively high, and these appear to have affinities with the tropical fauna. Thus, while in the tropics, species are able to maintain gene flow over a vast geographic range, they appear to speciate in temperate Australian waters. This phenomenon can be observed in other groups (e.g. *Microcosmus* and Polyzoinae) but is particularly conspicuous for *Polycarpa* (see Biogeography).

It is tempting to speculate that this results from loss of the larval ocellus and loss of capacity to select settlement sites. A consequent reduction in larval recruitment could cause isolation, especially in temperate waters where suitable habitats do not occur in such profusion as they do in the tropics.

A corollary of this hypothesis – that dispersal represents a particularly stringent selective pressure in this genus – is supported by the occurrence of the viviparous habit observed in the genus.

Key to the Species of *Polycarpa* Recorded from Australia

1. Polycarps grouped to form compound gonads 2
   Polycarps not grouped to form compound gonads 4
2. Polycarps in double rows and not embedded in body wall .... *P. biforis*
   Polycarps not in double rows and embedded in body wall 3
3. Stalk from anterior end of body .... *P. clavata*
   Stalk not from anterior end of body .... *P. aurata*
4. Polycarps upright and no endocarps on body wall outside gut loop 5
   Polycarps recumbent or polycarps upright amongst endocarps 6
5. Dorsal tubercle with multiple openings .... *P. fungiformis*
   Dorsal tubercle with inverted S-shaped opening .... *P. reniformis*
6. One or 2 large flat-topped endocarps in gut loop 7
   Endocarps in gut loop small, numerous or absent 18
7. Gonads not embedded in body wall .... *P. contecta*
   Gonads embedded in body wall 8
8. Gonads limited to ventral half of body .... *P. argentata*
   Gonads not limited to ventral half of body . 9

9. Branchial vessels contain white, fibrous thread ....*P. obscura*
Branchial vessels do not contain white, fibrous thread 10
10. Test thick, irregular with spongy outgrowths ....*P. nigricans*
Test not thick and irregular, no spongy outgrowths.....................................11
11. Long, cylindrical male follicles...*P. decipiens*
Pyriform male follicles...........................12
12. Test with coat of sand attached to long hairs ....*P. molguloides*
Test without coat of sand attached to long hairs 13
13. Dark, spherical vesicles usually present in body wall 14
No dark, spherical vesicles in body wall 15
14. Test hard, rigid; apertures on short siphons with blue lining in life; test not jet black in preservative .... *P. pigmentata*
Test thin, flexible; apertures inconspicuous with orange lining in life; test jet black in preservative .... *P. stirpes* n.sp.
15. Long gonoducts project into atrial cavity; reddish brown in life.........*P. pedunculata*
No long gonoducts project into atrial cavity; yellow in life...................................16
16. Test hard, sandy, black in preservative ....*P. flava* n.sp.
Test not hard, sandy, nor black in preservative 17
17. Vesicles in body wall 0.2 to 1.0 mm diameter *P. viridis*
Vesicles in body wall less than 0.2 mm diameter ....*P. ovata*
18. Gut straight or kinked; no gut loop formed 19
Gut forms loop 23
19. Stigmata 2 or 3 per mesh ....*P. procera*
Stigmata 4 to 8 per mesh 20
20. Gonads scattered over body wall .... *P. rigida*
Gonads not scattered over body wall........21
21. Male and female gonads separate .... *P. tinctorella* n.sp.
Male and female gonads not separate 22
22. Gonads in a single row each side of ventral border .... *P. tinctor*
Gonads a row of polycarps each side of both dorsal and ventral borders ..... *P. chinensis*
23. No endocarps in gut loop.......................24
Numerous endocarps in gut loop 28
24. Endocarps on body wall numerous .... *P. papyra* n.sp.
Endocarps on body wall not numerous 25
25. Stomach more than half the length of primary gut loop..26
Stomach less than half the length of primary gut loop..27
26. Thin, naked stalk present..*P. plenovata* n.sp.
Thin, naked stalk not present ....*P. sobria*
27. Gut loop narrow..................*P. lucilla* n.sp.
Gut loop wide .... *P. thelyphanes*
28. Hollow spines on and in siphons .. *P. olitoria*
No hollow spines on or in siphons 29
29. Gonads confined to ventral bands ....*P. intonata* n.sp.
Gonads not confined to ventral bands 30
30. Gonads cylindrical .... *P. aurita*
Gonads round or elliptical 31
31. Gonads upright .... *P. papillata*
Gonads not upright ....*P. nota* n.sp.

The following species recorded from Indonesia (Sluiter 1885, 1895, 1904; Millar 1975) and from Sri Lanka (Herdman 1906) have not been taken in Australian waters:

Polycarpa albopunctata (Sluiter, 1904) is a well-characterised species with white patches scattered in the body wall, a thin parchment-like test, a row of rounded polycarps along each side of the endostyle, a single endocarp enclosed in the rather short gut loop, and a very short stomach (ZMA V.TU976.3). The species is distinguished from *P. argentata* by the single row of polycarps on each side of the body.

Polycarpa colletti Herdman, 1906 has a very deeply curved gut loop and long rectum, crowded branchial vessels on the folds, polycarps embedded in the ventral part of the body wall, and endocarps on the gut loop (BM 1907.8.30.19).

Polycarpa glebosa (Sluiter, 1904), spherical individuals with thick, cartilaginous test and a flat branchial sac in which the branchial folds are represented only by crowded internal longitudinal vessels (ZMA V.TU976.14, TU1261).

Polycarpa palinorosa (Sluiter, 1895) and *Polycarpa ambonensis* (Sluiter, 1904) appear to be very similar to one another. Externally they resemble *Polycarpa papillata* and have similar numbers of endocarps on the body wall but have a less voluminous gut and a dark siphonal lining that persists even in the type specimens (ZMA V.TU103.6 and V.TU976.4 respectively). As the gonads are not present in these specimens, it was not possible to determine their affinities accurately.

Polycarpa patens (Sluiter, 1885) has numerous internal branchial vessels; in this and other

TABLE VII — SUMMARY OF CHARACTERS OF SPECIES OF *POLYCARPA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	[3]Branchial sac	Dorsal tubercle slit	Curve of gut loop	[4]Stomach length	[5]Endocarps	[6]Gonads position	[7]Spherical vesicles	Additional features
P. reniformis	WP	Norfolk I. - Torres St	2–5 (13),6–8	entire	shallow	2/3	1;0	ventral (u)	—	upright body
P. fungiformis	—	Moreton Bay – Lizard I.	1–2 (15);15	complex	obtuse	1/2	"	dorsal (u)	B	stalked; black in preservative
P. biforis	—	Heron I. – Cockburn Sd	4–5 (20);6	entire	acute	3/4	"	scattered (u)	—	gonads grouped
P. pedunculata	—	Dongara – Moreton Bay	4 (12);6–10	"	variable	2/3	"	scattered (e)	C	gonoducts protrude
P. flava	—	Spencer Gulf	2 (12)10–15	"	obtuse	1/3	"	"	"	stalked; black in
P. viridis	—	Cockburn Sd – Port Jackson	2–3(15);9–10	"	acute	1/2	"	3–4 rows (e)	"	stalked; body wall greenish or purple
P. ovata	WP	Moreton Bay – Trinity Bay	2–3 (16);1–10	"	obtuse	"	"	"	"	stalked; test naked; apertures sessile
P. stirpes n.sp.	WP	Townsville – Cape Melville Melville	6 (17);12	entire – complex	straight	"	2;0	scattered (e)	B	stalked; black in preservative
P. molguloides	—	Bass St	3 (10);10	entire	acute	1/3	"	3–4 rows (e)	"	sandy coat
P. pigmentata	—	Bass St – Cockburn Sd	3-8(15-24);8-12	entire – complex	obtuse	"	"	scattered (e)	B,C	laterally flattened; brown with blue siphon lining in
P. obscura	WP	Bass St – Cape Jaubert	5–6 (20);10	"	"	"	"	"	B,C	stalked; black; white threads in vessels; long male follicles
P. nigricans	WP	Heron I. – Cockburn Sd	3 (12);9–10	"	"	1/2	"	"	—	aggregates; black with white siphon lining in life
P. argentata	WP	Moreton Bay – Rowley Shoals	5–11 (20) 8–15	entire	"	"	"	ventral (e)	—	black in preservative; viviparous

P. decipiens	WP	Bowen – Weymouth Bay	1-2 (15);15	"	"	1/3	"	"	"	long branched male follicles
P. sobria	WP	Abrolhos	2-3 (9);6-8	"	obtuse	2/3	0;0	3-4 rows (p)	"	gastric caecum
P. plenovata n.sp.	—	Bass Strait	1 (8–10);6	"	straight	"	0;0	2 rows (p)	—	siphons diverge; fine stalk; gastric caecum
P. rigida	—	SA - NSW	6-8 (15–22);4-6	"	no loop	short	0; + + +	scattered (p)	—	sandy rigid test
P. chinensis	WP	Bass St – Cockburn Sd	2-4 (6–10);4-6	entire – complex	"	"	"	marginal rows (p)	—	"
P. procera	WP	circum Aust.	6-40(16-50);2-3	"	"	"	"	ventral row (p)	—	"
P. tinctor	—	NSW	8 (16) 4–6	entire	"	"	"	"	—	sandy rigid test; viviparous
P. tinctorella n.sp	—	Vic.	1-3 (5–14);4–6	"	"	"	"	"	—	gonads dioecious
P. papyra n.sp.	—	Townsville	6 (12);6	"	straight	2/3	"	?	—	sandy rigid test
P. lucilla n.sp.	—	Cape Jaubert – Townsville	5(11);3-5	"	obtuse	1/3	0;0	2-3 rows (p)	—	sandy rigid test; siphonal pigment spots; delicate
P. thelypanes	WP	mid WA – Bass St	1-6 (7–16);2-8	"	open loop	"	0; + +	ventral rows (p)	—	sandy rigid test; gonads elongate
P. nota	—	Heron I.	2 (6) 3	entire	obtuse	1/3	+ + ; + + +	scattered (p)	—	"
P. intonata	—	Bowen – Townsville	4 (12);4-7	"	acute	"	"	ventral (p)	—	sandy flexible test; viviparous
P. papillata	IWP	NW Aust – NE Qld	3-6 (20);12	entire – complex	variable	1/2	"	1-3 rows (u)	—	gut eviscerates; male follicles in single row
P. longiformis	—	NE Qld	3 (15);12	entire	obtuse	"	"	1 row (u)	—	"
P. olitoria	WP	Bass St – Shark Bay	6-10 (20);8	"	"	1/4	"	1 row (p)	—	gonads elongate; large conical siphonal spines; male follicles in single row; gut sometimes eviscerates.
P. aurata	WP	Heron I. – Torres St	3-5 (25);12	complex	acute	1/2	"	scattered (e)	—	gonads grouped, long body axis curved
P. clavata	WP	Dampier Arch. – Coral Sea	6 (18);8	"	"	2/3	"	"	—	gonads grouped; fleshy stalk from anterior end of body
P. aurita	Pan-tr	Moreton Bay – Cape Jaubert	6-12(20-50);2-4	entire	"	1/2-2/3	"	"	-	gonads long, overlap

WP, western Pacific. [2]Range given anti-clockwise around continent. [3]Internal longitudinal vessles: between folds (on folds); stigmata/mesh. [4]As fraction of ascending limb of gut loop. [5]In gut loop; outside gup loop. [6](e) embedded; (u) upright; (p) prostrate and not embedded, [7]B, black; C, colourless.

characters it resembles *P. aurita*. However it is distinguished by its loosely attached polycarps and open gut loop (ZMA V.TU1042). It also resembles *P. thelypanes*.

Polycarpa psammodes (Sluiter, 1904) has a spirally wound ovarian tube and more vessels in the interspace than on the folds.

Polycarpa sluiteri: Herdman, 1906 (the name is preoccupied by *P. sluiteri* Herdman, 1899 < *P. rigida*) and *P. twynami* Herdman, 1906 also appear to be very similar to one another. They both have a voluminous gut enclosing tall endocarps resembling those of *Polycarpa papillata*. Their gonads are elongate and are lightly attached to the body wall and not embedded in it as Herdman (1906) reported (BM 1907.8.30.23 and BM 1907.8.30.24 respectively).

Polycarpa vankampeni Sluiter, 1915 from Indonesia has a terminal branchial aperture, smooth surface and loosely attached polycarps. No other characters of the two known specimens are recorded by which its affinities can be determined.

Polycarpa willisi Herdman, 1906 and *Polycarpa palkensis* Herdman, 1906 from Sri Lanka have both been redescribed by Michaelsen (1923). Both species have apertures at opposite ends of the body and simple, tight gut loops enclosing a single endocarp.

Polycarpa argentata (Sluiter, 1890)
(Fig. 66)

Styela argentata Sluiter, 1890, p.340.
Styela nutrix Sluiter, 1904, p.86.
Polycarpa iwayamae Tokioka, 1950, p.143; 1967a, p.174.

DISTRIBUTION

NEW RECORDS: Western Australia (Rowley Shoals, WAM 943.83 947.83). Queensland (off Moreton Bay, QM GH371; Heron I., QM GH2560 GH2718 GH3056 GH3095; Britomart Reef, QM GH273; Cape Kimberley, QM GH2348; Lizard I., QM GH2217 GH2680).

PREVIOUSLY RECORDED: Indonesia (ZMA V.TU993 Sluiter 1890; ZMA V.TU976.18 V.TU976.99 Sluiter 1904). Palau I. (Tokioka 1950 1967a). Gilbert Is., Marshall Is. (Tokioka 1967a).

DESCRIPTION

EXTERNAL APPEARANCE: Tokioka (1967a) has described specimens from 2 to 6 cm long. A specimen from Heron I. (QM GH2560) is only 2 cm long, with a thick stalk the same length. The body is more or less oval, laterally flattened and fixed posteriorly. The atrial aperture is about one-third of the body length distant from the terminal branchial aperture. Both apertures are on short siphons, the branchial sometimes turned to the right. The test is tough, but rather flaccid. It is thin and flexible in smaller specimens, but more leathery in the larger ones. The surface has some scale-like thickenings and is irregular, rough and wrinkled, with some longitudinal creases and epiphytes. Preserved specimens are deep greenish black the internal surface of the test is grey and glistening. A specimen of almost 4 cm was 'vermilion in life' (Tokioka 1967a, p.175). One from Heron I. (QM GH3095) was orange chrome (Ridgeway 1886) with geranium red pigment cells in the black and white mottled siphon linings.

INTERNAL STRUCTURE: The body wall, which adheres closely to the test, is rather flaccid when removed. Circular muscle bands form a more or less regular, but not dense, layer on the right side of the body. On the left, the muscle-bands form a more or less irregular mesh, leaving the swollen postero-dorsal area (over the gut) relatively free of muscles. There are 12 to 20 rather short, finely pointed and widely spaced tentacles. The opening of the neural duct, in a shallow peritubercular area, is entire and U-shaped, with horns turned in or out, or S-shaped, with both ends spiralling inwards.

The branchial folds are wide and overlapping, but often contracted. There are up to 20 internal longitudinal vessels on the folds and up to 11 between them. In larger specimens, each mesh has up to 15 stigmata (Tokioka 1967). However, in specimens 3 cm long or less, there are only 8 to 10 per mesh and longitudinal vessels are arranged according to the following formulae: E4(8)4(12) 3(10)3(6)2DL (3 cm, QM GH2217); DL1(6)2(9) 2(10)2(9)2E (1.5 cm, ZMA V.TU976.18).

The gut loop is relatively short and simple. It is oriented obliquely across the postero-dorsal corner of the body and is open at the pole, where it encloses a large, circular endocarp. The stomach is relatively short and elliptical, with internal folds (which are not always evident from outside the stomach). The short, wide rectum extends forward to form an obtuse angle with the primary loop. The anal border has up to 20 rather short, rounded lobes.

The gonads are numerous, small, almost spherical polycarps completely, but not deeply, embedded in the ventral half of the body wall. They become more crowded toward the ventral mid-line. The male follicles, which are not numerous, are pyriform and sometimes branched, completely surrounding the almost circular ovary. Vasa efferentia cross the surface of the ovarian

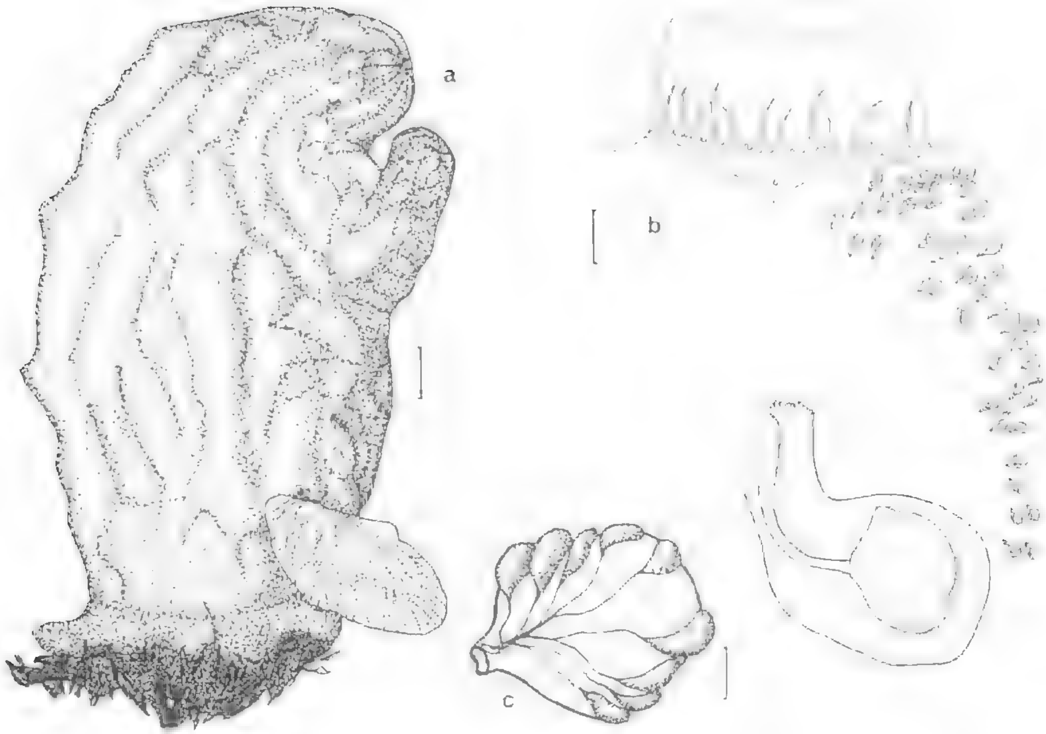


FIG. 66: *Polycarpa argentata* — a, external appearance (QM GH273); b, gut, gonads and endocarp (QM GH2217); c, gonad (QM GH273). (Scales: a, 1.0 cm; b, 2.0 mm; c, 0.25 mm).

sacs and converge to the short male opening on the mesial surface of the equally short oviduct.

There may be 2 or 3 small endocarps enclosed in the gut loop in line with the large circular one enclosed in the pole, but endocarps are otherwise absent from the body wall.

REMARKS: This species bears a superficial resemblance to some specimens of *Polycarpa obscura*; the circular endocarp in the gut loop reinforces that resemblance. However, the present species is distinguished by the colour of the living specimens; the less crowded musculature; the uninterrupted opening of the neural gland; the small, almost spherical polycarps in the ventral half of the body wall; the short anal lobes and pear-shaped male follicles that surround the ovary; and the absence of vesicles in the body wall.

Polycarpa stirpes n.sp. has similar gonads, but they are scattered all over the body wall rather than being limited to its ventral half.

Tokioka (1967a) found a larva present in a specimen from the Marshall Is., suggesting that this large species may be viviparous. This possibility is supported by the position of the gonads in the ventral part of the body, distant from the excurrent aperture.

The type specimen (ZMA V.TU993) is identical with the Australian specimens, and within the range examined by Tokioka. Individuals of *Styela nutrix* (ZMA V.TU976.18, V.TU 976.99) are small (1.5 to 2 cm) with an irregular and flaccid cartilaginous test and appear to be synonyms of *P. argentata*.

Polycarpa aurata (Quoy and Gaimard, 1834)
(Fig. 67; Pl.IIIc)

Ascidia aurata Quoy & Gaimard, 1834, p.559.
Styela aurata: Sluiter, 1904, p.57.
Polycarpa aurata: Herdman, 1906, p.319. Sluiter, 1915, p.30. Hastings, 1931, p.74. Harant and Tuzet, 1932, p.4. Tokioka, 1955b, p.53; 1967a, p.169; 1970, p.93.
Pandocia aurata: Van Name, 1918, p.94.
Polycarpa sulcata Herdman, 1882, p.179. Drasche, 1884, p.379. Traustedt, 1885, p.48. Michaelsen, 1905, p.97. Millar, 1975, p.288.
Styela psoloessa Sluiter, 1890, p.337.
Styela (Polycarpa) pneumonodes Sluiter, 1895, p.179.

Polycarpa pedunculata: Pizon, 1908, p.216.
Pandocia botryllifera Michaelsen, 1912, p.146.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM G9371; Tryon I., QM GH1408; Swain Reefs, QM GH1420 GH2808; Broadhurst Reef, QM GH312; Davies Reef, QM GH2343; Lizard I. QM G8571 G9732 G9734 G11850 GH1460; northern Reefs, QM G9819 GH299 GH300; Raine I., QM GH299 GH300 GH2088; Murray I., QM G9816–8 GH311).

PREVIOUSLY RECORDED: (Great Barrier Reef — Hastings 1931). Sri Lanka (Herdman 1906). New Guinea (Quoy and Gaimard 1834). Indonesia (Herdman 1882, Drasche 1884, Sluiter 1890 1895 1904 1915, Michaelsen 1912, Harant and Tuzet 1932, Millar 1975, Pizon 1908). Caroline Is (Tokioka 1967a). Palau Is (Tokioka 1955b). Philippines (Van Name 1918, Tokioka 1967a, Millar 1975).

This Indo-West Pacific species is strictly tropical, its most southerly record being at the southern end of the Great Barrier Reef. It is taken in waters from 3 to 20 m deep.

DESCRIPTION

EXTERNAL APPEARANCE: The colour of the living individuals is striking, being an opaque white or cream with purple and yellow markings. The siphonal lining is bright yellow. In preservative, the colour changes fairly rapidly to orange-brown and sometimes subsequently to black. Individuals are large and solid, up to 10 cm in length. The body is slightly flattened laterally and strongly curved along the longitudinal axis, with a deep concavity in the dorsal surface from which the atrial aperture arises. Deep creases with wide, rounded ridges between them extend from the branchial aperture parallel to the wide curve of the ventral border, but usually fade out on the wide, rounded posterior end of the body. Individuals are fixed by an area on the postero-ventral to mid-ventral margin where a short, broad stalk sometimes develops to raise the horizontally oriented animal off the substrate. The body narrows toward the branchial aperture at one end, while the other (posterior) end is wide and rounded, expanding dorsally almost at right angles to the long axis of the anterior part of the body to emphasise the dorsal concavity. Apertures are on rather short but conspicuous, deeply sulcate siphons. The test is tough, thick and smooth, without incrustations and epibionts.

INTERNAL STRUCTURE: The body wall is thin and closely adheres to the test. Fine but rather irregularly placed muscles extend from both the siphons and the intersiphonal region to form a continuous layer that fades out over the ventral border. The branchial tentacles are widely spaced. In large specimens, there are often as few as 10, with some minute rudimentary ones; they are more numerous in smaller specimens. The dorsal tubercle is large, completely filling the peritubercular area. The very numerous openings of the neural duct are punctate to elongate slits.

The branchial folds are rather narrow but flat; they do not overlap. There are 17 to 25 internal longitudinal vessels crowded on them and 3 to 5 more widely spaced between the folds. There are up to 12 stigmata per mesh. The folds are deeply curved, the dorsal lamina being short in relation to the length of the endostyle and the wide ventral curve of the body.

The gut forms a fairly narrow, deeply curved loop around the wide posterior end of the body. The internally pleated stomach is long and cylindrical, occupying almost the whole of the ascending limb of the gut loop. It tapers slightly at the pyloric end, where it opens into the wide intestine (which is of even diameter throughout its length). The rectum extends forwards to the base of the atrial siphon. The anal opening is fringed by 10 sometimes irregularly rounded lobes. A ligament firmly holds the middle part of the stomach to the body wall and a conspicuous gastro-intestinal connective runs from the pyloric part of the stomach.

The gonads are scattered and deeply embedded in the body wall. They are rounded to irregular and of variable size. Each gonad is compound consisting primarily of a circle of ovaries, each at right angles to the surface of the body wall, and each with a central duct that opens into the atrial cavity. Unbranched, club-shaped testis follicles are present in a circle around each ovary, their ducts converging to a common duct that opens with that of its associated ovary amongst the endocarps on the body wall. Each gonad spreads out in the body wall; sometimes adjacent gonads appear to be confluent. The primarily circular arrangement of ovaries in each compound gonad is obscured with maturity.

Up to 7 tall endocarps are enclosed in the gut loop. Angular endocarps are also present here and there on the body wall, but they are not crowded. The body wall covering the gonads is also produced into shorter endocarps.

REMARKS: The shape of the body, the colour of the test, the compound polycarps, the well-spaced tentacles, the shape of the stomach and the position of the ligament binding it to the body wall are distinctive. The similarity of the dorsal tubercle to that of *Polycarpa papillata* has caused some confusion between the species, which has been

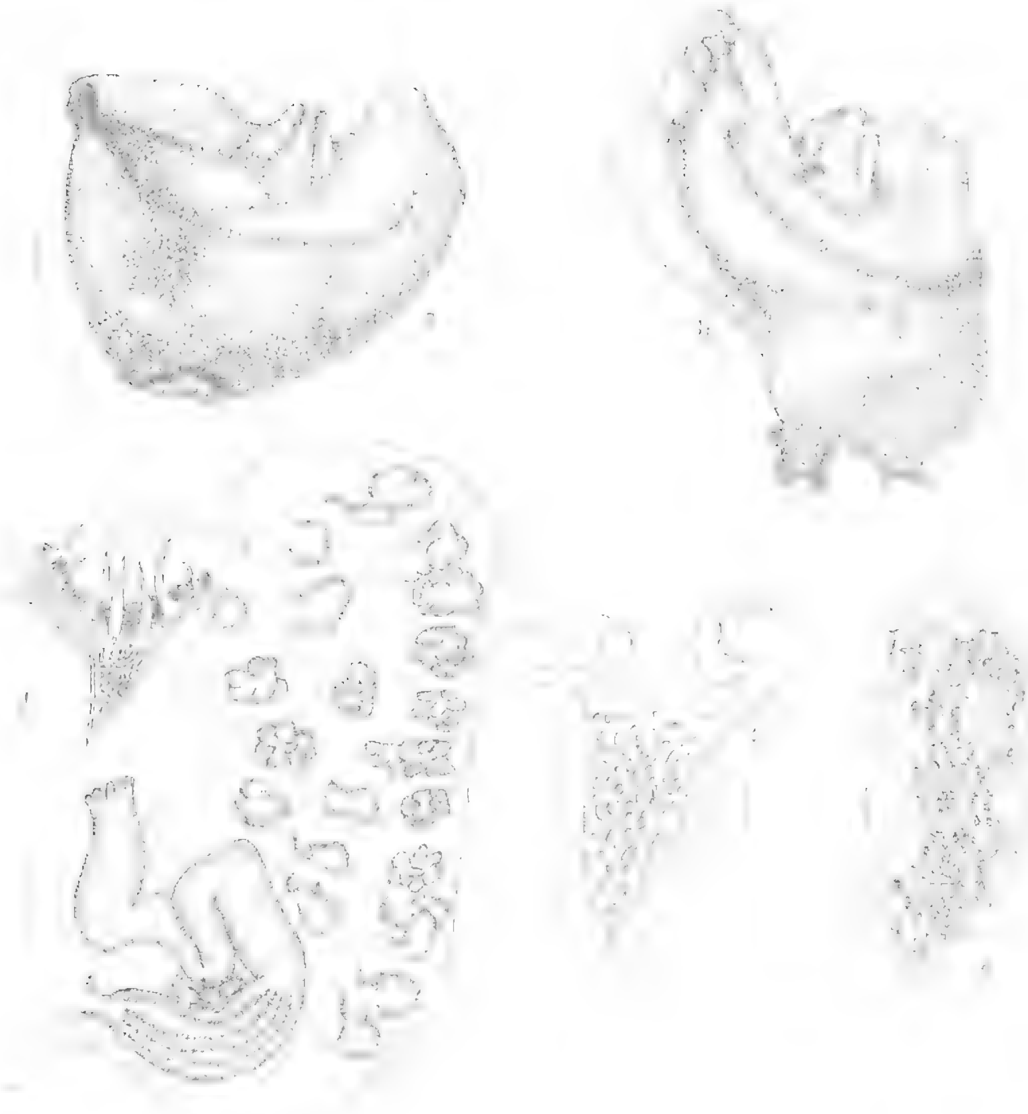


FIG. 67: *Polycarpa aurata* — a, b, external appearance (QM G9816); c, dorsal tubercle (QM GH288); d, internal structure (QM G9513); e, gonad (QM G8571). (Scales: a, b, d, 1.0 cm; c, e, 0.5 mm).

reinforced by the specimens of *P. papillata* that have a conspicuously swollen posterior end of the body. However, in the present species, the area of adhesion to the substrate, or the point of origin of the stalk, is always along the ventral border, so that the individual lies horizontally with the rounded swelling of the posterior end of the body projecting upwards, emphasising its deep dorsal concavity. *Polycarpa papillata* is generally fixed by the posterior end or postero-ventral corner of the body. Only in the largest specimens is the narrow, attenuated, curved body horizontally oriented and fixed by the posterior part of the ventral surface. The voluminous, pear-shaped stomach with its very fine folds; the tall crowded endocarps; the long flattened anal lobes; and the polycarps with a single row of male follicles are also characters by which *P. papillata* is distinguished from the present species.

Cnemidocarpa pedata (Herdman) has a similarly swollen body; which led Hartmeyer (1919) to regard it as a synonym of the present species. In *C. pedata*, however, ovaries are tubular structures and although they branch and coalesce in the body wall, gonoducal openings are present only at their distal ends, around the atrial siphon.

Polycarpa aurita (Sluiter, 1890)

(Fig. 68)

Styela aurita Sluiter, 1890, p.338; 1904, p.59.

Polycarpa aurita: Hartmeyer, 1919, p.81. Sluiter, 1915, p.3. (Not: Kott, 1952, p.234, = *P. papillata*)

Styela circumarata Sluiter, 1904, p.70.

Pandocia circumarata: Hartmeyer, 1909, p.1363. Van Name, 1918, p.92.

Polycarpa circumarata: Van Name, 1921, p.428; 1945, p.261. Vasseur, 1967b, p.134. Millar, 1975, p.285.

Tethyum australiense Michaelsen, 1912, p.128 (part, not type specimen).

Polycarpa polyphlebodes Hartmeyer, 1919, p.72.

Cnemidocarpa polyphlebodes: Hartmeyer and Michaelsen, 1928, p.382.

Styela ramificata Kott, 1952, p.214; 1964, p.138; 1972c, p.241, 1972e, p.51.

?*Styela robusta* Sluiter, 1904, p.79.

Distribution

New Records: Western Australia (Shark Bay, WAM 1217.83; off Dongara, WAM 967.83 1216.83; Cockburn Sound, QM G9667), Queensland (Moreton Bay, QM G4988 G5147 G6127–38; Heron I., QM GH1423 GH3093; Wistari Reef, QM GH2717 GH3071; Gladstone Harbour, QM G9682 G9800; Abbot Point, QM GH666 GH687 GH716; Lizard I., QM GH1461–2).

Previously Recorded: Western Australia (Cape Jaubert — Hartmeyer 1919; Sharks Bay, Cockburn Sound — Hartmeyer and Michaelsen 1928). New South Wales (Port Jackson — Michaelsen 1912). Queensland (Moreton Bay — Kott 1952 1964 1972c; Bowen — Michaelsen 1912). Northern Territory (Gulf of Carpentaria — Kott 1972e). Indonesia (Sluiter 1890 1904). New Caledonia (Vasseur 1967b). Philippines (Van Name 1918, Millar 1975). Atlantic Ocean (Gulf of Mexico, Caribbean, Venezuela — Van Name 1921 1945).

This pan-tropical species occurs from low tide down to about 40 m on silt, sand and coral substrates. It has not yet been reported from the eastern Atlantic or from the western Indian Ocean.

Description

External Appearance: Individuals up to 12.2 cm in length have been reported (Millar 1975), although the newly recorded specimens are not more than 5 cm in length. They are from one half to two-thirds as broad as they are long and are slightly laterally flattened, although this may be obscured by contraction. The branchial aperture is terminal; the atrial aperture is from one- to two-thirds of the distance down the dorsal surface. The apertures are on very short siphons, but these are very often so strongly contracted that the apertures appear to be completely sessile. There are sometimes, but not always, short rounded projections of the external test in the vicinity of the siphons. The body is more or less club-shaped, rounded posteriorly and gradually narrowing to the terminal branchial aperture. Occasionally there is a short stalk posteriorly. Many of the specimens, especially those completely invested with sand, probably lie free on the substrate, although those with posterior stalks were clearly held in an upright position.

The specimen from Cockburn Sound (QM G9667) has a specimen of *Microcosmus squamiger* attached to its upper surface between the branchial and atrial apertures. The atrial aperture in this specimen is well posterior, apparently resulting from the presence of the commensal. It is clear from the orientation of both siphons that the specimen was lying on its long ventral surface rather than standing upright. The long axis of commensal and host were parallel and oriented in the same direction, so that their feeding currents were mutually reinforced.

The test varies greatly. It is sometimes a thin, translucent and rather flaccid membrane, covered with fine but irregular hair-like extensions. Sand adheres to the hairs and is embedded in the test all over the body, obscuring the position of the apertures. Specimens with similar white, translucent but thicker and firmer test have the same hairs and included sand (e.g., QM G9682 G9800, and from Moreton Bay). Other individuals (e.g., QM GH666 GH687 GH716) have a cartilaginous to tough, rigid test. It is opaque,

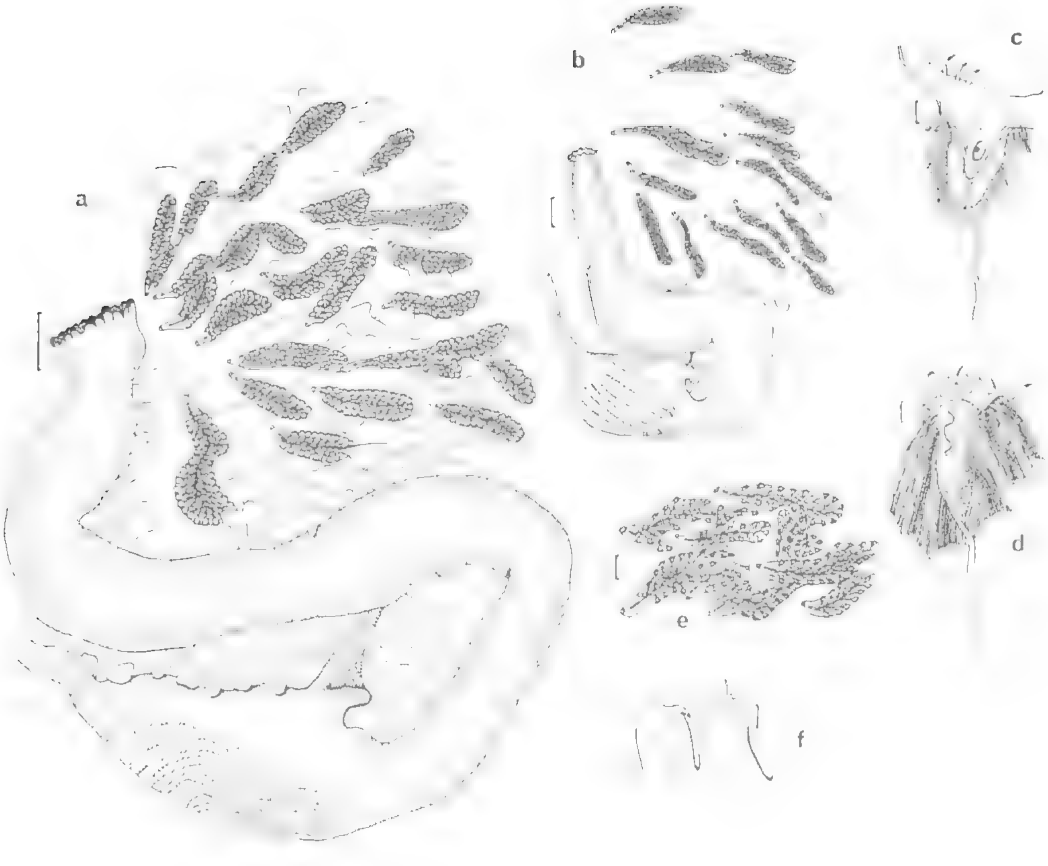


FIG. 68: *Polycarpa aurita* — **a**, **b**, gut, gonads and endocarps (QM G6132, GH666); **c**, **d**, dorsal tubercles (QM GH687); **e**, gonads branching and overlapping (QM GH4988); **f**, papillae in siphonal lining (QM GH4988). (Scales: **a**, 2.0 mm; **b**, 1.0 mm; **c** – **e**, 0.5 mm; **f**, 0.1 mm).

brick or light brown, and without hairs, but with pebbles and sand particles embedded in or adhering directly to it except in the region around the apertures. The test tends to grow out in irregular extensions for added adhesive strength. Living specimens have been described as maize yellow (Ridgeway 1886) buff yellow, yellow brown or coppery. They are about twice their size when preserved. Even narcotised specimens do not regain the smooth distended condition of the undisturbed, living individual. There is often some black or purple pigment in vessels in the siphon lining and around the siphons of preserved specimens.

INTERNAL STRUCTURE: When freshly preserved, the body wall is bluish-grey but subsequently fades to cream, brown or pinkish purple. However, the darker grey colour persists for some time around the siphons and in the siphonal linings. The musculature consists of a thin but almost continuous outer layer of circular muscles and inner longitudinal bands. It is especially strong anteriorly. In larger specimens, and in smaller specimens that are strongly contracted, the body wall is thick and completely opaque; however, in less mature specimens, when the musculature is relaxed, the internal organs can be seen through the wall. The rim of the apertures turns in when contracted.

The siphonal lining is produced into regular rows of rounded swellings, each usually with a minute terminal tentacular process, as described for *P. polyphlebodes* Hartmeyer, 1919. There are up to 32 relatively short branchial tentacles of 3 orders, 8 long; 8 moderately long; and alternating minute tentacles. The prebranchial area is very narrow. The dorsal tubercle is a very conspicuous raised cushion that completely fills the V of the peritubercular area. The opening of the neural gland is especially large, and varies from a wide circular, pit-like opening to a C-shape, an E shape, or a coiled or divided slit with conspicuous lips. There is usually a plain, unperforated area of branchial sac around the peritubercular area in all but the smallest (1.5 to 2 cm) specimens. The long dorsal lamina becomes wider toward the oesophagus, which is at the posterior end of the body.

The branchial sac is tough. It has four folds, with 20 to 30 ribbon-like internal longitudinal branchial vessels crowded on each. The contracted folds are low, with the vessels so crowded that they are difficult to count. However, the relaxed folds are broad and overlapping. In the interspace are no more than 6 to 12 longitudinal vessels, fairly close together, with only 2 to 4 stigmata per mesh. There are very tough connectives between the branchial sac and body wall. They are also wide in some specimens, and extend for a considerable length along the transverse branchial vessels. Parastigmatic vessels are present.

The gut forms a long, narrow loop across the ventro-lateral corner of the body. The rectum bends anteriorly and, owing to contraction of the narrow body, usually forms an acute angle with the primary loop. The anus is bordered by 12 to 24 shallow lobes that are regular in some specimens, irregular in others. The oesophagus is short. The voluminous stomach is from one- to two-thirds of the length of the ascending limb of the gut loop. In mature specimens, the stomach folds in to form a typhlosolar fold anterior to the suture line. This effects a decrease in the external diameter of the stomach without reduction in its internal surface area. Occasionally the stomach typhlosole is not present (QM GH687) and the stomach is very wide. The fold is held in place by connective tissue. Internal longitudinal glandular folds are not always apparent on the surface of the stomach. They extend obliquely over the typhlosolar fold to meet the suture line on its anterior border; on its posterior border, the glandular folds lie mainly parallel to the line. The curved caecum at the pyloric end of the stomach has a gastro-intestinal connective attached at the curve. There is also a conspicuous typhlosole around the inner curve of the gut loop. From 4 to 6 tall, narrow endocarps are enclosed in the pole of the gut loop.

The gonads are numerous, elongate polycarps scattered over the body wall, radiating toward the atrial aperture. In juvenile specimens, these polycarps are long, narrow and sometimes sinuous. With maturity, the gonads increase in width and number, overlapping one another (which gives the appearance of branching), and become more deeply embedded in the body wall. Up to 12 pairs of rounded to oval male follicles are present beneath each ovarian tube.

There are very numerous thin and sometimes flattened endocarps on the body wall between the gonads, as well as in the loop of the gut. In larger specimens, well-developed gonads embedded in the body wall raise it around the scattered endocarps, which then appear to rise from pits in the body wall. Vascularisation of the endocarps is often very conspicuous.

REMARKS: Variations in the thickness of the test of this species are perplexing. Hairy individuals with thin, flaccid, sand-embedded, membranous test were present in large numbers at Abbot Point (Queensland) in June 1982. In November 1981 only a single hirsute specimen was taken, but numerous individuals with thicker, hard, sand-encrusted test were taken. It is likely, therefore, that the test thickens and loses its hairs with maturity.

The species is readily identified by the large dorsal tubercle with its wide opening, the large number of branchial vessels on the folds and in the interspace, the strong branchial connectives, the imperforate area of pharynx behind the dorsal tubercle, the roomy stomach with its caecum, gastro-intestinal connective and typhlosolar fold, and the dark pigmentation around the siphons. The minute, tentacular projections on swellings in the siphon lining are also distinctive, but are not easily observed. The long polycarps are a useful diagnostic character, overlapping in more mature specimens, but in juveniles being long and narrow, less numerous, not overlapping, and not so deeply embedded in the body wall.

In view of the many distinctive characters of this species, it is surprising that the synonymy of *Polycarpa aurita*, *P. circumarata* and *P. polyphlebodes* has been overlooked for nearly 60 years.

In *Styela robusta* Sluiter, 1904, the gonads are embedded in the body wall and are very probably overlapping polycarps as in the present species, although Sluiter believes them to be irregularly branching. The nature of the test and shape of the body, the strong branchial sac with its broad connectives and numerous longitudinal vessels, the long narrow endocarps and the large dorsal tubercle are also similar to those of *P. aurita*; the species are very likely synonymous.

Polycarpa biforis (Sluiter, 1904)
(Fig. 69)

Styela biforis Sluiter, 1904, p.78.
Polycarpa biforis: Millar, 1975, p.289.

NEW RECORDS: Western Australia (Cockburn Sound, QM G9651). Queensland (Heron I., QM GH2683 GH3054). Coral Sea (Lihou Reef, QM GH 256; Marion Reef, QM GH255). Philippines (Tawitowi anchorage, Sulu Archipelago, on xanthid crab, 2 m, coll. D.P. Abbott).

PREVIOUSLY RECORDED: Indonesia (Sluiter 1904, Millar 1975).

This is a relatively uncommon tropical species in the West Pacific. Its range extends south to Cockburn Sound on the west coast of Australia, although there are no records for the eastern Australian mainland coast.

EXTERNAL APPEARANCE: Preserved specimens from 3 to 7 cm long and from 2 to 4 cm wide are known. The body shape varies. Smaller specimens are round (see Millar 1975), with almost sessile apertures. The atrial aperture is one-third of the body length distant from the terminal branchial aperture. In specimens of 3 to 4 cm (QM G9651), the apertures are on short conspicuous siphons. The one-third of the body anterior to the atrial siphon is narrow and the terminal branchial siphon is turned ventrally. Larger specimens (5 to 7 cm, QM GH255-6) are considerably attenuated anteriorly and the posterior end of the body is curved dorsally, the atrial siphon projecting sideways from the middle of the dorsal concavity. These large, attenuated specimens are fixed along part of the ventral border and are probably more or less horizontally oriented on the substrate, while the smaller specimens are fixed by the thickened posterior test. The surface of the test is wrinkled, with deep longitudinal furrows. Larger specimens have epiphytes. The test of the preserved specimens is beige to brown, and sometimes black posteriorly.

INTERNAL STRUCTURE: The body wall is brown-black in the recently preserved material, although the living specimens may be orange. The body musculature is moderately well developed. There are about 30 very long, slender tentacles. The dorsal tubercle is large and fleshy, with a more or less S- or C-shaped slit.

On each side of the branchial sac are 4 folds (of which the most dorsal is the narrowest). The folds are wide at the base and rather loose. In one specimen, the branchial sac is contracted and longitudinal vessels are crowded on the folds and in the interspaces. There are up to 22 ribbon-like internal longitudinal vessels on the folds; 4 in the interspace. Each mesh has about 6 short, rectangular stigmata. Parastigmatic vessels are not present.

The oesophagus, from the posterior end of the branchial sac, is fairly long. The stomach is very long, narrow, cylindrical and internally folded. It occupies the greater part of the ascending limb of the gut loop. The gut loop is narrow and deeply curved, enclosing a narrow, flat-topped, comma-shaped endocarp in its pole. The gut is only loosely attached to the body wall. The anus has a few irregular lobes on its border.

The gonads are unique and arranged in groups. Each group consists of 2 rows of 2 to 8 upright, elliptical polycarps, attached by a small part of their proximal end, along each side of the flat,

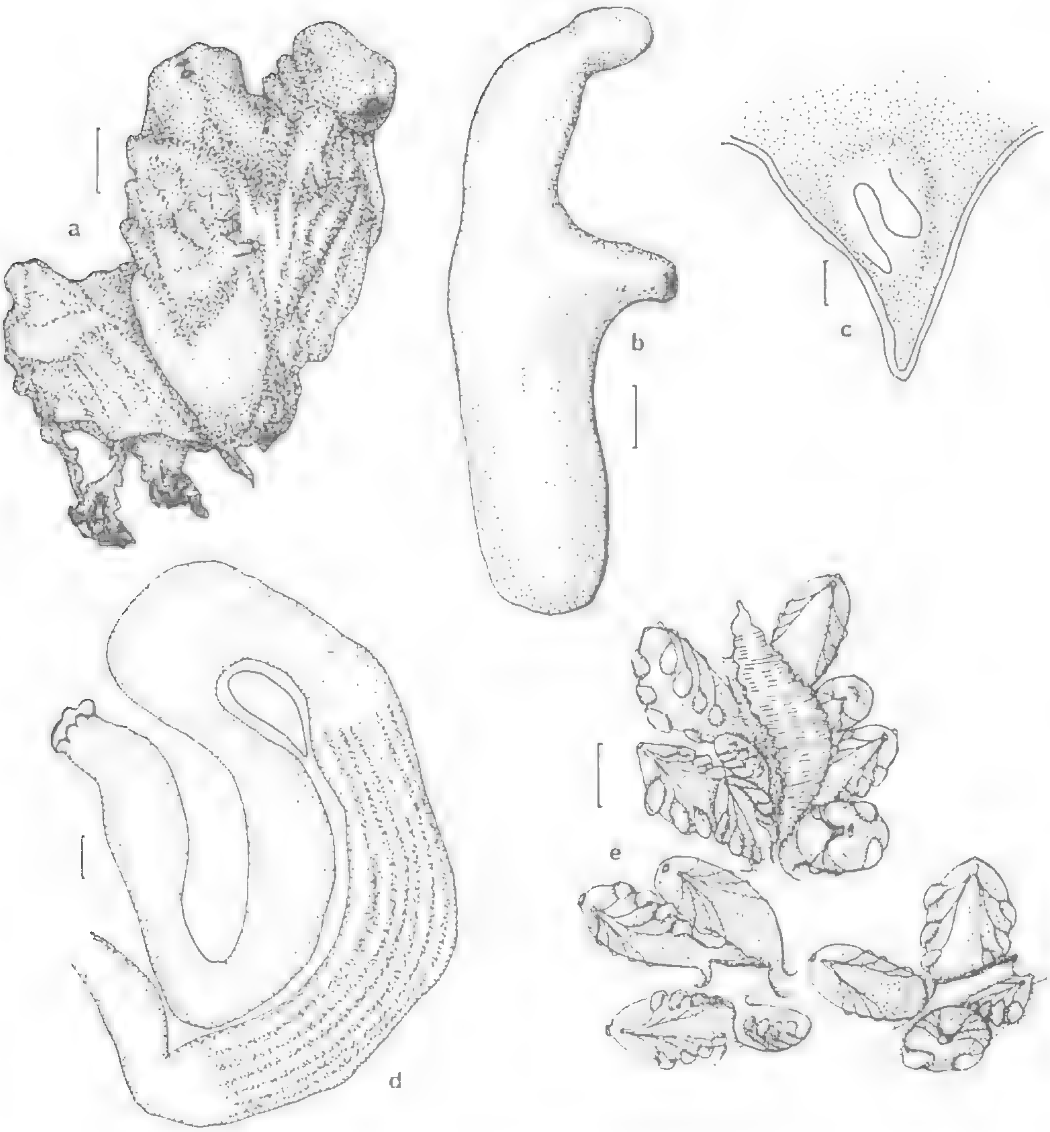


FIG. 69: *Polycarpa biforis* — **a**, external appearance (QM G9651); **b**, body removed from test (QM GH256); **c**, dorsal tubercle (QM GH256); **d**, gut loop and endocarp (QM GH256); **e**, gonads clustered around branchial connectives with portion of branchial sac shown *in situ* (QM G9651). (Scales: **a**, 1.0 cm; **b**, 0.5 mm; **c** – **e**, 1.0 mm).

broad branchial connectives that extend between the outer wall of the peribranchial cavity and the branchial sac. The upright gonads, otherwise vulnerable to dislodgement, may be protected by these branchial connecting vessels. The unbranched male follicles are in two rows, each of about 6 follicles, along the side of the ovary distant from the protective branchial ligament. Their ducts pass around the ovary to join a short, common vas deferens that opens into the atrial cavity near the oviducal aperture on the free end of the ovary. The groups of gonads are scattered over the internal surface of the body wall, but are especially clustered around the ventral half of the right side.

There are no endocarps present on the body, apart from the one enclosed in the gut loop.

REMARKS: The condition of the gonads appears to represent a stage between simple polycarps that occur in most species of the genus and the compound polycarps of *P. aurata* and *P. clavata* in which numbers of ovaries and their associated male follicles are more closely associated, often with the branchial connectives passing through the centre of the compound gonad. The dark colour of preserved specimens also resembles that of *P. aurata*, although the test of the latter species is always naked, smooth and sulcate, rather than wrinkled. The species also resembles *P. aurata* in its low, rounded branchial folds with crowded longitudinal vessels, and in its long, cylindrical stomach. The upright gonads and the single endocarp enclosed in the gut loop resemble *P. fungiformis* which is distinguished by its ungrouped gonads and spongy dorsal tubercle. With maturity, specimens of the present species resemble those of *P. papillata*, however, the species are readily distinguished by their very different gonads and endocarps, and by the opening of the neural gland on the dorsal tubercle which remains entire in even the largest individuals of *P. biforis*.

Polycarpa biforis is characterised by its gonads; its straight and slender branchial tentacles; the endocarp enclosed in the gut loop and the absence of other endocarps; its deeply curved gut loop and long cylindrical stomach; its smooth-rimmed bilabiate (rather than lobed) anal border; its low, rounded branchial folds; the reduction of its dorsal fold; and the colour of its body wall. Pontonine shrimps are often present in the peribranchial cavity.

Polycarpa chinensis (Tokioka, 1967)
(Fig. 70)

Cnemidocarpa chinensis Tokioka, 1967a, p.188.
Polycarpa chinensis: Millar, 1975, p.282.
Polycarpa tinctor: Kott, 1964, p.134 (part, specimens from Moreton Bay); 1972c, p.242.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 415.83; Cockburn Sound, WAM 1213-5.83). Victoria (Bass Strait, NMV H375 H749). Queensland (off Moreton Bay, QM G4922 G10081; Moreton Bay, QM G4746 G4921 G4780–1 G5026 G6110-6120 G10077 G12670–2 GH1371 GH2689; Gladstone Harbour, QM G9686 G9721 G9805 G11879; Calliope River, G11879; Mackay, G9980; NW of Bowen, QM GH633–49 GH1367–9; Townsville, QM GH743 GH746; Nymph I., QM GH1370; Temple Bay, QM GH766, GH3050; Murdoch Point, QM GH3049; between Cape Flattery and Lizard I., QM GH3048; Murray I., QM G9820).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1964 1972c). China (Hsia-men — Tokioka 1967a). Vietnam (Millar 1975).

The species has a wide range in temperate and tropical waters and is sympatric with the closely related *P. procera*.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals of this species are sexually mature when less than 1 cm long, although they grow to 6 cm or more. During growth, their external appearance and proportions change dramatically, although at all stages the test is hard and rigid and the body is usually conspicuously laterally flattened. Sand is thickly embedded in the test except in some of the larger specimens, where it is absent from a large part of the surface.

The smallest specimens available are about 7 mm long (QM GH2689 from Moreton Bay). The body is more or less flattened on the anterior surface. It is slightly elliptical in transverse section, folded sharply around the ventral and dorsal mid-line. The test, which is heavily impregnated with sand, is hard and brittle. Both apertures are sessile and depressed into the anterior surface, the branchial aperture ventral and the atrial aperture antero-dorsal. Many of these small specimens taper posteriorly to a single extremely fine, long, sand-covered, hair-like extension of the test (which may have some fine branches along its length). Other specimens have numerous long, hair-like threads from around the postero-ventral, sharp, border of the body. More often there are tufts of short hairs, with adherent sand, distributed around the postero-ventral, posterior and postero-dorsal border of an almost circular (or oval or wedge-shaped), laterally flattened body, which is wider anteriorly than posteriorly.

With growth, the length to width ratio of the body increases; specimens from 4 cm in length are narrow and sickle-shaped, curved in a long arc and concave dorsally, often with a long furrow down the centre of each side. The posterior end of the body is often produced into a short, thick stalk into which the body wall extends. The branchial aperture is either terminal or at the anterior end of the dorsal surface. The atrial aperture is from quarter to halfway along the dorsal border. Both apertures, although sessile in small specimens, are on short siphons in these larger individuals. The test is thin and usually impregnated with sand, and is accordingly very hard and brittle. Sometimes the larger, curved specimens have a tough test, whitish in preservative, with patches of encrusting sand that is not always embedded. Tufts of hair-like roots, similar to those in the smaller specimens, are supported on solid, short and thick extensions of the test along the ventral border as well as around the posterior end and on the posterior part of the dorsal border. Individuals may be crowded, but do not adhere to one another. They lie with their dorsal border uppermost and their long axis horizontal, or at an oblique angle, to the surface of the substrate. The postero-ventral part of the body is usually embedded in the sand and held in place by the root-like processes of the test that develop around the postero-dorsal and ventral border of the laterally flattened body.

In life the test is reddish-orange, where it can be seen through the sand. The colour is lost in preservative.

Internal Structure: The body wall is closely applied to the inside of the test. Although there is an outer layer of circular and inner longitudinal bands, these are very thin indeed and often difficult to demonstrate. The prepharyngeal area is very narrow. The dorsal tubercle is a rounded, rather inflated and sometimes lobed cushion in a shallow peritubercular area. The slit may be S- or U-shaped and entire, or convoluted and often interrupted. There is a conspicuous atrial velum with relatively long tentacles on its rim.

The branchial folds are very low ridges, with 6 to 10 internal longitudinal vessels on the largest fold and 2 to 4 widely spaced vessels between the folds. There are 4 to 6 stigmata per mesh in the interspace. Parastigmatic vessels are present. In smaller specimens, some of the branchial folds are often almost completely flat, being represented by a few internal longitudinal vessels which are closer together than those between the folds. A branchial formula from a small (0.8 cm) specimen from Moreton Bay (QM GH2689) is E1(4)1(5)2(5) 2(4)1DL 0(3)1(4)3(6)1(4)1E.

In small specimens, the gut is S-shaped, forming a short intestinal loop, the descending limb not extending further posteriorly than the pyloric end of the stomach before it curves anteriorly into the long, straight rectum. This S-shaped kink in the gut loop is present in many larger specimens, but often it is lost and the gut extends anteriorly in a smooth, simple arc from the oesophagus at the posterior end of the body to the base of the atrial siphon. The stomach is characteristically short and barrel-shaped, with narrow, parallel longitudinal folds that are not always conspicuous externally. Very rarely the gastric folds are slightly convoluted. The anal border is bilabiate, with from 12 to 24 rounded lobes on the mesial lip only. The gut loop is covered with a thick layer of body wall that is especially conspicuous in small specimens. The gut is attached to the parietal body wall by a thin but continuous membrane.

The gonads are recumbent and oval to elongate, only loosely attached to the body wall and arranged in a row along each side of the dorsal and ventral mid-line. On the right, the row is continuous around the posterior end of the body, although continuity between dorsal and ventral rows is interrupted by the gut on the left. The long axis of each polycarp radiates toward the atrial aperture. There are up to 25 gonads on the right of the mid-ventral line and up to 20 on the left. The less numerous gonads on each side of the dorsal mid-line are usually confined to the posterior half of the body. The gonads consist of a double row of up to 12 pairs of elongate male follicles beneath, and sometimes projecting up into, the ovarian tube.

There are small, rounded, papilla-like endocarps scattered on the body wall. In some of the largest specimens, these are more crowded and longer and more pointed in the vicinity of the atrial aperture.

Remarks: Millar (1975) proposed that the S-shaped intestinal bend and the dorsal rows of polycarps of the present species distinguished it from *P. procera* and *P. tinctor*. This has been confirmed in the present study: the dorsal gonads form a reliably constant feature, although the S-shaped intestinal kink is not always present. The species is further distinguished from *P. procera* by its fewer and less crowded internal longitudinal vessels on and between the folds, and the greater number of stigmata in each mesh between the branchial folds. The branchial folds of the present species are especially low ridges, which further

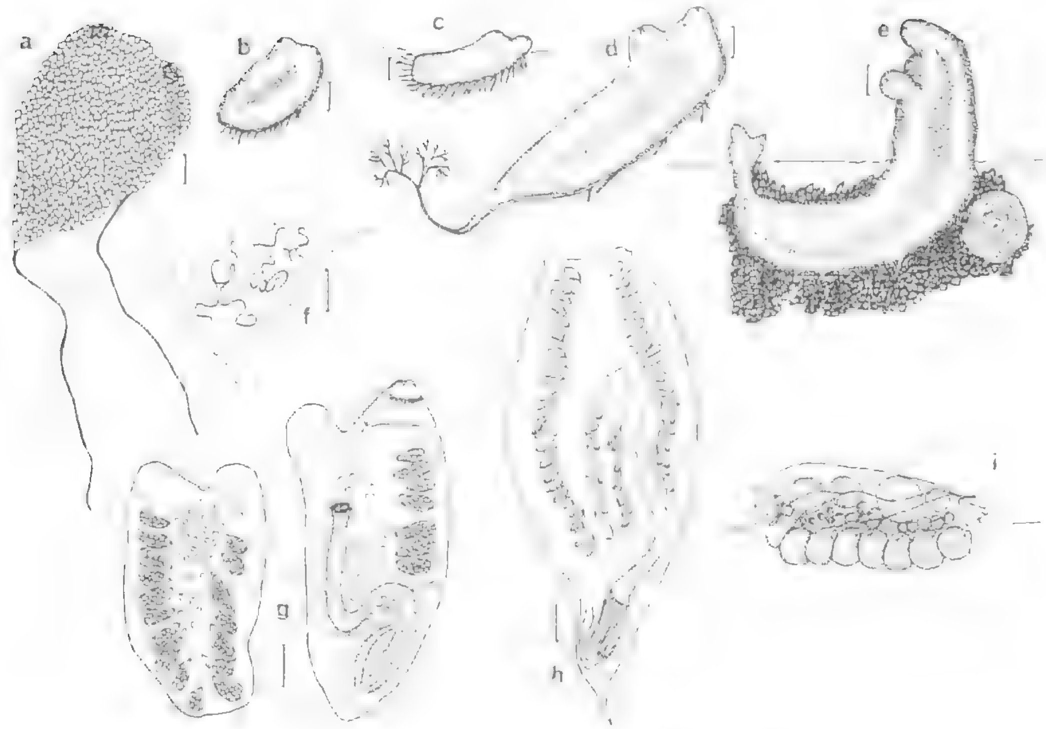


FIG. 70: *Polycarpa chinensis* — a – e, external appearance showing progressive maturation (QM GH2689, G4921, GH633, G4921, GH639); f, dorsal tubercle with convoluted and divided slit; g, h, gut, gonads and endocarps of young and mature specimens, respectively; i, profile of gonad on body wall. (Scales: a, 1.0 mm; b – e, 5.0 mm; f, 0.25 mm; g, 1.0 cm; h, 4.0 mm; i, 0.1 mm).

distinguishes it from both *P. procera* and *P. tinctor*.

The gonads of the present species, like those of *P. procera*, are elongate and the male follicles are below the ovarian tube. In both *P. rigida* and *P. tinctor* the gonads are wide — even almost circular — with a short, wide ovarian sac; the testis follicles are around the sides of the ovary rather than beneath it.

Polycarpa chinensis can also be distinguished by the very flat, elongate, sickle shape of the larger specimens, by the strong rootlets supporting tufts of hairs that develop around the edges of the body, and by the bilabiate anal border that is lobed only on the outer lip.

Polycarpa clavata Hartmeyer, 1919
(Fig. 71; Pl.IIId,e)

Polycarpa aurata: Hartmeyer, 1919, f. clavata p.40. Hartmeyer and Michaelsen, 1928, f. clavata p.363. Kott, 1952, f. clavata p.236. Tokioka, 1961, f. clavata p.123. Vasseur, 1967b, f. clavata p.133.

Polycarpa clavata: Kott, 1972a, p.33; 1972b, p.186. Millar 1963, p.723.

DISTRIBUTION

NEW RECORDS: Western Australia (Cape Preston, WAM 1083.83; Carnarvon, WAM 1071.83; Learmonth, WAM 1079.83; Houtman's Abrolhos, WAM 1080–1.83; Shark Bay, WAM 1072–3.83; Yanchep, WAM 1068.83; Cockburn Sound, WAM 937.83 1070.83 1074–8.83 1082.83 1084.83; Geographe Bay, WAM 117.75 1069.83, QM G9516; Albany, WAM 118.75). South Australia (Hotspot, QM GH938; Top Gallant I., QM GH932). Queensland (Oyster Reef, QM G11984; Yonge Reef, QM G10176 GH313; Marion Reef, QM GH275; Lihou Reef, QM GH274; Trinity Bay, QM GH777).

PREVIOUSLY RECORDED: South Australia (Kott 1972a,b). NW Australia (Hartmeyer 1919, Hartmeyer and Michaelsen 1928). SW Australia (Millar 1963). New Caledonia (Tokioka 1961, Vasseur 1967b).

The range appears to be primarily in Australian waters, from temperate latitudes around the southern coast and north to the tropics. It extends out into the Coral Sea and to New Caledonia. Specimens are found on both sandy and rocky bottoms from a few metres depth down to 40 m.

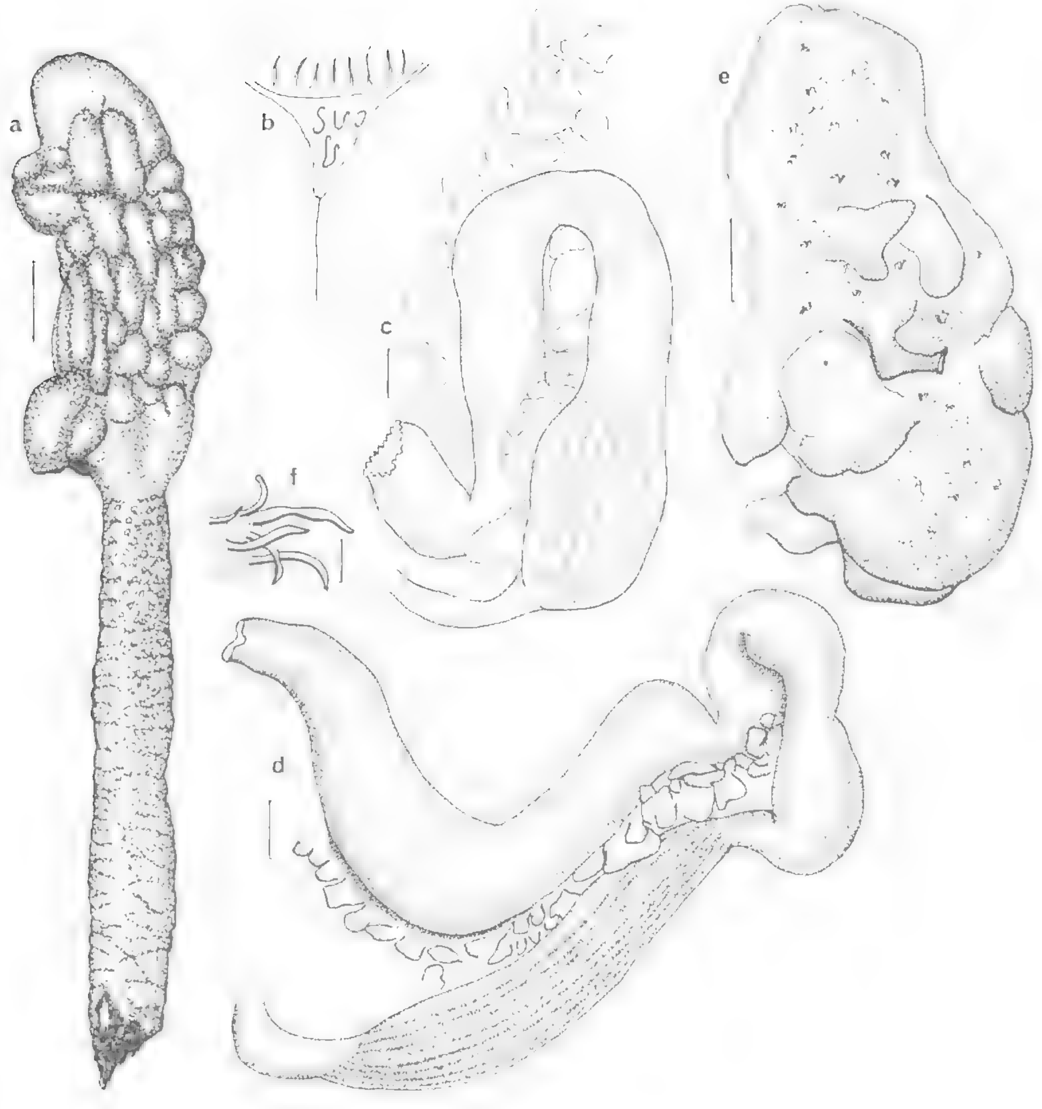


FIG. 71: *Polycarpa clavata* — **a**, external appearance (QM GH313); **b**, dorsal tubercle (WAM 1075.83); **c**, **d**, gut loop and endocarps (WAM 1075.83, QM GH275); **e**, gonad, with severed branchial connective in the centre; **f**, hair-like processes on surface of stalk (QM GH275). (Scales: **a**, 2.0 cm; **c**, **d**, 2.0 mm, **e**, 1.0 mm; **f**, 0.1 mm).

DESCRIPTION

EXTERNAL APPEARANCE: Large individuals up to 8 cm long and 3 cm wide supported on a fleshy stalk that is usually at least twice the length of the body are known. Occasionally specimens are found in which the stalk is shorter than the body. The stalk is slightly constricted where it joins the body. It is up to 2 cm in diameter at the upper end, increasing to as much as 3 cm at the base where it is attached to the substrate. The body has longitudinal furrows and rounded ridges that are sometimes interrupted along their length by transverse creases. The upper, free end of the body (its posterior end) is smooth and rounded. The apertures are on one side. The atrial aperture is about one-third of the body length from the free end and is directed obliquely upwards. The branchial aperture from the lower one-third of the dorsal side is directed down toward the substrate. The individuals are thus supported upside down on the stalk, the stalk extending from the anterior end of the body.

Millar (1963) and Kott (1972a) have described the remarkable circular concavities that are always present around the stalk. In the large specimens from NE Queensland (all with long stalks), these richly vascularised organs are not generally present, although in some specimens, there are circles of crowded, vascular ampullae around the top of the stalk.

The test is thick and quite firm, but is not tough and is cut very readily. The brilliant orange of living specimens fades in preservative to orange brown. Most of the pigment is in the surface layer of test, which is very richly supplied with terminal ampullae of blood vessels. A living specimen from South Australia (QM GH2375, Pl.IIId) has a greyish blue body, although orange pigment is present in the vascularised organs in the stalk. Other specimens from South Australia are the characteristic orange colour found in the tropical forms. Internally the test is whitish and translucent. The transversely wrinkled test of the stalk has minute hairs about 0.25 mm long and about 0.1 mm apart.

INTERNAL STRUCTURE: The body wall is thin and adheres closely to the test. Longitudinal muscle-bands are inside the layer of transverse muscles. The orange-coloured body may extend a short distance into the stalk. The branchial tentacles are large, wide basally and tapering. The dorsal tubercle completely fills the peritubercular area. The slit is continuous in smaller specimens, but in larger specimens is divided into crowded oval to punctate openings that give it a spongy, porous appearance.

The branchial sac is strong, with thick longitudinal vessels. The folds are straight, low and rounded, with from 8 to 18 vessels crowded on them. There are up to 6 internal longitudinal vessels in the interspaces which have 8 to 10 stigmata per mesh, crossed by parastigmatic vessels. Transverse vessels are arranged according to the formula, 1332332331. The vessels connecting the branchial sac with the outer wall of the peribranchial cavity are conspicuously white, very wide and exceptionally tough.

The oesophagus is short. The stomach is long and cylindrical, with internal folds. It occupies most of the ascending limb of the gut loop, which is narrow and deeply curved in the postero-ventral quarter of the body. The anal border has shallow lobes, but these disappear in the large specimens.

The gonads are scattered over the body wall, in 3 more or less irregular rows on each side of the body. In juvenile specimens, they are attached to the body wall by the tissue ligament along their lateral surface. With age, they become progressively embedded in the body wall. In larger specimens the gonads are deeply embedded, identifiable only by a swelling that projects into the peribranchial cavity. They are compound organs consisting of about 10 short, perpendicular ovaries, each with a separate opening into the peribranchial cavity. Rather short, unbranched testis follicles surround each ovary and are connected to a short vas deferens that opens with the oviduct on a small papilla on the body wall. The gonads are therefore not homologous with ordinary polycarps. The tough, wide connecting vessels that extend between the branchial sac and the outer wall of the peribranchial cavity sometimes extend up through the centre of a gonad.

The surface of the body wall over each polycarp may be produced into angular endocarps. Tall endocarps are also present between the gonads and around, and enclosed by, the gut loop.

REMARKS: The species is most closely related to – and was once regarded as a sub-species of – *P. aurata*, which it resembles in the form of its stomach and gut loop and the presence of compound gonads. However, the shape and orientation of the body, the nature of the test and its pigmentation, the straight rather than curved branchial folds, and the absence of well defined anal lobes clearly distinguish *P. clavata*.

Polycarpa contecta (Sluiter, 1904)
(Fig. 72)

Styela contecta Sluiter, 1904, p.66.

DISTRIBUTION

NEW RECORDS: Queensland (Townsville, QM GH1452–4).

PREVIOUSLY RECORDED: Indonesia (lectotype ZMA V.TU1019.1, paratypes ZMA V.TU1019.2 Sluiter 1904).

The species has been recorded from 10 to 36 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are from 1 to 3.5 cm long. They are more or less circular or elongate, and laterally flattened. The apertures protrude slightly from the upper surface and are directed away from each other in rounded specimens; long, oval specimens have a terminal branchial aperture and a dorsal atrial aperture. The test is moderately thick but flexible, and slightly translucent in preservative, with some sand adhering to the surface and to rootlike projections from the ventral part of the body.

INTERNAL STRUCTURE: The body wall is opaque and fleshy, though the muscles are not crowded. It is brown in preservative. The internal longitudinal muscles are visible through the thin, external circular layer. The siphons are short. The dorsal tubercle is represented by a fleshy thickening of the body wall that completely fills the wide, V-shaped peritubercular area. The opening of the neural gland is always an inverted S-shape in which the tongues of tissue in each curve of the S are depressed, causing the aperture to appear circular. The dorsal lamina is long, the oesophagus opening at the posterior end of the body.

The narrow branchial folds are long and rather straight. Posteriorly they curve dorsally and terminate around the posterior end of the oesophageal opening. There are up to 14 thick, ribbon-like internal longitudinal vessels on the folds, and up to 6 in the interspace. Branchial formulae are: E1(9)2(9)2(11)2(10)0DL (1 cm long individual); E3(9)3(14)6(11)6(10)3DL (3 cm long, lectotype ZMA V.TU1019.1). The branchial sac is very contractile, however, and when contracted formslow, rounded folds, on which the longitudinal vessels are crowded, with those in the interspace crowded against the base of the folds. The long stigmata are crossed by parastigmatic vessels. There are 6 to 8 per mesh.

The gut forms a narrow, curved loop, open at the pole where it encloses a single, large endocarp. In small specimens, the gut occupies much of the ventral curve of the body. In larger specimens, it is confined to the posterior half. The longitudinally pleated stomach is very long occupying at least three-quarters of the ascending limb of the gut loop. The rectum is long. The anal border has 8 to 10 rounded lobes.

The gonads are robust, broad and flask-shaped. They are arranged in about 2 to 3 very irregular, sometimes overlapping, rows down the centre of each side of the body. On the left, the gonads of the middle row extend down into the curve of the gut loop. They are always directed toward the atrial aperture. There are 5 to 15 gonads on the right side of the body and 6 to 15 on the left. These polycarps are not embedded, and are attached to the body wall by a membrane along the proximal half of each sac. There are up to 6 crowded pairs of rather long, lobed male follicles beneath the ovary.

There are no endocarps on the body wall, except the one enclosed in the gut loop.

REMARKS: Sluiter's (1904) type material (ZMA V.TU1019) was examined and found to include specimens of *Ascidia scaevola, Styela canopus, Seriocarpa littoralis* and *Herdmania momus*, together with two specimens of the present species. The last specimens agree with the description set out above in all respects; discrepancies in Sluiter's description probably resulted from the confusion of other material with the present species.

The species resembles *Polycarpa decipiens* in having a single endocarp enclosed in the gut loop, in the form and arrangement of the gonads, and in its lobed anal border. However, in *P. decipiens* the gonads are attached to the body wall along the whole of their length; the male follicles are larger, less crowded and more branched; there are fewer internal longitudinal vessels in the interspace and more stigmata per mesh; and the branchial folds are not so straight. The long stomach and single endocarp enclosed in the gut loop resemble the organs of *P. reniformis*, but the species are distinguished by their gonads. *Polycarpa pedunculata* has a similar long stomach and deeply curved gut loop enclosing a single endocarp. It also has similar (although longer and embedded) gonads, but has shorter, more numerous, stigmata.

Polycarpa palaoensis Tokioka, 1950 from the Palau Is. is distinguished mainly by its testis follicles, which are bunched rather than arranged in 2 rows. In *P. maculata* Hartmeyer, 1906 the gonads are connected to the body wall by a ligament (Tokioka 1959a, Nishikawa and Tokioka 1976); however, the dark vesicles embedded in the body wall and the short stomach distinguish it from *P. contecta*.

FIG. 72: *Polycarpa contecta* (ZMA V.TU1019.1) — a, gut, gonads and endocarps; b, opening of neural gland. (Scales: a, 2.0 mm; b, 0.2 mm).

Polycarpa contecta is characterised by its conspicuous S-shaped slit on the dorsal tubercle; long stomach; thick, oval, recumbent but not embedded, polycarps; and the circular endocarp enclosed in the gut loop.

Polycarpa decipiens Herdman, 1906
(Fig. 73)

Polycarpa decipiens Herdman, 1906, p.324.
Polycarpa sigmilineata Millar, 1975, p.287.

DISTRIBUTION

NEW RECORDS: Queensland (NW of Bowen, QM GH680 GH733 GH735 GH737 GH1484-5 GH1490 GH2201-7; Cleveland Bay, QM GH742 GH1487-9; Lizard I., QM GH1486 GH1491; SE Cape Sidmouth, QM GH780).

PREVIOUSLY RECORDED: New Guinea (Port Moresby — Millar 1975). Singapore (Millar 1975). Sri Lanka (BM 1907.8.3.20 Herdman 1906).

In Australia, the species has been taken in large numbers at from 8 to 30 m on silt and sand substrates. The records suggest that it has a wide range in the Indo-West Pacific, although it has not often been collected outside Australia. At Singapore, it is common at low-tide level (Millar 1975).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens examined are up to 2 cm in diameter across the upper surface and slightly higher than their greatest diameter. The body is characteristically top- or pear-shaped, with completely sessile apertures on the rather flat, circular, upper surface. Usually the basal or ventral surface tapers to a short stalk that is hollow in its upper part where it joins the body. The test is smooth, firm on the upper surface but very thin and flaccid on the basal half of the body. Terminal branches of test vessels expand into ampullae in the superficial layer of test. They contain brown pigment. Circular patches of diffuse particles of brown pigment are also present in the inner lining of the test.

INTERNAL STRUCTURE: The body wall is rather fleshy, but quite flaccid. Inner longitudinal muscle-bands radiating from the siphons to about halfway down the body can be seen through the thin, outer, circular muscle layer, which thickens in the lower half of the body, especially around the base of the body where it extends into the hollow stalk. In smaller specimens, pale brownish vesicles in the surface layer of the body wall are especially conspicuous on the lower half of the body where they are surrounded by dark patches of pigment. There are about 40 quite crowded branchial tentacles of moderate length. The dorsal tubercle is not raised off the surface of the body wall; an S-shaped slit is oriented horizontally or vertically in the centre of the peritubercular area.

The branchial folds are low, with up to 15 very wide longitudinal vessels. The vessels are crowded on the folds but not in the interspace, where there are only 1 or 2 vessels and about 15 stigmata in each long mesh. Typical branchial formulae for specimens 1 cm and 2 cm in diameter respectively are: DL 0(4)1(4)1(5)1(6)1 E; DL 0(15)2(10)2(14) 4(6)1 E. Transverse vessels are also wide.

The gut is voluminous and forms a long, closed loop in the lower half of the body. The rectum curves up to the atrial aperture against the descending limb of the primary loop to form a deep secondary loop. The oesophagus is of moderate length. The stomach is more or less barrel-shaped to elliptical and rather narrow, with 12 longitudinal folds. The intestine is voluminous and has a deep typhlosolar fold that extends around its inner curve. The rectum is also voluminous. The anal border is deeply divided into up to 20 lobes.

There are 2 or 3 irregular rows of short, oval and rather plump gonads. They are embedded in the body wall, but not deeply, and form a horizontal band about halfway down the body. On the left, they extend into the secondary gut loop. There are paired rows of 3 or 4 long, branched male follicles along the sides of each ovary, extending beneath it as the follicles proliferate. In

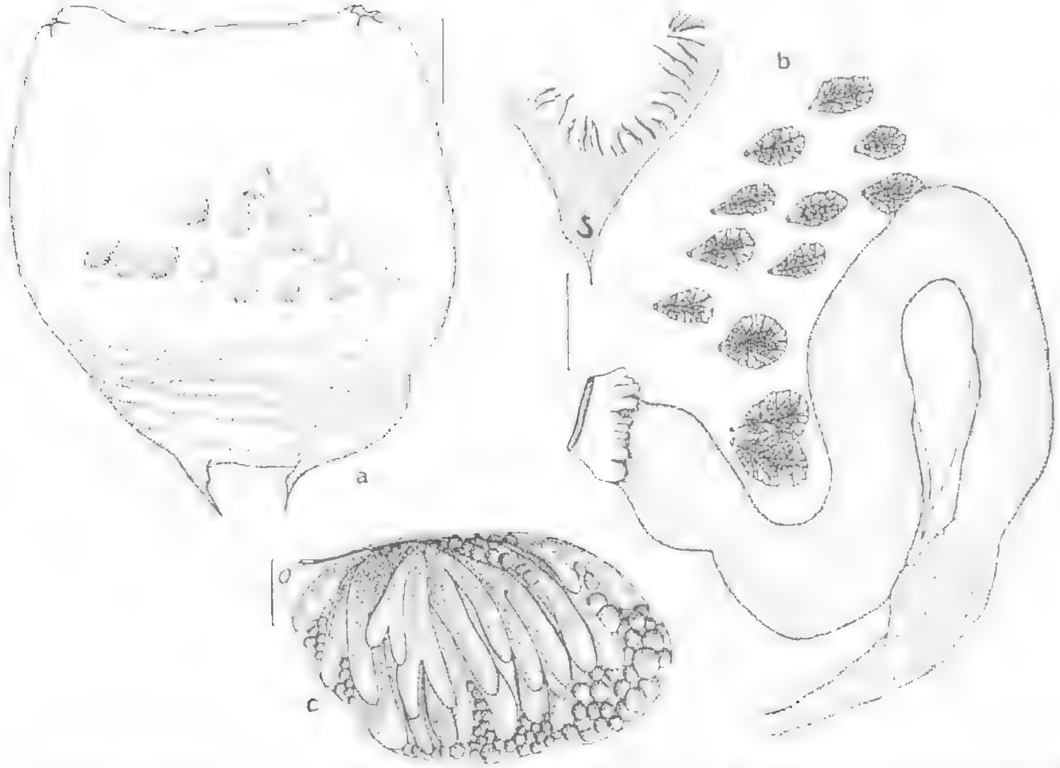


FIG. 73: *Polycarpa decipiens* — **a**, gonads seen through right side of body (QM GH737); **b**, inner body wall, left side (QM GH2203); **c**, profile of gonad. (Scales: **a**, 4.0 mm; **b**, 1.0 mm; **c**, 0.5 mm).

the mature condition, they form a solid block beneath the distal end of the ovary. Male follicles are also sometimes present on the mesial surface of the ovary.

There is a single, large, comma-shaped to narrow elongate, endocarp that completely occupies the primary gut loop distal to the stomach. Apart from the single endocarp enclosed in the gut loop, there are no others on the body wall.

REMARKS: The type specimen of *Polycarpa decipiens* (BM 1907.80.30.20) is very small (1.0 cm diameter) and is dorso-ventrally flattened. It has fine test hairs on the lower half of the body. The body wall is very thin and adheres closely to the test. A single, internal longitudinal vessel lies in the interspace between the third and the most ventral fold, but longitudinal vessels are otherwise absent between the folds. There are 9 stigmata per mesh. The stomach is short and the intestine is rather wide. The anal border is deeply divided into 12 lobes. The gonads are mature and are identical with those of the present specimens in form and arrangement, including the same long, branched male follicles. The differences between this specimen and those in the present collection (differences in numbers of internal longitudinal vessels, stigmata and anal lobes and in the development of an endocarp in the gut loop) may be related to size; the species appear to be conspecific.

Polycarpa obscura, P. pigmentata and *P. fungiformis*, also have a single endocarp enclosed in the gut loop; strong, wide, protruding longitudinal branchial vessels; and wide branchial meshes. However, they have large spherical vesicles that are quite different from the patches of pigment in the present species, which is further distinguished by its rounded, top-shaped body; S-shaped opening of the neural gland; tight gut loop; especially long meshes in the interspaces; and arrangement and form of the gonads (especially the long branched male follicles).

Polycarpa obscura has long male follicles, but they are confined to the distal end of the ovary and are not usually branched. *Polycarpa molguloides* and *P. pigmentata* have branched male follicles, although each branch is not as long as in the present species. As well, they have more internal longitudinal vessels in the interspace and lack the long anal lobes of the present species.

Millar (1975) has suggested that *P. pustulosa* (Sluiter, 1904) resembles the present species. However, *P. pustulosa* has a greater number of internal branchial vessels in the interspaces, a larger stomach, and less deeply divided anal lobes.

Polycarpa flava n.sp.
(Fig. 74)

Polycarpa pedunculata: Kott, 1972a, p.35 (part, specimens, black in preservative); 1972b, p.186 (part, black specimens); 1975, p.13 (part, small, smooth, black individuals).

DISTRIBUTION

TYPE LOCALITY: Victoria (Point Nepean, low reef, heavy surge, 16 m, coll. J.E. Watson, 16.7.80, holotype QM GH48).

NEW RECORDS: South Australia (upper Spencer Gulf, paratype QM GH2798; Kingston, QM G10135). Tasmania (Orford Beach, QM GH1334). Victoria (Cape Wooloomai, paratype QM G10010; Bass Strait, NMV F51826 H404, QM G9654).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1975; Spencer Gulf — Kott 1972b; St Vincent Gulf — Kott 1972a).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are usually spherical (up to 4 cm diameter) to more or less top-shaped, and either taper to a stalk from the posterior or postero-ventral aspect of the body or are sessile. The stalk varies from short and thick to long. Apertures are sessile, about one-third of the body length apart. Other specimens are upright and more elongate; their atrial apertures are on a laterally projecting conical protruberance. The test is smooth and rigid, and has a thin layer of sand embedded in the surface.

Living specimens are always bright yellow, but black in preservative.

INTERNAL STRUCTURE: The body wall is black to blackish brown. There is a layer of strong circular muscles. Large bladder cells are present in the body wall between the muscles and often crowded in the inner, muscle-free, layer to give it a foamy appearance. The dorsal tubercle is a circular cushion with a deep U- or S-shaped slit. There are up to 40 branchial tentacles.

The branchial sac has conspicuous, thick internal longitudinal vessels crowded on the folds. There are especially wide meshes each side of the endostyle and to the right of the dorsal lamina. The branchial formula for a specimen from Victoria (QM GH48) is E2(10)2(12)2(12)3(16)1DL.

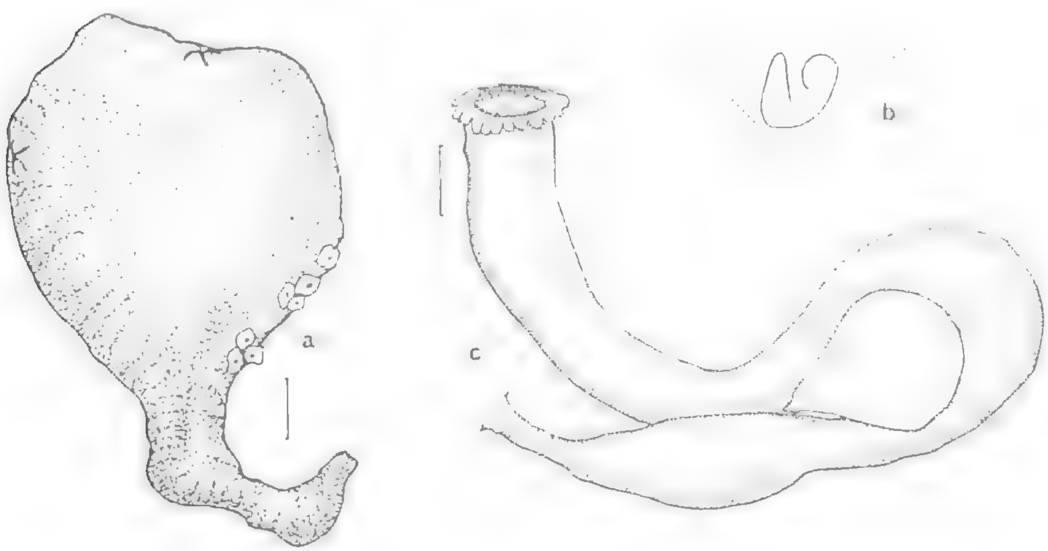


FIG. 74: *Polycarpa flava* n.sp. (QM GH48) — **a**, external appearance; **b**, dorsal tubercle; **c**, gut loop and endocarps. (Scales: **a**, 5.0 mm; **c**, 2.0 mm).

There are 10 to 12 stigmata in narrower meshes in the interspace, but up to 15 in the wider meshes.

The gut loop is long and forms a shallow curve around the posterior curve of the body. The elliptical stomach occupies about half of the ascending limb of the loop. The longitudinal glandular folds are not visible from the outside of the stomach. The rectum is about half the total length of the loop. The anal border is divided into at least 12 shallow, rounded lobes.

The gonads are embeddded in the body wall. They are spherical to oval and often are crowded, overlapping and very numerous. Pyriform, lobed male follicles are present around the sides of, and projecting beneath, the ovary. The short gonoducts open onto small papillae projecting from the body wall.

REMARKS: Preserved specimens are distinguished by the black, sand-engrained, smooth test; the absence of the dark vesicles that occur in the body wall of *P. obscura* and *P. molguloides*; and the absence of the white thread that occurs in the blood vessels of the former species. The colour of living individuals is yellow, resembling *P. viridis* in this and their embedded bladder cells, sessile apertures, embedded gonads and single, flat-topped endocarp in the gut loop. However, *P. viridis* has longer and fewer anal lobes, a naked test without sand and gonoducts that do not open into a papilla projecting from the body wall.

Polycarpa pedunculata is often the same shape as the present species and has a sandy test, but it is a different colour from the present species both in life and in preservative. Its elongate gonads, long projecting gonoducts and small bladder cells also distinguish it clearly from the present species.

Probably the most closely related species is *Polycarpa stirpes* n.sp., which has similar round gonads with short pyriform male follicles, wide branchial meshes with short stigmata and a similarly scalloped anal border. However, it has a complex dorsal tubercle, few branchial tentacles and a markedly laterally flattened body.

Polycarpa fungiformis Herdman, 1899
(Fig. 75)

Polycarpa fungiformis Herdman, 1899, p.43. Hastings, 1931, p.75. Kott, 1964, p.137; 1972c, p.242.

DISTRIBUTION

NEW RECORDS: Queensland (Moreton Bay, QM G4909 G5133 G5137 G5158 G5436 G6087–98; Hay Point, QM G9981 G9987; Townsville, QM GH2740 H2742–8; Innisfail, QM GH2741; Lizard I., QM G9733).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Herdman 1899; Kott 1964 1972c; Low Isles — Hastings 1931).

This relatively large, conspicuous species appears to be one of the few indigenous forms in Australian tropical waters. It has an unusually restricted range, from Moreton Bay to Lizard I. It is taken from sand, shell and grit substrates from about 5 to 30 m. It appears to be restricted to the mainland coast and adjacent locations. Spawning probably takes place between March and June in Moreton Bay (Kott 1972c).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens from about 2 to 5 cm in length are quite black in preservative, and are characteristically fungoid or potato-shaped, with their long axis horizontal. There is a short, cylindrical stalk from the middle of the lower surface. Both apertures are on the upper, rounded surface, quite close together and sessile. The test is relatively thin, but hard and tough. It is rough externally and has horizontal wrinkles. There is sometimes a sparse encrustation of sand on parts of the outer surface, although specimens are more often naked.

Juvenile specimens are upright and oval, with the apertures on opposite sides of the narrow upper surface. The test is very thin and grey in these small preserved specimens, with some hair-like extensions and a fairly thick coat of sand. With growth, the body becomes wider, the test tougher, the sand investment is lost, the stalk develops and the short, rather pointed, siphons are reduced. Brown vesicles like those in the body wall are present in the test of some of these smaller individuals. Living specimens are orange.

INTERNAL STRUCTURE: The body wall is completely opaque. It is brownish black and its most conspicuous feature is the embedded black vesicles beneath the ectoderm on the external surface and on both sides of the atrial cavity. These vesicles raise the surface into small pimples. The inner body wall has minute papillae, as Herdman (1899) had also observed on the dorsal lamina. There is a thick external layer of circular muscles. Longitudinal muscle-bands are deeply embedded in a thick, parenchymatous internal layer of the body wall.

There are about 40 fairly crowded tentacles, varying in size and often with black tips. The peritubercular area is wide and almost completely filled with the dorsal tubercle. Herdman (1899) noted the foamy appearance of this low, rather flat swelling with its numerous small, inconspicuous slits and/or punctate openings on the surface. In even the smallest specimens (less than 1 cm) the dorsal tubercle has this appearance.

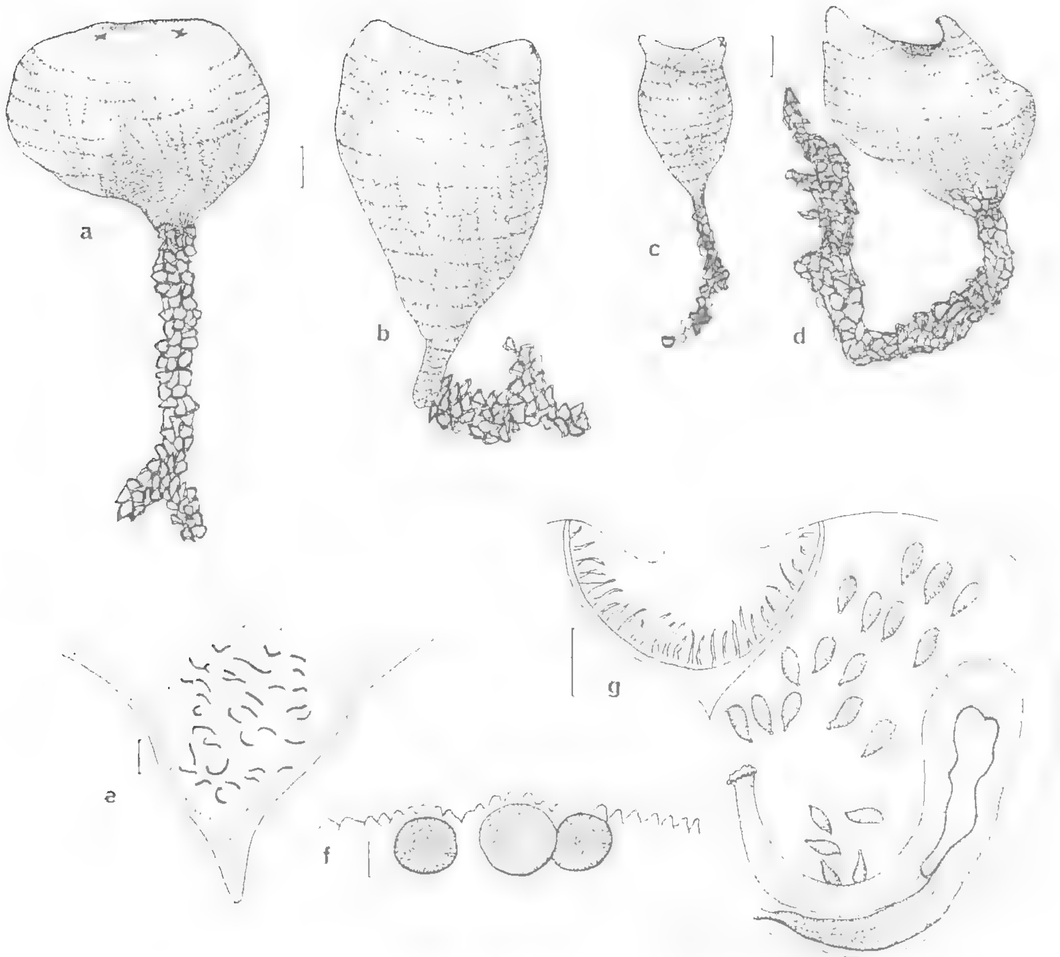


FIG. 75: *Polycarpa fungiformis* — **a** – **d**, external appearance (**a**, QM G9983; **b** – **d**, G9986); **e**, dorsal tubercle; **f**, black, spherical vesicles embedded in body wall; **g**, internal body wall, left side (QM G9984). (Scales: **a** – **d**, 1.0 cm; **e**, 0.5 mm; **f**, 0.1 mm; **g**, 4.0 mm).

The branchial sac is very tough, with wide longitudinal and transverse vessels. The folds are low and rounded, with up to 15 crowded longitudinal vessels. There are only one or two vessels in the interspace, but the very wide meshes have up to 15 stigmata. The branchial connectives to the body wall are exceptionally long and tough. Each connective is associated with a gonad; they may, to some extent, protect the gonads that project into the peribranchial cavity.

The gut is firmly fixed to the body wall, but is not embedded in it. The layer of the body wall that covers the gut contains the characteristic randomly distributed, black-brown vesicles and minute papillae. The gut forms a rounded loop, enclosing a rather elongate, comma-shaped endocarp. The stomach is fairly long, with longitudinal folds that are not conspicuous externally. The rectum extends anteriorly, forming an angle with the primary loop. The anus is bordered with about 20 slightly irregular rounded lobes. There is a typhlosolar fold in the intestine.

The gonads are scattered over the dorsal half of the body wall, but are absent from the ventral part. They are upright and flask-shaped, attached only by a strip of the body wall at their rounded proximal end. The layer of body wall that covers the polycarps has the usual vesicular cells and minute papillae. The thick ovarian tube occupies the centre of each polycarp and opens at the free end. The male follicles are obscure, however, and appear to be minute and diffuse, forming an almost continuous layer in the body wall covering the dorsal side of the ovary. The male ducts are usually obscured by the overlying layer of opaque body wall with the male follicles embedded in it, but can be seen from inside the dissected ovary. They extend around it to join the vas deferens on the ventral side in the usual way.

A single, circular, flat-topped endocarp is enclosed in the gut loop; endocarps are otherwise absent from the body wall.

Remarks: The species is distinguished from all others by the large dorsal tubercle with its many openings (which is present in even the smallest individuals), its remarkable projecting gonads and characteristic fungoid shape. Vesicles similar to those found in the body wall are also present in *P. pigmentata, P. obscura* and *P. molguloides*. Although this characteristic, together with their strong branchial sacs, suggests close relationships, the unusual projecting gonads and diffuse male follicles of *P. fungiformis* do not support that view. *Polycarpa maculata* Hartmeyer, 1906 from Japan has the same vesicles embedded in the body wall and also has upright gonads. But the opening of its neural gland is S-shaped, not complex as in the present species.

The upright, projecting gonads resemble those of *P. reniformis*, but other characteristics of the species — especially the dorsal tubercle — are distinct.

Polycarpa intonata n.sp.
(Fig. 76)

Distribution

Type Locality: Queensland (Abbot Point, Euri Creek, 15–20 m, sandy mud, coll. C. Roberts and L. Hammond, Ockleman Sledge, 19.3.81, holotype QM GH681; Abbot Point, paratypes QM GH669 GH682–3 GH732 GH738).

Further Records: Queensland (Cleveland Bay, QM GH3033).

Specimens representing large populations were taken from 4 to 20 m on sand, and sand and silt, bottoms.

Description

External Appearance: The soft, egg-shaped to oval, or kidney-shaped individuals with a dorsal concavity, apparently lie free on the substrate. They are up to 3 cm long and are completely encrusted with a thick coat of sand that adheres to the rather long test hairs (which are longest on the ventral surface). The test is very thin, easily torn, membranous, and either flexible or brittle with sand. Apertures are 4-lobed, inconspicuous and completely sessile. They are both present along the dorsal side, the branchial aperture toward the anterior end and the atrial aperture from one-third to half of the body length distant. There are especially dense, fine test hairs around the apertures.

Internal Structure: The faintly mauve-coloured body wall is delicate, almost diaphanous, and adheres to the test. There are delicate muscle bands radiating from the siphons extending only halfway down the body. Some large vesicles are embedded in the body wall.

The branchial tentacles are relatively sturdy, but are not crowded. The prebranchial region is very shallow and minutely papillated. The large, wide dorsal tubercle occupies most of the shallow, open peritubercular area and extends forward almost to the base of the tentacles. The opening is U-shaped, with both horns turned out.

The branchial sac is delicate. The branchial folds vary from low, rounded swellings to narrow but flat rather than rounded, folds. The dorsal fold on the right usually flattens out posteriorly. Between 6 and 12 internal longitudinal vessels are crowded on the folds and 3 or 4 in the interspaces.

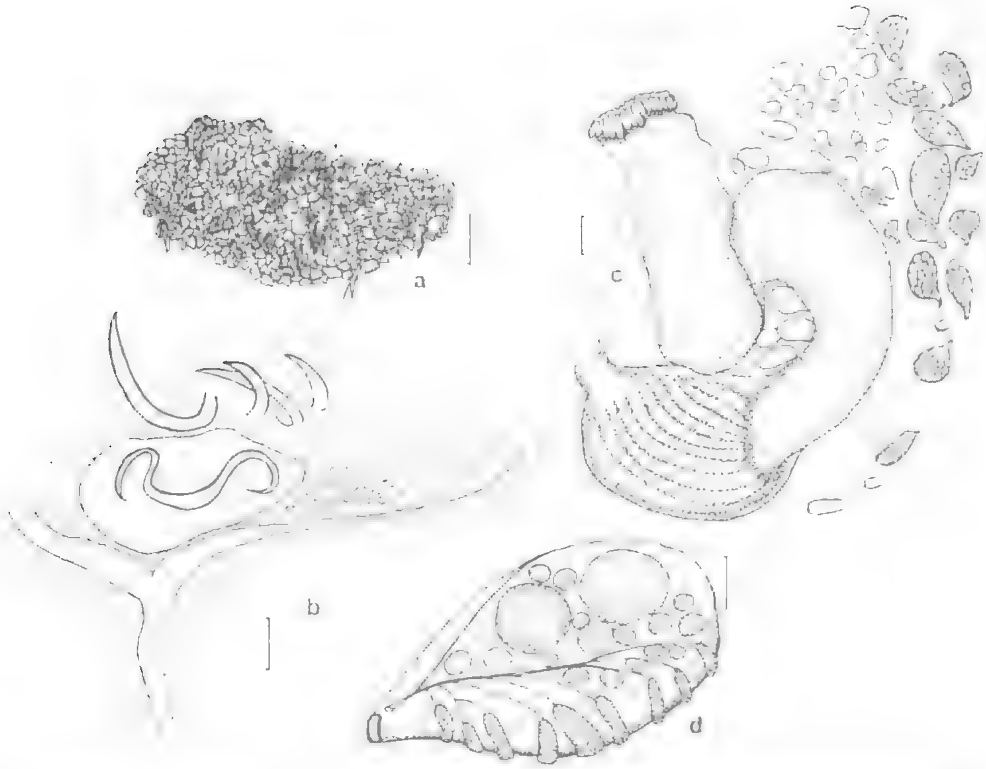


FIG. 76: *Polycarpa intonata* n.sp. — a, external appearance (QM GH681); b, dorsal tubercle (QM GH681); c, gut, gonads and endocarps (QM GH681); d, profile of gonad (QM GH682). (Scales: a, 5.0 mm; b, 0.2 mm; c, 1.0 mm; d, 0.25 mm).

There are 4 to 7 stigmata per mesh. The branchial formula for the holotype is E4(10)4(11)4(12) 4(8)1DL.

The gut is fairly voluminous and forms a narrow loop. The rectum extends forwards to form a deep secondary loop. The oesophagus is short. The stomach is short, with longitudinal folds. It narrows slightly to the intestine at its pyloric end. The anal lobes are regular and rounded, but shallow.

One or 2 irregular rows of flask-shaped polycarps extend around the ventral border on each side of the endostyle. Occasionally a row of polycarps also extends across the body wall in front of the gut loop. The polycarps lie on, rather than being embedded in, the body wall. Their pointed distal ends where the ducts open are rather irregularly directed ventrally and posteriorly, or sometimes toward one another. Each polycarp has up to 8 pairs of oval to elongate, unbranched male follicles beneath or along the sides of the ovary. The ducts curve around each side of the ovary to meet the short vas deferens that opens on the mesial side of the gland at the base of the oviduct. A few of the eggs in each ovarian sac are especially large. Small, rounded endocarps are scattered over the body wall, and a group of 3 or 4 small endocarps is enclosed by the gut loop.

Small larvae are present in the peribranchial cavity of specimens from Cleveland Bay (2.9.81). The narrow larval trunk is only 0.6 mm long and the stumpy tail is about the same length. Anteriorly there are the usual adhesive organs arranged in a triangle. The small otolith is halfway along the trunk.

REMARKS: The arrangement of the gonads in the ventral part of the body wall, with ducts directed away from the atrial opening is an adaptation favouring viviparity. The species resembles the viviparous species *P. tinctor* and *P. tinctorella* n.sp in the position of its gonads, although their gonoducts are directed dorsally and development is direct, no larva being formed. The gut loop and the soft flexible hairy test, distinguish the species from *P. tinctor* and related species (*P. rigida* and *P. procera*), all free-living species with gonads in rows on each side of the ventral mid-line, but with the gut forming a simple arc and with a hard and brittle test. *Polycarpa colletti* Herdman, 1906 (type specimen BM 1907.8.30.19) from Sri Lanka has similarly arranged gonads. However, the hard, naked test, the muscular body wall, and the presence of endocarps on the intestine distinguish it. *Polycarpa argentata*, which also has gonads only in the ventral half of the body, has a rough, naked test; a laterally flattened body; and a large flat-topped endocarp enclosed in the gut loop.

Specimens assigned to *Polycarpa quadrata* Herdman, 1882 from the Philippines and Arafura Sea (Van Name 1918 and Tokioka 1952 respectively) have gonads confined to a row each side of the endostyle. However, both the body shape and the nature of the test are different from the present species, and the gut loop is simple and rather straight, rather than deeply curved. *Polycarpa quadrata* Herdman, 1882 is a species of *Cnemidocarpa*. The type specimen (BM 1887.2.4.161-3) has 2 long gonads on the left and 3 on the right, a few endocarps on the body wall, a short gut loop enclosing a small endocarp across the posterior end of the body; a rectum that extends forwards at right angles to the gut loop; only 5 transverse vessels, and unusually long stigmata.

Polycarpa intonata is characterised by its oval, hairy form and sessile apertures, its thin test and body wall, and its ventrally placed gonads with ducts directed away from the atrial aperture and simple undivided male follicles.

Polycarpa longiformis Tokioka, 1952
(Fig. 77)

Polycarpa longiformis Tokioka, 1952, p.119; 1955a, p.213. (Not: Kott, 1966, p.298, < *P. papillata*).

Distribution

New Records: Western Australia (Port Hedland, WAM 1086.83). Queensland (Lizard I., QM G9730; Martha Ridgeway Reef, QM GH310; Cape Weymouth, QM GH767; Raine I., QM GH309; Murray I., QM G9820 GH254).

Previously Recorded: Arafura Sea (Tokioka 1952). Japan (Tokioka 1955a).

The species has a restricted range in tropical waters of southeast Asia and northern Australia down to 40 m.

Description

External Appearance: Individuals are elongate and cylindrical, up to 20 cm long and only about 1 cm in diameter. Both apertures are anterior, projecting from opposite sides of the anterior surface and are both on long siphons. The branchial siphon is directed laterally; the atrial siphon is directed upwards at an angle of about 45° to the long axis of the body. It is the more conspicuous of the two, projecting further anteriorly than the branchial siphon. The basal part of the body is produced into a wide stalk that is almost the same diameter as the long body. The preserved specimens are opaque white, with a smooth surface. The stalk is brownish, and transversely wrinkled. The base of the stalk may be broken into root-like extensions. In section, the outer layer of test is seen to be filled with densely arranged bladder cells, 0.06 mm in diameter. They are absent from the inner layer of test.

Internal Structure: The body wall adheres closely to the test and is rather delicate. The external transverse muscles form a continuous but thin layer. Very delicate internal longitudinal muscle-bands extend the whole length of the body. Both internal siphons are long and delicate. There are 12 simple branchial tentacles, each with a band of muscle along their anterior margin, which causes them to coil up. The dorsal tubercle is large, filling the peritubercular area. The slit is long, S-shaped or V-shaped, with either or both horns turned in or out. It is never divided.

The specimens from Lizard I. (QM G9730) are all heavily infested with long, vermiform notodelphid (?) copepods incubating nauplius larvae threaded through the body wall.

In most specimens, the branchial sac and gut are not present. Only in the specimen from Raine I. (QM GH309) were these eviscerated organs still attached to the branchial aperture. The branchial sac has about 15 internal longitudinal vessels on the wide, overlapping folds and about 3 between the folds. As in *P. papillata*, the anterior end of the endostyle meanders.

The oesophagus is short; the stomach long and finely pleated. The cardiac end of the stomach is about the same diameter as the oesophagus; the pyloric end is wide and voluminous. The stomach opens into a wide duodenal area. There is a thin-walled, voluminous mid-intestine in the pole of the gut loop. The rectum extends anteriorly in a straight line up the length of the body to open at the base of the atrial siphon. The anal border is divided into 12 long, flattened lobes.

There are small rounded to tall endocarps over the body wall and in the loop of the gut (as in *P. papillata*). The height of the endocarps is probably related to the condition and age of the specimen.

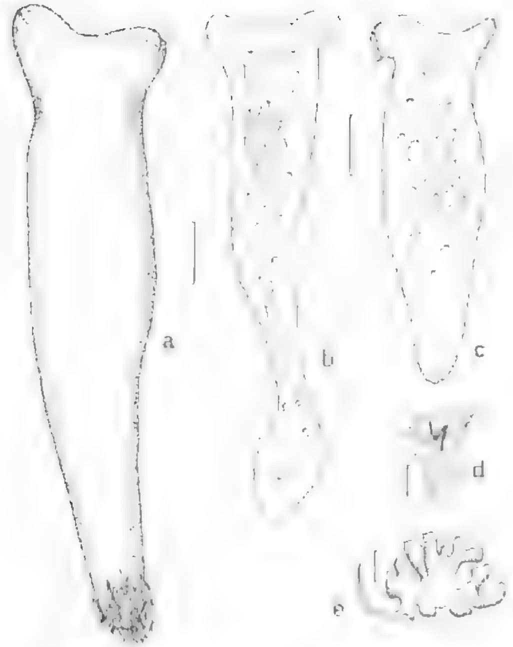


FIG. 77: *Polycarpa longiformis* — a, external appearance (QM GH309); b, c, internal body wall, left and right sides respectively, gut not present (QM GH309); d, dorsal tubercle (QM G9730); e, testis follicle (QM G9730). (Scales: a - c, 5.0 mm; d, 0.4 mm; e, 0.2 mm).

The gonads are oval, directed toward the atrial aperture. They are sometimes all over the body wall on both sides of the body and sometimes present in only 1 or 2 irregular rows. The gonads are recumbent and, although they are fixed to the body wall by about the distal one-third to the whole of their length, they are readily detached. The male follicles are long, very much branched, and fan shaped, flattened in a plane at right angles to the surface of the ovary. They are in a single row along the side or beneath the ovary, projecting up into it and often forming a rod of male tissue embedded in the under (lateral) side of the ovary. Ducts from one side of the male follicles curve around to join the vas deferens, which extends along one side of the ovary to open above the aperture of the female duct.

REMARKS: The species is closely related to *Polycarpa papillata* in the condition and proportions of the gut, the type of polycarps and endocarps, and the branchial sac and endostyle. It also shares with *P. papillata* a tendency to eviscerate the gut when disturbed. The bladder cells in the test are slightly smaller in the present species, the body is narrow, the slit on the dorsal tubercle is always entire and the gut loop is vertical. It is possible that forms will be found that are intermediate between these two species; that will indicate that the range of variation is greater than is known at present; and show *P. longiformis* to represent unusually elongate specimens of *Polycarpa papillata*.

Polycarpa lucilla n.sp.

(Fig. 78)

Polycarpa tinctor: Kott, 1975, p. 13 (part, U-shaped specimen)

DISTRIBUTION

TYPE LOCALITY: Queensland (Abbot Point, 20 m, sandy mud, coll. C. Roberts and L. Hammond, Ockleman Sledge, 18.3.81, holotype QM GH1396).

NEW RECORDS: Western Australia (Cape Jaubert, WAM 1292.83). South Australia (Upper Spencer Gulf, QM GH1432). Queensland (Gladstone Harbour, QM GH2087; Abbot Point, paratypes QM GH1401-2 GH1404; Euri Creek, QM GH1335; Townsville, paratype QM GH1403)

PREVIOUSLY RECORDED: South Australia (Kott 1975).

Although it occurs frequently at those Queensland localities from which it is recorded, the species is fragile and sandy and is readily overlooked. The scattered records suggest a wide Australian tropical to temperate range.

DESCRIPTION

EXTERNAL APPEARANCE: The body is elongate, from 1 to 3 cm long and is sometimes curved, with a dorsal concavity. It is round in section and only slightly laterally flattened. The branchial aperture is at the anterior end of the body on a very short siphon. The atrial aperture is postero-dorsal, or at least in the posterior half of the dorsal surface, and usually projects forwards, forming a cleft between the anterior part of the body and the atrial siphon. The test is thin, but hard and brittle and impregnated with sand.

INTERNAL STRUCTURE: The body wall is very thin and delicate and is closely adherent to the test. Muscles are present only around the siphons, terminating around their base. There are yellow spots in the siphonal lining of preserved specimens. About 16 short branchial tentacles of variable length are present at the base of the short siphon. There is a wide prebranchial area. The dorsal tubercle is small, with a simple U-shaped slit.

The branchial sac is delicate, with wide, flat internal longitudinal vessels. The branchial folds are narrow. The branchial formula of a specimen of 3 cm is DL1(7)5(10)5(11)2(6)3E. However, occasionally there are as few as 4 internal longitudinal vessels on a fold. There are 3 to 5

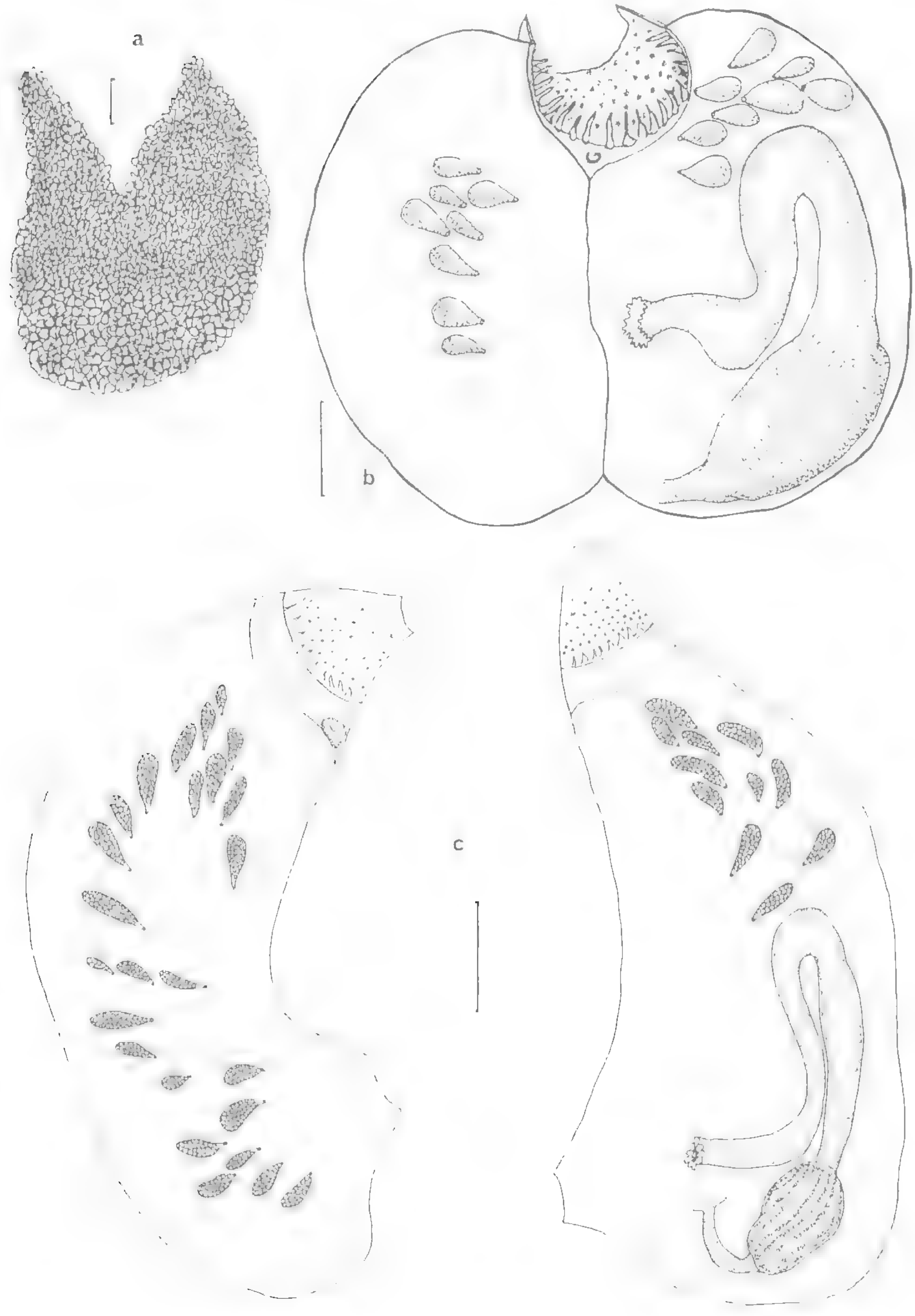


FIG. 78: *Polycarpa lucilla* n.sp. — **a**, external appearance (QM GH1432); **b**, **c**, internal structure (WAM 1292.83, QM 1335). (Scales: **a**, 3.0 mm; **b**, 2.0 mm; **c**, 4.0 mm).

long, oval stigmata per mesh, crossed by parastigmatic vessels.

The gut forms a long, narrow, gently curved loop confined to the posterior half of the body. The rectum sometimes turns anteriorly, depending on the postion of the atrial aperture. The stomach is very short and barrel-shaped, with rather irregular longitudinal folds. The anal border has about 10 small, rounded lobes.

The gonads are elongate and consist of 2 rows each of up to 6 unbranched male follicles beneath a tubular ovary. They are only very lightly attached to the body wall in 2 or 3 irregular rows, extending the whole length of the body wall on the right but terminating anterior to the gut loop on the left. On the right, there are up to 12 polycarps in one row, but the rows are seldom complete. On the left, there are never more than 6 in a row. The polycarps are oriented toward the atrial aperture. There are no endocarps on the body wall.

REMARKS: The species most closely resembles *Polycarpa granosa* Tokioka, 1953a. The single Japanese specimen is the same shape and has a similar test, body wall, gonads and gut loop. It is distinguished only by the greater development of branchial folds. *P. thelyphanes* is similar in its test and the position of its atrial aperture and gonads, but is distinguished by its open gut loop and more numerous branchial vessels. *Polycarpa tinctor* and *P. procera* also have the same stiff, brittle test, short stomach and gonads, but their gut does not form a loop and their atrial apertures are not posterior. *Polycarpa palkensis* Herdman, 1906, and *P. willisi* Herdman, 1906 both from Sri Lanka, have similar gonads and posterior atrial siphons, but they also have endocarps.

Polycarpa manaarensis Herdman, 1906 from Sri Lanka (type specimen BM 1907.8.30.14) has the same body shape, brittle test and branchial sac. A small part of the branchial sac with gonads attached and a very small fragment of body wall are the only soft parts of the type specimen remaining. These fragments do not confirm Herdman's report of 'many large polycarps embedded in the thick mantle', and the species appears to be closely related to the present one.

The stiff, brittle test; very delicate body wall; yellow spots in the siphons; lightly attached, elongate polycarps; long, narrow gut loop, short, barrel-shaped stomach; posterior atrial aperture; absence of endocarps and muscles; and the widely separated and narrow branchial folds distinguish the species.

Polycarpa molguloides Herdman, 1882
(Fig. 79)

Polycarpa molguloides Herdman, 1882, p.172. Hartmeyer, 1927, p.168.

DISTRIBUTION

NEW RECORDS: Victoria (off Lakes Entrance, NMV 73/22 H383 H414 H471 F51825).

PREVIOUSLY RECORDED: Victoria (Bass Strait — BM 1887.2.4.99–100 Herdman 1882).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are oval, up to 7 cm long, 3 cm high and 4 cm wide, rounded at both ends and dorso-ventrally flattened. The apertures are both on the long upper surface, the branchial aperture near the anterior end and the atrial aperture about one-third of the body length distant from it. Each aperture is sessile and surrounded by 4 rather solid projecting lobes of test that are covered with sand. The basal test is very thin and without sand, but the remainder of the test is firm and cartilaginous, with an outer layer of sand and quite crowded hair-like projections to which sand also adheres. The inside of the test is silvery purple.

INTERNAL STRUCTURE: The body wall is fleshy and opaque and is brown or brownish black. It has large black, brown and colourless spherical vesicles embedded in the inner and outer layers of muscle and amongst the connective tissue of the inner body wall. The outer layer of circular muscles is rather thin, interrupted by the large vesicles. The inner layer of longitudinal muscles is relatively strong and thick. There are about 40 crowded, and rather robust, branchial tentacles. The dorsal tubercle is small, with a C-shaped or U-shaped aperture with both horns turned in.

The branchial folds are moderately wide, but do not overlap. They are all more or less the same size. Internal longitudinal branchial vessels are wide and ribbon-like. They are crowded on the folds but wide apart in the interspace, where there are 6 to 8 stigmata per mesh. There are 9 or 10 internal longitudinal vessels on each fold and 3 or 4 in the interspace. Connecting vessels between the branchial sac and body wall are numerous and strong.

The gut loop is narrow and deeply curved, enclosing one or 2 large, flat-topped endocarps in the upright part of the loop, distal to the stomach. The stomach is voluminous, regularly and conspicuously pleated and only loosely connected to the body wall. It occupies slightly more than a third of the ascending limb of the primary loop. However, the oesophagus is short and the stomach does not extend far into the upright part of the gut

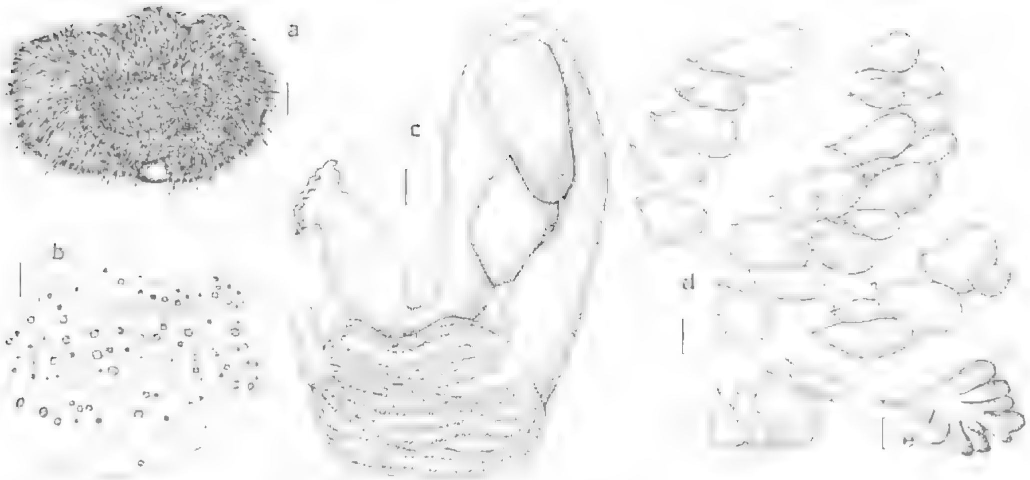


FIG. 79: *Polycarpa molguloides* — **a**, external appearance (NMV 73.22); **b**, body removed from test showing vesicles (NMV 73.22); **c**, gut loop and endocarps (NMV 75.22); **d**, gonads overlapping one another in body wall (NMV H414); **e**, male follicle (NMV H414). (Scales: **a**, 3.0 mm; **b**, 2.0 mm; **c**, **d**, 0.5 mm; **e**, 0.25 mm).

loop, which is formed by the long intestine. The anal border is divided into rounded lobes.

The internal body wall is thick and very fleshy, with flask-shaped gonads embedded in it. The long, wide male follicles with narrow branches are in a row along each side of, and beneath, the ovary. The gonads appear to be arranged in 3 or 4 longitudinal bands, each containing overlapping polycarps.

There are no endocarps on the body wall outside the gut loop.

REMARKS: The species resembles *P. pigmentata* in its dark, embedded vesicles, robust internal longitudinal branchial vessels, flat-topped endocarps in the gut loop, short anal lobes and short, branched male follicles. It is distinguished from the latter species by its thin, hairy test with its glistening purple lining and its rounded body shape and long, deeply curved intestinal loop. It is less easily distinguished from hairy specimens of *P. obscura* although it lacks the white fibres in the blood vessels. *Polycarpa flava* is also black and is sympatric. However, it lacks black vesicles, long hairs and the 2 endocarps of the present species.

Polycarpa nigricans Heller, 1878
(Fig. 80; Pl.IIIf)

Polycarpa nigricans Heller, 1878, p.2. Hartmeyer, 1905, p.390. Vasseur, 1967a, p.115. Tokioka, 1970, p.91.
Not *Gynandrocarpa nigricans*: Sluiter, 1904, p.91.
?*Polycarpa erecta* Pizon, 1908, p.202.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 183.75 981.83, 1067.83). Queensland (Heron I., QM G10029 GH351 GH357 GH3101 GH3112-4; Townsville, QM GH726 GH2736; Lizard I., QM GH2226; Britomart Reef, QM GH276 GH385 GH2739; Deltaic Reef, QM GH2738; Raine I., QM GH277; Flinders Reef, QM GH2240).

PREVIOUSLY RECORDED: Philippines (Tokioka 1970). West Indian Ocean (Mauritius — holotype ZMC Heller 1878; Ile Maurice — Vasseur 1967a). Indonesia (Pizon 1908).

This species is found in places where there is strong water movement, as on vertical channel faces, down to 20 m.

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are in aggregates or in compact but irregular colonies, sometimes separate from one another but sometimes apparently embedded in the very tough test with their anterior ends projecting. Separate individuals are up to 4 cm long and 3 cm wide. In preservative they are laterally flattened. Distended living specimens are spherical to elongate. The surface, sometimes smooth and with a thin layer of sand adhering to it, is often naked, slightly wrinkled and rough. The body tapers to the terminal branchial aperture, which is inclined away from the atrial aperture, the latter on a conical siphon directed antero-laterally or laterally from the middle of the dorsal surface. The test is grey to black in preservative and is thick and very hard.

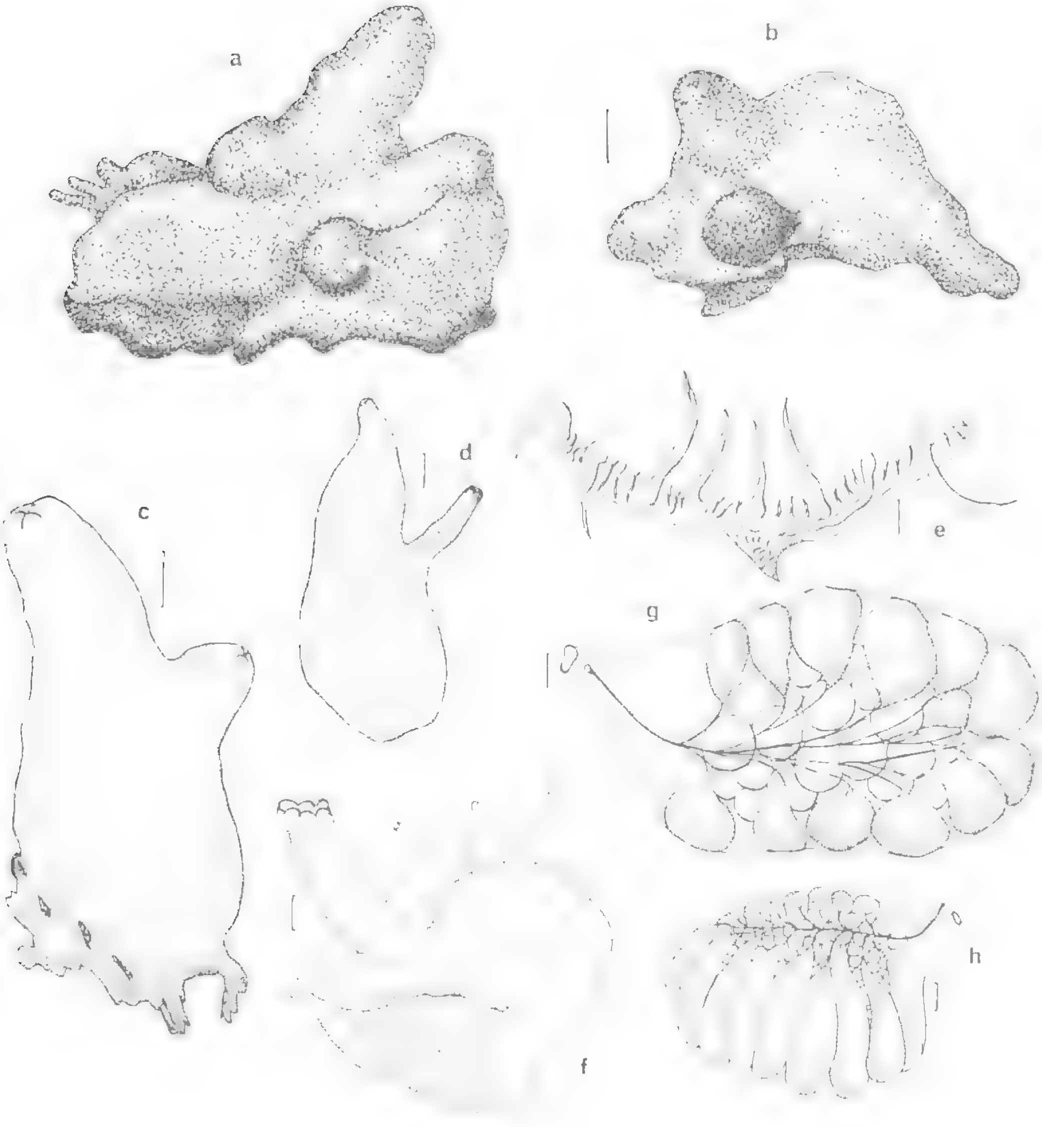


FIG. 80: *Polycarpa nigricans* — **a**, **b**, zooids embedded in common test with spongy outgrowths (QM GH2736); **c**, external appearance separate individual (QM GH2739); **d**, body removed from test (QM GH2739); **e**, branchial tentacles and dorsal tubercle (QM GH680); **f**, gut loop, endocarps and a few gonads embedded in the body wall (QM GH680); **g**, **h**, a gonad from above and from the side, respectively. (Scales: **a**, **b**, **d**, 5.0 mm; **c**, 4.0 mm; **e**, **h**, 0.25 mm; **f**, 0.5 mm; **g**, 0.1 mm).

Most individuals have 1 or 2 rounded projections of the test, sometimes with a slight constriction partially separating them from the rest of the body. These contain spongy test and a profusion of terminal ampullae of the test vessels. Living specimens are black with white siphon lining and brick-red to orange body wall.

INTERNAL STRUCTURE: The body wall is very muscular. When contracted it is very black and shiny and does not adhere closely to the test. Boththe branchial and atrial siphons are narrow and rather pointed. Spherical vesicles do not appear to be present in the body wall. There are up to 24 robust branchial tentacles, sometimes without alternating rudimentary tentacles. In some specimens, 4 large tentacles alternate with 4 slightly smaller ones and groups of 3 rudimentary tentacles are present between the 8 larger tentacles. The dorsal tubercle is a fleshy area that completely fills the peritubercular area. The opening of the neural gland varies from a U-shaped slit with both horns turned out to a complex opening in which the slit is subdivided into very numerous perforations.

There are 4 wide, overlapping folds. The thick internal longitudinal vessels of a specimen 3 cm long are arranged according to the formula DL2(8)2(12)3(11)3(6)3E. There are 6 stigmata in the dorsal mesh of the interspace and 9 to 10 in the wider ventral mesh. The external vessels of the branchial sac are tough and fibrous.

The gut forms a short, rounded loop across the posterior end of the body. The rectum extends antero-dorsally at a slight angle to the loop. A round endocarp is enclosed in the intestinal part of the loop, and a second endocarp fits between the stomach and the proximal part of the rectum. The endocarps are separated by a gastro-intestinal ligament. The stomach is elliptical, with internal longitudinal folds and a small, curved caecum at the distal end. The anal border is divided into about 6 shallow lobes.

The gonads are deeply embedded in the body wall and cannot be seen on its internal surface. They consist of flask-shaped ovaries with up to 8 long, cylindrical, undivided male follicles standing vertically to the surface of the body wall along each side of the ovaries.

REMARKS: The colonial habit and spongy test projections; the muscular body, with a fairly long atrial siphon often at right angles to the longitudinal axis of the body; the thick, hard, black test; the tough branchial sac; the few branchial tentacles; and the long, cylindrical, vertical male follicles around the border of the ovary are the characteristics of this species.

It appears, from the apparently embedded individuals that vegetative reproduction occurs. If it does, there is a possibility that all the members of the tight aggregates are vegetatively derived (although some have already lost their organic connection to others in the colony). No secondary reduction in size, or other morphological adaptations associated with budding have been observed, however, and in view of its close relationships with other *Polycarpa* spp., the species is more conveniently treated as a species of that genus than of *Polyandrocarpa*.

Pizon's (1908) single specimen had an identical body shape, and the branchial tentacles and branchial sac appear to be the same as those of the newly recorded specimens. However, although the gonads are reported to have been embedded in the body wall, Pizon's specimen was not sexually mature, so the exact position of the male follicles relative to the mature ovary is not known.

The tough external longitudinal branchial vessels contain fibres reminiscent of the single fibre present in the internal longitudinal vessels of *P. obscura*. *Polycarpa obscura* is also a similar colour to the present species, but has longer anal lobes, and more stigmata per mesh.

Polycarpa flava n.sp. most closely resembles the present species in external appearance, but it has pyriform, lobed male follicles around and beneath the ovary.

Of the species of *Polycarpa* with embedded gonads only *P. obscura* has long male follicles, but they are underneath (lateral to) the ovary. *Polycarpa stirpes* n.sp. and *Polycarpa argentata* both have sac-like ovaries surrounded by male follicles, but their ovaries are more circular and their male follicles are pyriform rather than cylindrical.

In *Polyandrocarpa, P. simulans* appears to be related but is a very much smaller species, recorded only from southern Australia.

Polycarpa nota n.sp.
(Fig. 81)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., undersurface of a boulder, intertidal rubble zone of reef flat, coll. P. Kott, July 1976, holotype QM GH940).

DESCRIPTION

EXTERNAL APPEARANCE: The holotype only is available. It is almost spherical, 1 cm in diameter. The short siphons, present on the upper surface,

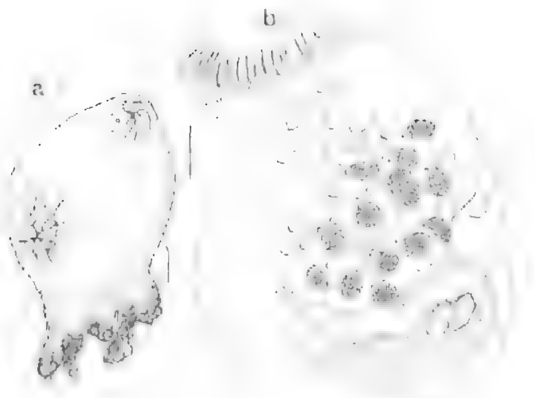


FIG. 81: *Polycarpa nota* n.sp. (QM GH940) – a, external appearance; b, internal body wall, left side. (Scale: 1.0 mm).

have brown stripes along their length. The test is white, wrinkled and tough.

INTERNAL STRUCTURE: The body wall is muscular, with an outer circular coat and inner longitudinal bands. The branchial tentacles are quite long and crowded. The dorsal tubercle is a circular cushion with a simple, U-shaped slit in the centre of the usual V-shaped peritubercular area.

The branchial folds are represented by slightly raised ridges with up to 6 crowded internal longitudinal vessels. There are only 1 or 2 vessels in the interspace, and 2 or 3 stigmata per mesh.

The gut is white in this specimen. It forms a simple loop across the posterior end of the body and is only very slightly curved. The stomach is short and wide, narrowing at each end. It is internally folded, but the folds are not evident externally.

The gonads are robust, rounded polycarps scattered over the mid- to ventral part of the body wall, their ducts directed toward the atrial aperture. There are rounded endocarps on the body wall between the polycarps, and 2 or 3 tall, narrow endocarps clustered in the pole of the gut loop.

REMARKS: The gonads are reminiscent of those of *P. contecta*. However, that species has only a single (and flat-topped) endocarp enclosed in a more deeply curved gut loop and does not have endocarps scattered on the body wall outside the gut loop. *Polycarpa contecta* is further distinguished by its very long stomach. The very low branchial folds and small number of internal longitudinal vessels are also characters by which the present species may be distinguished from others.

Polycarpa obscura Heller, 1878
(Fig. 82)

Polycarpa obscura Heller, 1878, p.22. Michaelsen, 1905, p.107. Hartmeyer, 1919, p.44. Hartmeyer and Michaelsen, 1928, p.367. Kott, 1952, p.245; 1964, p.137.
Styela cryptocarpa: Sluiter, 1885, p.210; 1890, p.333.
Polycarpa cryptocarpa: Hartmeyer, 1906, p.17. Michaelsen, 1912, p.152. Oka, 1915b, p.17. Hastings, 1931, p.75. Tokioka, 1967a, p.173 (part, black specimens only).
Styela albomarginata Sluiter, 1904, p.65.
Polycarpa unilineata Kott, 1952, p.246.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, QM GH2795). Victoria (Bass Strait, QM G12733 GH2192, NMV F51828). Queensland (Moreton Bay, QM GH2764; Heron I., QM G9769 GH316 GH356 GH2191; Tryon I., QM GH1412; Swain Reefs, QM GH1408; NW of Bowen, QM GH724 GH728 GH736 GH2757–60 GH2762 GH2766 GH2768–72; Townsville, QM GH725 GH727 GH2751–4 GH2756 GH2765; Innisfail, QM G4948; Green I., QM G10078; N of Cape Grafton, QM G11985; Lizard I., QM G9774 GH2761 GH2763; Trinity Bay, QM GH2755; Martha Ridgeway Reef, QM GH240; Cape Flattery, QM GH761; Deltaic Reef, QM GH2767; Murray I., QM G9824 GH236 GH237 GH242; Britomart Reef, QM GH2773).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919). Victoria (Bass Strait — Heller 1878, Michaelsen 1905). Queensland (Mackay — Kott 1952; Innisfail — QM G4948 Kott 1964; Low Is — Hastings 1931). Indonesia (Sluiter 1885; *P. albomarginata* type ZMA V.TU991–2 Sluiter 1904). Western Pacific (Tokioka 1967a). Japan (Hartmeyer 1906, Michaelsen 1912, Oka 1915b).

DESCRIPTION

EXTERNAL APPEARANCE: The test is always black the siphon lining is orange in living specimens, becoming black in preservative. Specimens up to 5 cm in length are oval in outline, with a terminal branchial aperture and an atrial aperture slightly posterior to it along the dorsal surface. The apertures are on small, wart-like siphons. The body is laterally flattened. In larger specimens (up to 10 cm) there is usually a thick, cylindrical posterior stalk that is sometimes as long as the rest of the body. The posterior end of the body is rounded and expanded. It is cylindrical for most of its length, but it narrows anteriorly (usually from the level of the atrial siphon). With growth, the siphons become short and cylindrical and the branchial aperture is usually directed ventrally, though occasionally posteriorly. The atrial aperture, directed anteriorly, is up to half the body length distant from the branchial opening. There are sometimes epibionts and foreign particles on the surface of the test. The surface is wrinkled and rough, often with parallel longitudinal creases, especially in the larger specimens.

The test is flexible and, although not thick, is very tough. Its inner wall is white and glistening. The body wall adheres closely to it.

Mature specimens are usually black externally with orange-chrome siphon linings.

This is one of the largest solitary species in coral reef habitats. It occurs in quite shallow water, from 2 or 3 m, on the edge of reefs, where it can be seen swaying on its thick stalk, its recurved branchial aperture facing the on-coming current.

INTERNAL STRUCTURE: The internal siphons are very short, even in the largest specimens. The external circular muscles and internal longitudinal bands form very strong layers. There is a thick, fleshy layer of body wall inside the muscle layers. The body wall is always greyish-purple to beige in preservative, but is yellow-orange with some black in the living specimens. Some of the large, spherical cells or vesicles embedded in the body wall are colourless, others contain dark pigment, resembling the dark vesicles of *P. pigmentata*. These vesicles are very conspicuous over the body organs on the inner body wall. Branchial tentacles are not crowded, and about 20 large alternate with smaller ones. The dorsal tubercle is large, filling the peritubercular V-shaped area. In smaller specimens, the slit is S-shaped, transversely or vertically oriented. However, the horns spiral in and become convoluted with growth and the slit is interrupted. In larger specimens, the dorsal tubercle has a spongy appearance, with very numerous small openings. The dorsal lamina is ribbed.

A conspicuous white line in the internal longitudinal branchial vessels extends out into the ribs of the dorsal lamina. In the less opaque body wall of smaller specimens it can also be seen in the fine network of blood vessels in the body wall. It is a tough fibrous thread, which can be pulled out of these vessels. The thread is less conspicuous in larger specimens in which the vessels are less transparent, but it can be seen by breaking the internal longitudinal vessels.

The branchial sac is robust, but the folds are relatively low, with up to 20 internal longitudinal vessels on the folds and 5 or 6 in the interspace. There are usually about 10 stigmata per mesh, though up to 13 have been found in some large specimens. Branchial formulae for specimens of 4 cm and 8 cm respectively are: E0(9)4(10)5(15) 4(9)4DL; E4(14) 5(13)(15)5(13)4DL. The internal longitudinal vessels are crowded on the edge of the folds, but spread out from one another toward the base.

The gut loop is curved and occupies a relatively large part of the left side of the body in smaller specimens; in larger specimens the gut loop is a short loop across the posterior end of the left side. The rectum extends anteriorly at right angles to the intestinal loop. There is a large, flat-topped endocarp enclosed in the intestinal loop and a second long, flat endocarp is present between the proximal part of the rectum and the stomach. The stomach, with parallel longitudinal glandular folds, is long and elliptical, extending to the posterior end of the first endocarp in the pole of the loop. The anal border is divided into 12 to 20 very long, tongue-shaped lobes. As specimens increase in length, the gut loop tends to project posteriorly, increasing the angle it forms with the rectum. The rectum is approximately the same length as the intestinal part of the gut loop.

The gonads are embedded in the thick, opaque body wall and only their short ducts can be seen on the surface. They are short and flask-shaped and set obliquely to the surface. The male follicles, which are long and finger-like, are usually not divided. They are present along the sides of the distal half of the ovary and stand vertically, at right angles to the surface. In some specimens, a mass of vertical, mature testis follicles is present at the distal end of the ovary, their ducts passing around the sides of the ovarian tube to join the short vas deferens on its mesial surface. The ovarian tube curves down behind the proximal (ventral) end of this clump of male follicles where it expands into a rounded sac.

REMARKS: Apart from its black colour, the species resembles *Polycarpa pigmentata* in its more conspicuous features, and the two have been confused (Kott 1952; Tokioka 1967a). However, living specimens are readily distinguished, the present species having a thick stalk, cylindrical body, black test and orange-yellow siphonal linings while *P. pigmentata* is sessile with a laterally flattened body, a brown test and blue siphon linings. Internally, both have opaque, strong muscle layers; a thick internal layer of tough, opaque, fibrous body wall with large spherical vesicles; simple to convoluted and interrupted openings of the neural duct; thick internal longitudinal vessels and wide branchial meshes; 2 large, flat-topped endocarps in the gut

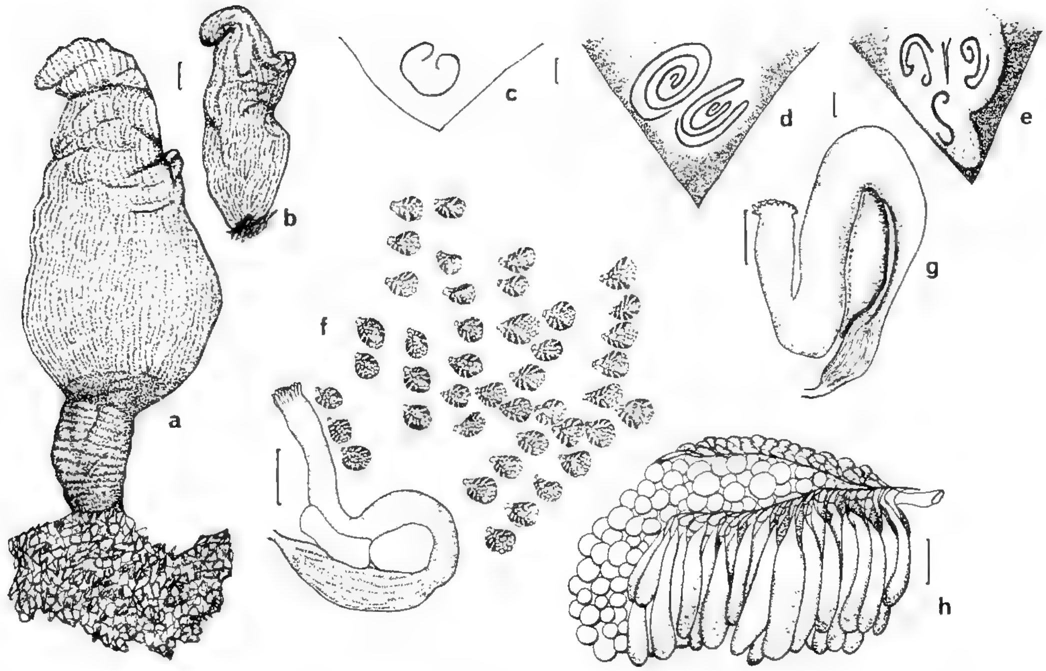


FIG. 82: *Polycarpa obscura* — **a**, **b**, external appearance (QM GH317, GH728); **c** – **e**, dorsal tubercles (**c**, QM GH1408; **d**, **e**, GH736); **f**, gut enclosing endocarps, and gonads embedded in body wall (QM GH774); **g**, gut and endocarps from specimen with sand-entangled test hairs (QM GH1408); **h**, gonad (QM GH1408). (Scales: **a**, **b**, 1.0 cm; **c** – **e**, 0.5 mm; **f**, **g**, 5.0 mm; **h**, 0.2 mm).

loop; and embedded gonads. The present species is distinguished by the longer, largely undivided, testis follicles that remain upright, do not protrude up into the ovary and are not present under the proximal end of the ovary; the long tongue-like anal lobes; and the tough white fibre in the blood vessels. Dark vesicles are not always present although colourless vesicles are crowded in the body wall as in *P. viridis*.

Polycarpa nigricans has white fibres in the external branchial vessels that resemble the single white thread in the internal longitudinal vessels of the present species.

Four specimens in the newly recorded material (QM GH1408 from the Swain Reefs, NMV H397 from Bass Strait, and QM GH761 and GH2755 from Cape Flattery and Trinity Bay respectively) are covered with hairs to which sand adheres. They resemble other specimens internally but the gut loop is longer and more deeply curved, the stomach is shorter, the endocarp enclosed in the gut loop is undivided and long, and the anal lobes are also shorter. The shape of the gut loop may be the result of a less upright body associated with a free-living habit.

Heller's (1878) type specimen of *P. obscura*, redescribed by Michaelsen (1905) has the characteristic long male follicles. It is possible that it had the irregular processes and sandy coat of the specimens referred to above.

Polycarpa mytiligera (Savigny, 1816) from the Red Sea has gonads that resemble those of the present species (Hartmeyer 1916), but its shorter stomach and laterally flattened body more closely resemble those of *P. pigmentata*. *Polycarpa decipiens* is a small species that can be confused with small specimens of the present species. However, it is top-shaped rather than tapering anteriorly; its long male follicles are subdivided; its gonads are not so deeply embedded; it does not have a white fibre in the vessels; and its branchial meshes are longer, there being only 1 or 2 internal longitudinal vessels in the interspace (in contrast to the 4 or 5 or more in the present species). *Polycarpa molguloides* resembles *P. obscura* in some features, but its testis follicles are short and branched and its anal lobes are shorter.

Polycarpa olitoria (Sluiter, 1890)
(Figs 83, 100a–d)

Styela olitoria Sluiter, 1890, p.341; 1904, p.60.
Styela solvens Sluiter, 1895, p.182.
Pandocia solvens: Sluiter, 1913, p.67.
Polycarpa solvens: Hartmeyer, 1919, p.61. Hartmeyer and Michaelsen, 1928, p.378.
Pandocia (Polycarpa) madagascariensis Michaelsen, 1912, p.139.
Styela elata: Sluiter, 1885, p.200; 1890, p.337 (Not *P. elata* Heller, 1878, p.25, < *P. papillata*).
Polycarpa seriata Michaelsen, 1905, p.112 (nom. nov. for *S. elata*: Sluiter, 1885).
Styela ascidioides Herdman, 1906, p.317

DISTRIBUTION

NEW RECORDS: Western Australia (Kendrew I., WAM 182.75). Victoria (Bass Strait, NMV H406 H478 H920). Queensland (Wistari Reef, QM GH1393; Abbot Point, QM GH686 GH688 GH693 GH713; Townsville; Cleveland Bay, QM GH717; Lloyd Bay, QM GH764; Cape Melville, QM GH2597; Murdoch Point, QM GH2596).

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Hartmeyer and Michaelsen 1928; Cape Jaubert — Hartmeyer 1919). Indonesia (ZMA V.TU1034 Sluiter 1885; Sluiter 1890 1895 1904 1913). Madagascar (Michaelsen 1912). Sri Lanka (BM 1907.8.30.14 Herdman 1906)

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright, usually sessile and fixed posteriorly. The posterior end of the body may be produced into a short stalk and/or roots. The branchial aperture is terminal and the atrial aperture is about one-third of the body length along the dorsal surface. Both apertures are on moderately long siphons marked externally with parallel grooves. When contracted, however, the test around the siphons has irregular swellings and rounded ridges around apparently sessile apertures. The test around the rim of each aperture is divided into broad lobes. In large specimens, the branchial siphon is often turned to the left. The atrial siphon usually projects forwards. Specimens are up to 6 cm long and 2.5 cm broad and are only slightly laterally flattened. The test is tough and uneven, with rounded swellings and grooves. It is usually cartilaginous, but may become leathery in older specimens. Anteriorly it is usually naked. Posteriorly, large sand and shell particles often adhere to the surface and to processes, including basal root-like processes where these are present. The test is beige to white in preservative, although living specimens are red. The test is especially firm and thick around the siphons, but is thinner and flaccid on the rest of the body.

There are relatively large (0.08 to 0.13 mm long), hollow, brown, horny spines evenly spaced on the external test. These spines are expanded basally, narrowing to a slightly curved, sharp point. They are especially conspicuous around the apertures and become less robust and more sparse toward the posterior half of the body, where they are absent altogether. The spines extend down into the outer part of the siphonal lining. The outer layer of test has crowded bladder cells, which extend up into the base of the hollow spines. In small specimens from Queensland, only a single bladder cell is associated with the base of each spine, but in large specimens from Kendrew I., which have larger spines, there is a group of about 3 bladder cells in their base.

INTERNAL STRUCTURE: The siphonal musculature is strong, but the remainder of the body wall is thin. It does not adhere very closely to the test. The external circular muscle layer is diffuse, the muscles very fine and the internal longitudinal bands clearly visible through it. The longitudinal muscle bands extend from both the siphons to halfway down the body. There are about 60 branchial tentacles of moderate length. The dorsal tubercle is large and often appears spongy, owing to the presence of bladder cells. It almost fills the V of the peritubercular space. The slit is U-shaped, the horns turned in or out.

The branchial folds are narrow, with the fine inner longitudinal vessels more crowded on the folds than in the conspicuously wide interspaces. There are up to 20 vessels on the folds and 6 to 10 in the interspace. The branchial formula of a specimen from Kendrew I. is E6(12)8(15)9(20)9(12)5DL. There are 8 stigmata per mesh in the interspace in the middle of the body wall.

The gut either forms a rounded loop across the posterior end of the body or is inclined backwards toward the postero-ventral corner. The long rectum forms an obtuse or right angle with the gut loop. The oesophagus is short, as is the stomach, which has the same diameter as the rather voluminous intestine. The very short stomach folds are usually not visible from the outside of the stomach. Internally, the intestine is seen to have a large typhlosole with stomach folds extending a little way on each side of it at its proximal end. The anal border has about 12 long, pointed lobes. In many of the preserved specimens the stomach is faintly red.

There are 9 to 15 long polycarp gonads on the left and 15 to 20 on the right. They are fixed along their whole length to the body wall in a single, often irregular, row down the centre of each side

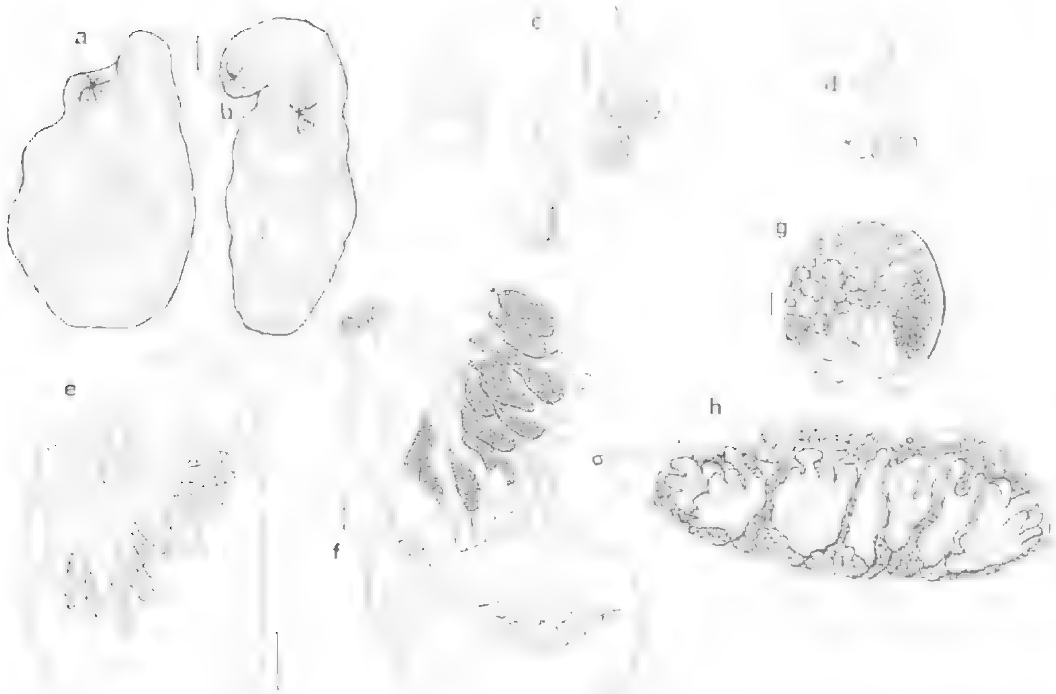


FIG. 83: *Polycarpa olitoria* — **a**, **b**, external appearance (WAM 182.75); **c**, **d**, siphonal spines (QM GH686, WAM 182.75); **e**, gonad on right side of body (QM GH686); **f**, gut, endocarps and gonads on left side (WAM 182.75); **g**, cross section through gonad (QM GH686); **h**, gonad from parietal surface (QM GH686). (Scales: **a**, **b**, 5.0 mm, **c**, **d**, 0.02 mm; **e**, 4.0 mm; **f**, 2.0 mm; **g**, **h**, 0.25 mm).

of the body, extending into the secondary gut loop on the left. Their ducts are directed toward the atrial aperture. Proliferation of gonads may produce an incipient second row of polycarps that overlap the proximal ends of those in the primary dorsal row. A single row of about 6 long, branched male follicles is present beneath the ovary, the ducts curving around the anterior side of the ovary to meet the vas deferens. Proliferation and branching of the male follicles force them up into the ovary from its lateral side.

There are about 5 tall and narrow to short and flat-topped endocarps crowded in the gut loop. Endocarps are also present on the body wall around and between the gonads but they are not crowded.

REMARKS: *Styela ascidioides* Herdman, 1906 and *S. elata*: Sluiter, 1895 (< *P. seriata* Michaelsen, 1905) appear to be identical to the present species. The spines of the type specimens of *P. olitoria* (ZMA V.TU1034) and of *S. ascidioides* (BM 1907.8.30.14) are not brown, but white and inconspicuous – the same colour as the test – and transparent and flexible. It is probable that these horny structures have deteriorated during their long period in preservative. Sluiter (1890) describes the type specimen of this species as having a smooth anal border. Unfortunately this could not be confirmed, as the type specimen is rather mutilated. Otherwise the type specimens of *P. olitoria* and *P. solvens* are identical in all important characters.

The species resembles *Polycarpa papillata* both in the bladder cells contained in the cartilaginous test and in the single rows of male follicles beneath the ovaries. However, in *P. papillata*, there is no adherent sand, the gut loop is larger, the gonads project into the peribranchial cavity and there are no spines on the test. As in *P. papillata*, the gut is only loosely attached to the body wall and may sometimes be ejected, as it appears to have been in some of Sluiter's (1904) specimens (see Hartmeyer 1919).

Living individuals are characteristically red. Although this colour is usually lost in preservative, the label in the jar is stained red in one specimen and the stomach retains some red pigment in another. Otherwise, the narrowing of the anterior part of the body; the conspicuous lobes around the apertures; the tough test; the minute, brown chitinoid spines anteriorly; the short stomach; the single, irregular row of gonads; and the large interspaces in the branchial sac are characteristic. The siphonal spines resemble those of *Cnemidocarpa intestinata* n.sp., but are more robust and conspicuous.

Polycarpa ovata Pizon, 1908
(Fig. 84)

Polycarpa ovata Pizon, 1908, p.211. Hastings, 1931, p.74. (Not: Van Name, 1918, p.102, < *P. stirpes* n.sp.).
Polycarpa moebii: Kott, 1952, p.244 (part); 1966, p.299.
Polycarpa pedunculata: Kott, 1964, p.137; 1972c, p.243.

Distribution

New Records: Queensland (Moreton Bay, QM G4945 G4903 G4908 G5148 G6099 G6100-6 G6108-9 G8684 G10075 G10078 GH341 GH2777; Hervey Bay, QM G2195; Heron I., QM GH1418; Mackay, QM G99786-7; NW Bowen, QM GH652 GH665 GH670 GH674-5 GH744 GH2778 GH2782-5; Townsville; Trinity Bay, QM GH 762).

Previously Recorded: Queensland (Moreton Bay — Kott 1964, 1972c; Hervey Bay — Kott 1966; Low Isles — Hastings 1931).

This species is most commonly reported from embayments from Moreton Bay, where it is common, and to the north. It has not been recorded from the western coast of the continent.

Description

External Appearance: Individuals are pear-shaped (rounded posteriorly) to more or less cylindrical, often with the body tapering postero-ventrally to a short to long cylindrical stalk that breaks into a tuft of long, thick roots basally. The stalk always arises from the postero-ventral part of the body. The longitudinal axis of the body is usually horizontal, at right angles to the stalk. However, sometimes the long axis of the body is upright, in line with the stalk. The apertures are small, sessile and inconspicuous, without lobes.

Occasionally, in contracted specimens, both branchial and atrial apertures are on conical protruberances, but these are not true siphons and merely result from contraction of body muscles. The branchial aperture is terminal, slightly toward the ventral side of the rounded anterior end in cylindrical specimens. The atrial aperture is one-third to one-half of the distance along the dorsal surface of the body. The test is usually naked, only rarely having a thin encrustation of sand. The basal roots of the stalk have a mass of sand adhering to them. The test is tough, opaque and rigid. The surface is smooth, becoming rather felty in larger specimens.

Living specimens are a dirty yellow, becoming white to beige or dirty white in preservative.

Internal Structure: The body wall is compact and muscular, the outer layer of circular muscles being continuous and thick. A feature of the species is the small (0.01 to 0.1 mm diameter), clear, spherical vesicles that are embedded between the muscle bundles and crowded in the inner, muscle-free, layer of test. The body wall is usually brown to black-brown in preservative.

There are from 20 to 40 branchial tentacles of varying length. The dorsal tubercle is a simple circular to heart-shaped cushion with an S- or U-shaped deep slit, variously oriented. The horns are turned in or out.

The branchial folds are low, with conspicuous, thick internal longitudinal vessels crowded on them. The stigmata are short and the meshes are very wide but irregular, with one mesh in the interspace wider than the others. This wide mesh has up to 10 stigmata, while the narrower meshes have 6 to 8. Meshes to the right of the dorsal lamina and on each side of the endostyle are very wide, with up to 16 stigmata. The transverse branchial vessels are wide and strong; parastigmatic vessels are rare. There are 2 or 3 vessels in the interspace and up to 16 on the folds.

The gut forms a relatively short loop across the posterior end of the body, enclosing a simple circular to irregular endocarp. The stomach is short and elliptical, never more than half the length of the ascending limb of the gut loop. The rectum, which is sometimes longer than the gut loop, extends anteriorly more or less at right angles to it. The anal border is divided into about 8 rather shallow lobes on the mesial side. The outside of the border of the anus projects forward and is rather irregularly indented. The stomach has internal glandular folds, which are not always conspicuous from the outside.

The gonads vary in number and shape with size and maturity of the specimen. They are arranged in 3 or 4 irregular rows, but are often crowded and slightly overlapping. They are flask-shaped, tapering toward the short ducts, which open on a small papilla at their distal (dorsal) end, directed toward the atrial aperture. The ovary is large and sac-like. There are about 6 pairs of wide, fan-shaped male follicles (lobed on their proximal border) beneath each ovary and projecting up into the centre of the sac. The gonads are embedded very deeply in the body wall but, in all but the

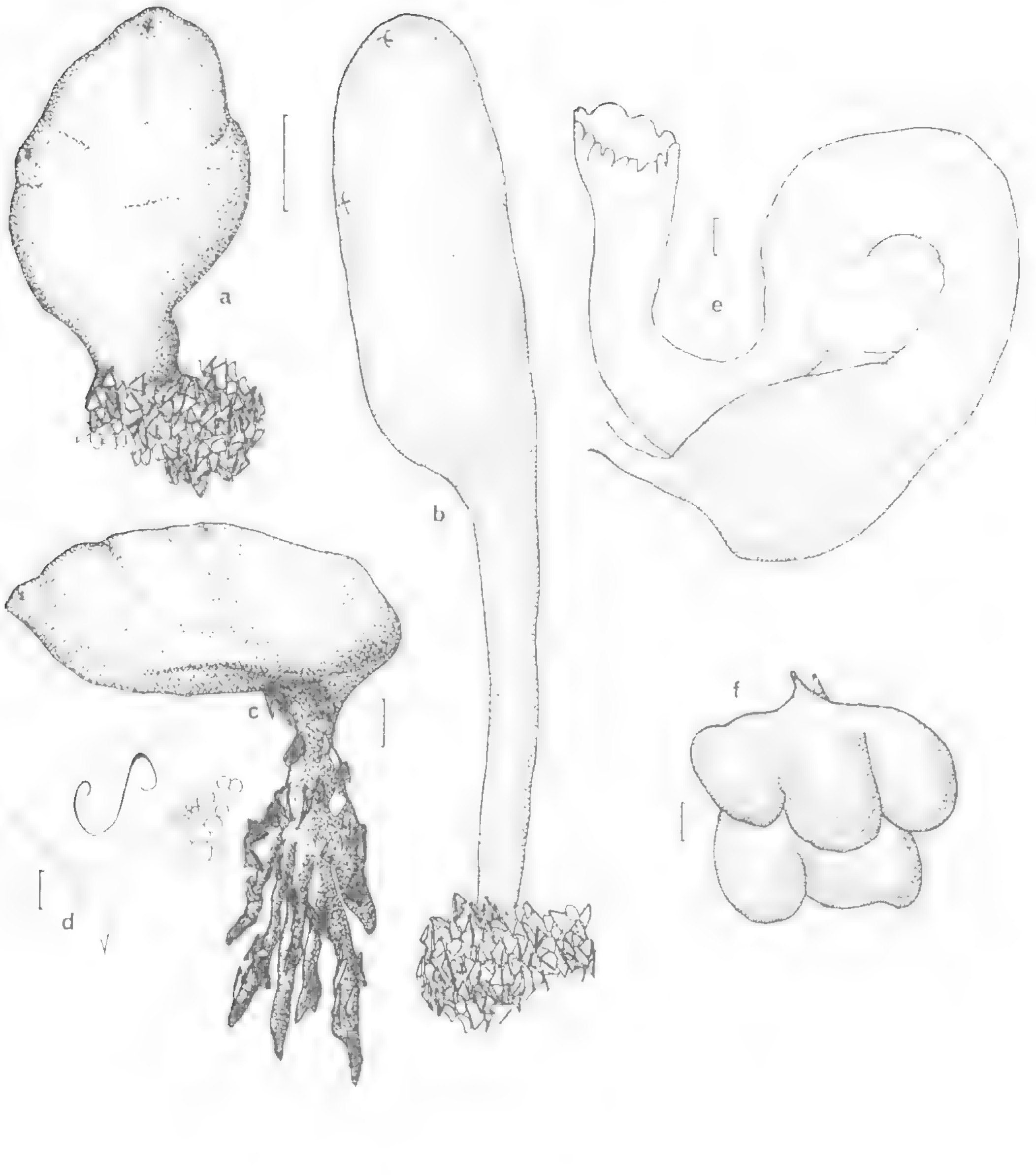


FIG. 84: *Polycarpa ovata* — **a - c**, external appearance (QM GH670, GH2777, G6106); **d**, dorsal tubercle, showing some bladder cells (QM GH1418); **e**, gut loop enclosing endocarp (QM GH341); **f**, male follicles (QM GH1418). (Scales: **a, b**, 1.0 cm; **c**, 0.5 cm; **d, f**, 0.1 mm; **e**, 1.0 mm).

largest specimens, are clearly visible from the inner surface. In some contracted specimens, the gonads are forced up onto the inner surface of the body wall.

REMARKS: Some horizontally oriented specimens of *Polycarpa viridis* (which is also yellow in life, naked and smooth, and occasionally has sessile apertures) resemble the present species. However, *P. ovata* can be distinguished by its very small vesicles and flask-shaped gonads with short ducts.

The type specimen of *P. ovata* Pizon has a the same compact body as the Australian specimens.

P. ovata is distinguished from the large *P. pigmentata* (which has a similar branchial sac and male follicles) by its body shape, colour, smooth test, small and colourless vesicles, short gut loop, short stomach and one endocarp, rather than 2, enclosed in the gut loop.

Polycarpa papillata (Sluiter, 1885)
(Fig. 85,86; Pl.IIIg)

!*Polycarpa elata* Heller, 1878, p.25.
Styela (*Polycarpa*) *papillata* Sluiter, 1885, p.192.
Styela papillata: Sluiter, 1890, p. 333.
Polycarpa papillata: Tokioka, 1952, p.117; 1970, p.99. Kott, 1972a, p 34. Vasseur, 1969, p.925
Styela (*Polycarpa*) *captiosa* Sluiter, 1885, p.202; 1895, p.181; 1904, p.60.
Styela captiosa: Sluiter, 1890, p.333.
Polycarpa captiosa: Tokioka, 1950, p.136; 1967a, p.171. Millar, 1975, p.292
Styeloides abranchiata Sluiter, 1885, p.219.
Styela (*Polycarpa*) *phaula* Sluiter, 1895, p.182; 1904, p.61.
Polycarpa aurata: Herdman, 1899, var. plana p.51.
Polycarpa attollens Herdman, 1899, p.53. Kott, 1952, p.235; 1972e, p.52.
Polycarpa mutilans Herdman, 1906, p.319.
Polycarpa aurita: Kott, 1952, p.234.
Polycarpa intestinata Kott, 1952, p.238.
Polycarpa capricornia Kott, 1952, p.239; 1964, p.135.
Polycarpa longiformis: Kott, 1966, p.298.
?*Polycarpa intermedia* Hartmeyer, 1919, p.69.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 201.75 1099.83; Kuri Bay, WAM 103.75; Learmonth, WAM 95.75; Port Hedland, WAM 1101–2.83; Shark Bay, WAM 1098.83; Kendrew I. WAM 161.75 183.75 214.75; Abrolhos, WAM 387.75; Cockburn Sound WAM 1095–7.83). South Australia (Port Noarlunga, QM GH9328). Victoria (SE Portland, NMV F51597). New South Wales (Port Jackson, AM G1150 U576). Queensland (Moreton Bay, QM G4919–20 G5133–36 G5138 G8570 G9573 G9600 GH342 GH361; Flinders Reef, QM G12814; Mudjimbah, QM G11911; Hervey Bay, QM G9388 G9391 G9573; Gladstone Harbour, QM G9714 G9807 G12709; Heron I., QM G10095-6 GH323 GH353 GH358 GH1416 GH2694 GH3015 GH3052; Wistari Reef Channel, QM GH2691; One Tree I., QM GH378; Keppel I., QM G11998; Swain Reefs, QM GH1414; NW of Bowen, QM GH598–610 GH617–8 GH650–1 GH730–1, GH739 GH741–3 GH2695; Magnetic I., QM G12003 G49574; Sarina, QM G4946 G4975; Mission Beach, QM G12859; Cooktown, QM GH765; Lizard I., QM G9729 GH 314; Britomart Reef, QM GH287; Thursday I., QM G9821 G9823; Murray I., QM G9822 GH308). Northern Territory (Gulf of Carpentaria, WAM 84–75; Darwin, NTM E5; NW Bathurst I., NTM E28).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1972a). New South Wales (Port Jackson — Herdman 1899, Kott 1952). Queensland (Moreton Bay — Kott 1952 1966; Central Queensland — Heller 1878; Great Barrier Reef — Kott 1952 1964; Thursday I. — Sluiter 1895, Kott 1952). Northern Australia (Darwin — Kott 1966; Gulf of Carpentaria — Kott 1972e). Ceylon (Herdman 1906). Madagascar (Vasseur 1969). Solomon Is (Kott 1952). Arafura Sea (Tokioka 1952). Indonesia (Sluiter 1885 1890 1895 1904). Palau Is (Tokioka 1950 1967a). Philippines (Tokioka 1970). Marianas Is (Tokioka 1967a).

This species has a wide range in tropical waters of the Indo-West Pacific, extending into temperate waters around the southern coast of Australia.

DESCRIPTION

EXTERNAL APPEARANCE: The species is very variable. Smaller specimens (up to 3 cm in length) have a tough, opaque, white test that is smooth or is marked with irregular, rounded swellings or ridges. In larger preserved specimens (from 3 to 8 cm long), the test is opaque and white with red longitudinal markings, or evenly beige or grey. The red colour fades in preservative. The surface is sometimes smooth all over, sometimes smooth only posteriorly, with swellings and ridges anteriorly. The largest specimens have a leathery, wrinkled surface.

The branchial aperture is always terminal, but the siphon may be curved ventrally or dorsally. The atrial aperture is at varying distances along the dorsal surface and is either directed forwards, at right angles to the long axis of the body, or posteriorly. Occasionally the apertures are almost sessile and relatively inconspicuous. Both apertures are surrounded by 4 conspicuous lobes or swellings that extend posteriorly as parallel, rounded ridges along the length of conical or cylindrical siphons (when these are present).

The body shape is also variable. The smallest specimens are rounded and almost spherical. Specimens 2 to 3 cm long may be almost rectangular, the atrial aperture being produced forwards nearly to the level of the branchial aperture. Very often, however, the anterior end of

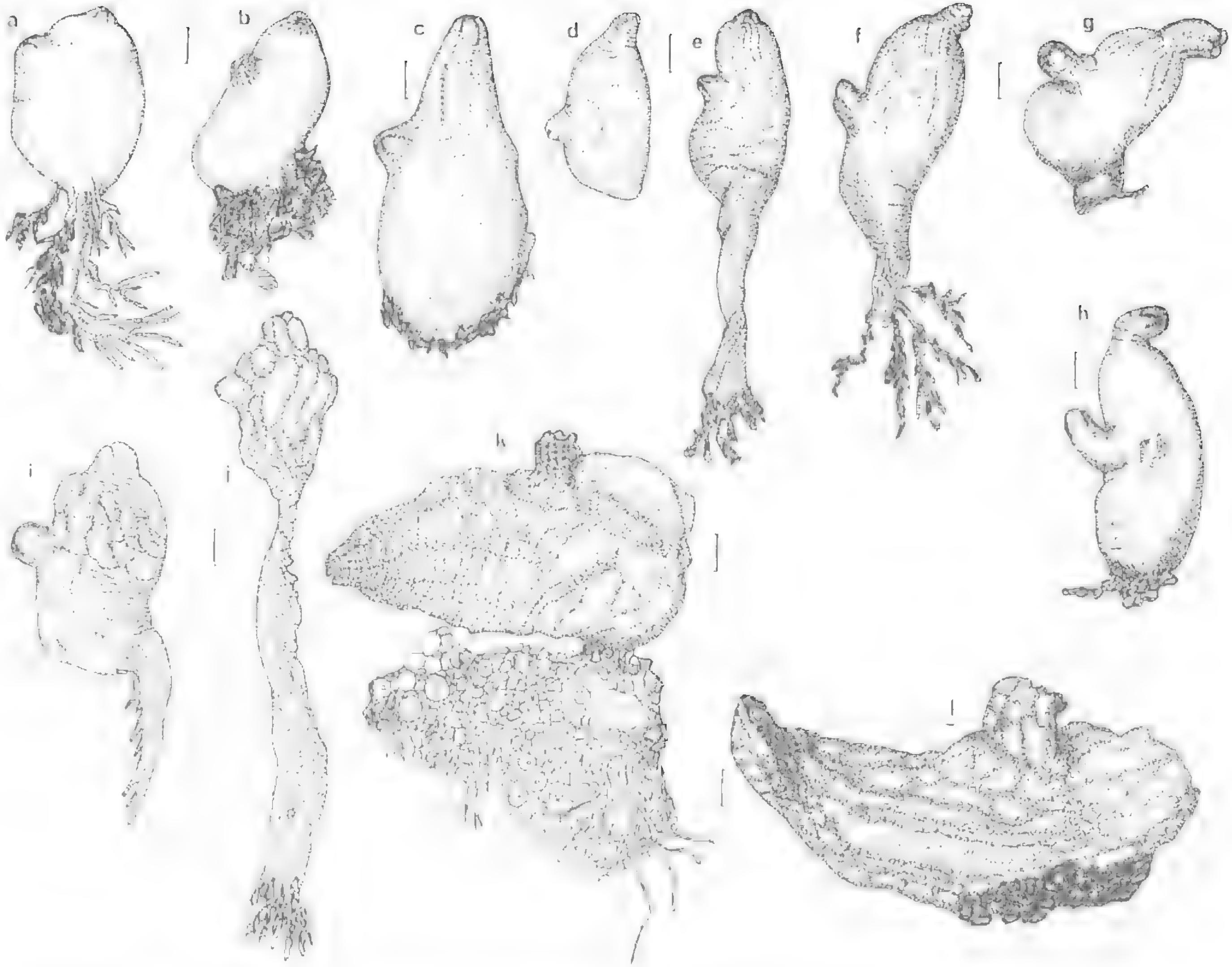


Fig. 85: *Polycarpa papillata* — variable external appearance (a, QM G9600; b, QM G5134; c, QM G11911; d, QM G9729; e, QM G4987; f, QM G5138; g, h, QM G4919; i, j, QM G9729; k, QM GH265; l, QM GH245). (Scales: a, b, d - j, l, 1.0 cm; c, k, 0.5 cm).

the body is attenuated and narrow; in larger specimens this is invariably the case. The longest specimen examined (14 cm, QM GH287) is more or less banana-shaped, concave dorsally, with the atrial siphon projecting forwards from the posterior third of the body. It is sessile and fixed by the posterior half of the ventral surface. More often, individuals are fixed either by extensive, root-like test extensions from the postero-ventral curve of the body or by a stalk that is up to 3 or 4 times the length of the body. The stalks or root-like extensions are hollow near the body and contain an extension of the body wall. A collection from Lizard I. (QM G9729) includes stalked, rooted and sessile specimens with smooth or furrowed tests. Their body-shapes vary from cylindrical to conical. Moreton Bay specimens are invariably smooth and swollen posteriorly. They may be grey-black, white with red stripes or beige-yellow in preservative.

In some individuals (AM E1840, U576), the posterior end of the body is swollen into an almost spherical hold-fast. The test thickness varies, generally being thicker when the surface is irregular, and relatively thin when it is smooth. Large bladder cells (0.085 mm diameter) are crowded in the outer layer of test, but they do not occur in the more compact inner layer.

Living specimens can be observed changing their shape by contracting the anterior part of the body.

INTERNAL STRUCTURE: The body wall is rather thin and adheres so closely to the test that it is sometimes difficult to remove from it. A thin outer layer of transverse muscles forms a continuous coat over a layer of longitudinal muscles. The branchial tentacles are usually crowded, except in the largest specimens, where they are well-spaced. Sometimes the tentacles are coiled in the preserved specimens. The dorsal tubercle is large, completely filling the deep and sometimes narrow peritubercular area. In smaller specimens, the opening of the neural duct is an undivided, generally U-shaped slit, with one or both horns turned in or out. In larger specimens, the slit divides into multiple, variable and complex openings, often densely distributed on the surface of the tubercle. The slit-like openings are either randomly placed, radial or parallel to one another. Long slits may either be present all over the tubercle; or confined to the anterior part of the tubercle with shorter, almost punctate, openings posteriorly.

The branchial sac is delicate, with 4 rather wide, flat folds that often overlap one another. There are up to 20 internal longitudinal vessels on the folds and 3 to 6 between. The number of vessels increases with the size of the individual. The longitudinal vessels are well-spaced, and only slightly more crowded on the folds than between them. There are up to 12 stigmata per mesh. Parastigmatic vessels cross some of the rows of stigmata in a random arrangement. Three intermediate-sized transverse vessels alternate with larger primary vessels. The anterior end of the endostyle undulates, the undulation having an amplitude of about 6 stigmata on each side of the mid-line (which may, however, be the result of contraction).

The gut forms an oblique to almost horizontal loop across the posterior part of the body, although the rectum projects forward to the atrial aperture, creating a secondary loop that is of variable depth, according to the position of the atrial aperture and the width of the body. The gut loop is only loosely attached to the body wall. In many specimens the whole branchial sac and gut eviscerate when the animals are collected. In one senescent specimen, the absence of the gut may be the result of predation by the pontoniid shrimps found in the peribranchial cavity. The oesophagus is short. It opens into a long, almost pear-shaped, stomach that is scarcely wider than the oesophagus at the cardiac end but expands greatly at the pyloric end. There are very fine longitudinal and oblique folds in its wall. The former extend the whole length of the stomach and the latter extend obliquely from both sides of the typhlosole at the pyloric end. Externally these folds may be obscured by the layer of body wall that covers the stomach. In large specimens, the roomy pyloric end of the stomach is almost divided into two chambers by a deep, wide typhlosole that projects into the lumen. The folds of the stomach cease abruptly where it opens into a wide duodenal area. An even more voluminous and very thin-walled, straight mid-intestine occupies the pole of the gut loop. The mesial wall of this mid-intestine is often distended and the pole of the gut loop bends dorsally, projecting into the atrial cavity. The rectum is also wide and extends anteriorly, to the atrial opening. The anal border is deeply divided into a variable number of pointed lobes.

The body wall is covered with tall, flattened endocarps, either straight or rounded on their free border, where they are sometimes expanded. Endocarps are also present between the limbs of the gut loop. With senescence, these endocarps shrink to little more than papillae on the body wall. Between these endocarps, the gonads are present in a wide belt (from 1 to 4 polycarps wide) down

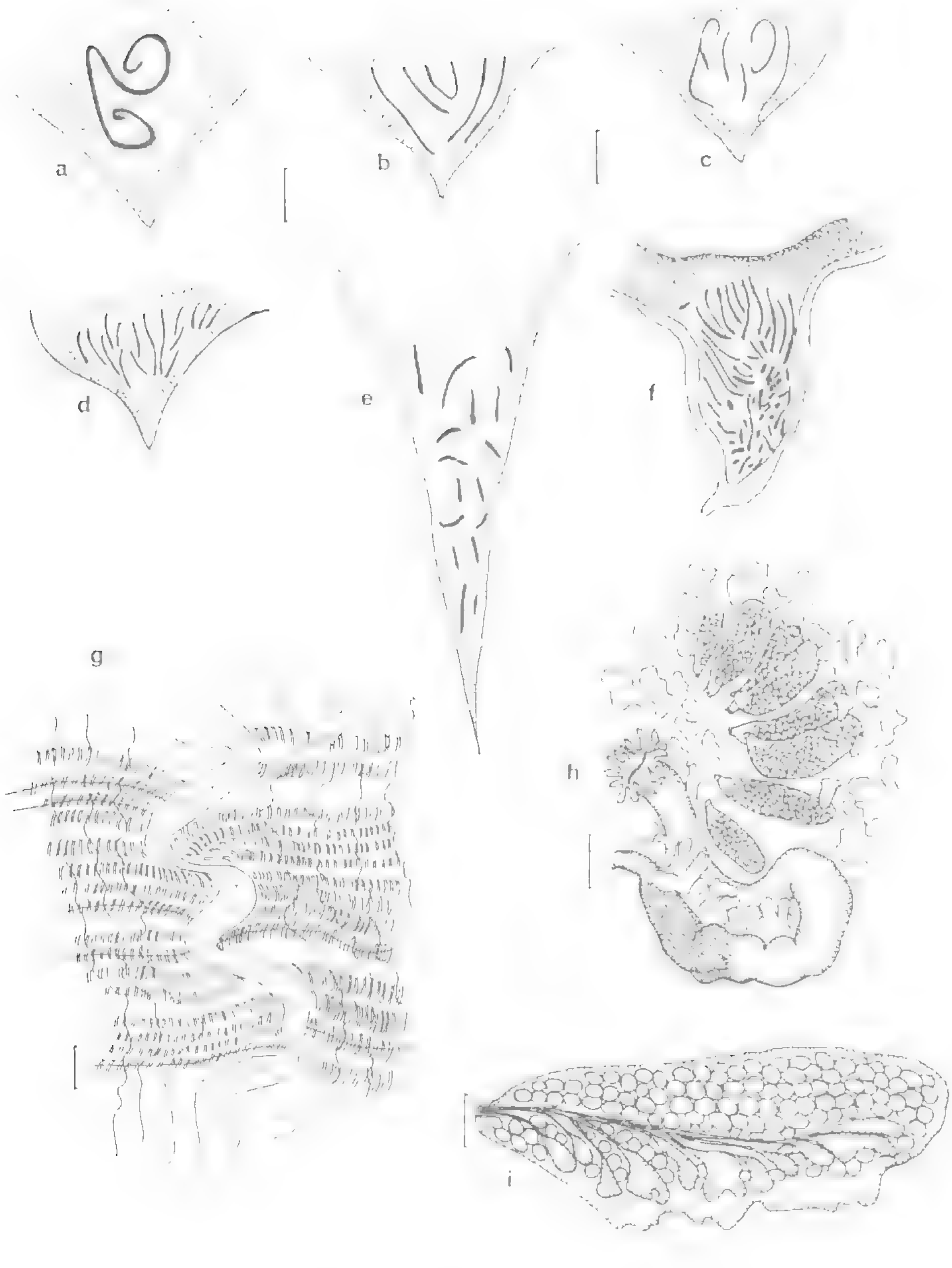


FIG. 86: *Polycarpa papillata* — **a** – **f**, variability in the dorsal tubercle; **g**, anterior end of the endostyle (QM G11998); **h**, gut, gonads and endocarps (QM G9729); **i**, profile of gonad (QM G10096). (Scales: **a** – **f**, 1.0 mm; **g**, **i**, 0.5 mm; **h**, 1.0 mm).

the middle of the body wall on each side of the body, forming an arc around the atrial aperture. The polycarps are almost elliptical, rounded proximally, the openings of male and female ducts at the narrowing distal end directed toward the atrial aperture. The gonads are either recumbent, or oblique or almost upright on the body wall, projecting into the peribranchial cavity. They are attached at their proximal end by a ligament that extends along one- to two-thirds of their length. The distal pointed ends of the gonads are free and often overlap polycarps dorsal to them. They are readily detached. There is generally only a single series of up to 10 much branched male follicles beneath the ovary, their ducts joining along one side before opening mesial to the oviducal opening. In senescent specimens, a rod of expended male follicles is embedded in the lateral side of the ovary. Very occasionally the gonads are scattered all over the body wall, instead of being confined to a mid-lateral belt.

REMARKS: Much of the variation in this species that has resulted in confusion over its identity has already been noted by Tokioka (1952) and Millar (1975). Colour variations may be genetic; however, others appear to be a result of age. They include the external appearance, the complexity of the dorsal tubercle and the decrease in size and number of endocarps and gonads. Otherwise, the internal structure is remarkably constant. The wide branchial folds with well-spaced longitudinal vessels, the undulating anterior extent of the endostyle, the voluminous stomach with its finely pleated wall and narrow cardiac end, the thin-walled mid-intestine in the pole of the gut loop, the tall endocarps and the long, narrow, pointed anal lobes are all characteristic and constant. The tendency of the gut to eviscerate is also a consistent and conspicuous feature of the species (see Tokioka 1970; and *P. mutilans* Herdman, 1906).

One of the inconsistencies in reporting the structure of this species that has led to the synonymy set out above has been the failure to recognise the narrow, almost cylindrical, cardiac part of the stomach as part of that organ rather than a continuation of the oesophagus. The stomach has often been recorded as short and elliptical, and the unique nature of the gut has been overlooked. The availability of large collections and especially of large samples from the populations of Moreton Bay, Lizard I. and Abbot Pt (near Bowen) has clarified the status of many of the characters formerly used to separate the species.

Specimens larger than 8 cm are taken only rarely. With the exception of its dorsal tubercle (which has multiple short openings on the posterior deep V of the tubercle and anteriorly is imperforate), the large (12 cm) specimen (QM GH308) from Murray I. is identical in all respects (including its size) with the largest *Polycarpa captiosa*: Tokioka, 1950, from the Palau Is. In both these specimens the body is attenuated and lies horizontally, fixed by the posterior end of the ventral border. The dorsal tubercles of Tokioka's larger specimens are identical with that of an 8 cm long specimen from Flinder's Reef (off SE Queensland, QM G12814). The specimens differ externally, however, the Flinder's Reef specimen being rounded and sessile and not the elongate, concave shape of some of the others. Millar (1975) suggested the synonymy of *P. captiosa* with *P. papillata*, which is confirmed by the specimens in this collection.

Polycarpa nebulosa Heller, 1878 and *P. elata* Heller, 1878 (both from Bowen) may be conspecific with the present species. But as details of their internal structure are not available, their affinity with *P. papillata* must be speculative, based on their external appearance (the test thickness and nature of its surface, and the shape of the body).

The shape of the body, the stomach, the anal lobes and the endocarps resemble those of *P. olitoria* (Sluiter), which is distinguished from the present species by its test spines.

Polycarpa papyra n.sp.
(Fig. 87)

DISTRIBUTION

TYPE LOCALITY: Queensland (Cleveland Bay, 4.6 km SSW John Brewer Reef, coll. P. Arnold and A. Birtles Sq 8e Stn 479, holotype QM GH1501; paratype QM GH1502).

This small, delicate and inconspicuous species has been taken from only one location.

DESCRIPTION

EXTERNAL APPEARANCE: The body is almost cylindrical, up to 2 cm long. The apertures are sessile. The atrial aperture is about two-thirds of the body length distant from the terminal branchial aperture. The test is moderately thin, sometimes naked, rough and more or less leathery. Some sand is embedded in the surface, making it stiff but not especially brittle.

INTERNAL STRUCTURE: The body wall is extremely delicate and closely adheres to the test. The muscles are very fine and inconspicuous. There are 12 rather short branchial tentacles. The

FIG. 87: *Polycarpa papyra* n.sp. (QM GH1501) - internal body wall, left side. (Scale: 2.0 mm).

prebranchial area is narrow. The dorsal tubercle, a small, rounded cushion in the centre of a V-shaped peritubercular area, has a simple vertical or oblique slit.

The branchial folds are low, narrow ridges with crowded internal longitudinal vessels. The vessels are arranged according to the formula E3(8)4(10) 6(9)3(12)3DL. There are 4 to 6 long, elliptical stigmata in each mesh, sometimes crossed by a parastigmatic vessel.

The gut forms a simple, narrow loop in the postero-ventral corner of the body. The pole of the loop only reaches halfway up the body. The pleated stomach is long, occupying about two-thirds of the ascending limb of the loop. The terminal part of the rectum curves anteriorly to the atrial opening. The anal border has about 20 narrow, sometimes bidentate, lobes.

Small, rounded endocarps are scattered on the body wall, and are especially crowded toward the ventral border. Those on the left are confined to the body wall anterior to the gut loop. There are no endocarps in the gut loop.

No gonads were present in these specimens.

REMARKS: The species is characterised by its narrow gut loop (curved only where the distal part of the rectum turns toward the atrial aperture), the very long stomach, the presence of small endocarps on the body wall and the absence of endocarps in the gut loop. *Polycarps biforis* and *P. contecta* have a similarly long, cylindrical stomach and rather numerous longitudinal branchial vessels in the interspaces. They both have an endocarp enclosed in the gut loop and none elsewhere on the body wall, a condition that is the reverse of that found in the present species.

Polycarpa pedunculata Heller, 1878
(Fig. 88)

Polycarpa pedunculata Heller, 1878, p.24. Michaelsen, 1905, p.98. Kott, 1952, p.232; 1972a, p.35 (part, reddish brown specimen); 1972b, p.186 (part); 1975, p.13 (part, sandy, reddish individuals). Millar, 1966, p.369. (Not: Hartmeyer and Michaelsen, 1928, f. typica p.366, < *P. pigmentata*; Pizon, 1908, p.216, < *P. aurata*).

Pandocia pedunculata: Hartmeyer, 1909, p.1364.

Polycarpa viridis: Herdman, 1899, p.47 (part, yellowish specimens with sand, Pl. Cyn. 18, Figs 5, 7).

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, WAM 1137.83; Cockburn Sound, WAM 101.72 34.75 164.75 168.75 194.75 222.82 872.82 920.83 1136.83 1138–9.83 1141.83 1144.83 1146–8.83 1154.83 259.84). South Australia (Spencer Gulf, QM GH2214; St Vincent Gulf, QM G9307 G9319–21 G9389 G9577 GH2774–6 GH2799–800 GH2804). Victoria (Bass Strait, QM G11852 G11876–7 G12734 G12750 G12752). Queensland (Tallebudgera, QM GH2198; Moreton Bay, QM G10075 GH367 GH1463–4; Mooloolaba, QM G11909 GH2449).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1975; Spencer Gulf — Kott 1972b; St Vincent Gulf — Kott 1972a). Victoria (Bass Strait — Heller 1878; Port Phillip Bay — Millar 1966). New South Wales (Port Jackson — Herdman 1899).

DESCRIPTION

EXTERNAL APPEARANCE: The shape is very variable: individuals range from spherical and stalked to upright and almond-shaped. The body is seldom more than 4 cm long (spherical specimens are shorter). The stalk is either longer than the body and relatively narrow, or short and thick. It arises from the ventral side of the posterior end or from the postero-ventral corner. The branchial aperture is subterminal, opening toward the ventral side; the atrial aperture is on the dorsal surface, usually very close to the

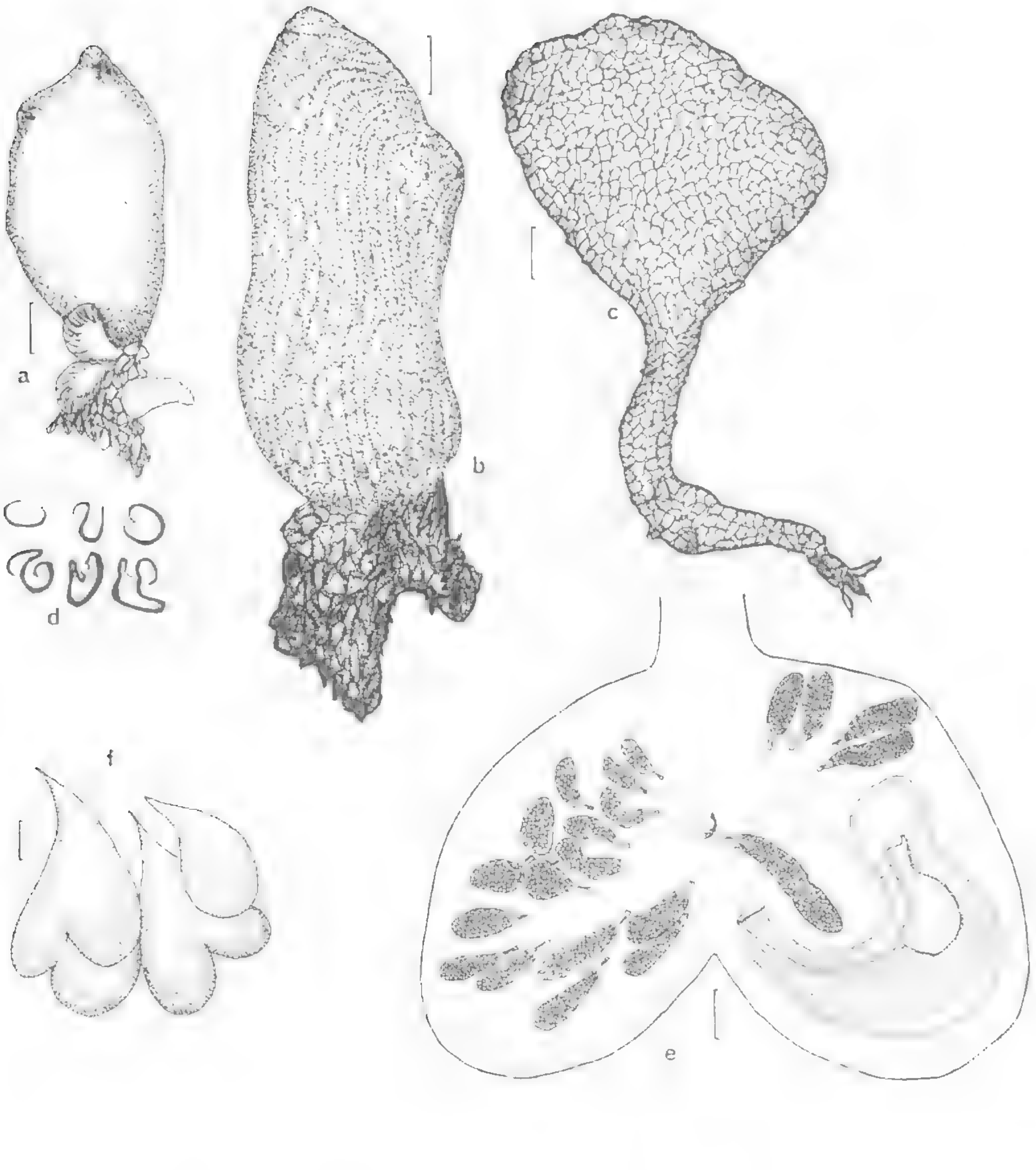


FIG. 88: *Polycarpa pedunculata* — **a**, individual with smooth surface (QM G10075); **b**, individual with wrinkled surface (QM G2198); **c**, stalked, sandy individual (QM GH2214); **d**, variation in opening of neural gland; **e**, internal body wall, showing gut, gonads and endocarp; **f**, male follicles. (Scales: **a**, **c**, 5.0 mm; **b**, 3.0 mm; **e**, 2.0 mm; **f**, 0.1 mm).

anterior end of the animal but sometimes about halfway down the dorsum.

Both apertures are sessile, but are not inconspicuous. Each is surrounded by 4 small lobes. The body is often (but not always) laterally flattened. The test is relatively thin, white in section and either smooth or rough with wrinkles and creases, mainly longitudinal but also with some irregular furrows and swellings. Specimens are often covered with a layer of sand that makes the test rather brittle, but are also sometimes naked.

The test is reddish brown in the living specimen. Preserved specimens are white to beige.

INTERNAL STRUCTURE: The body wall is muscular and in preserved specimens, often has a very faint greenish tinge. The outer circular muscle layer is continuous. Small, spherical vesicles (not more than 0.05 mm diameter) are embedded in the body wall, giving the inner muscle-free layer a rather fluffy appearance. There are about 40 branchial tentacles of varying sizes. The dorsal tubercle is a large, circular cushion with a very deep U- or S-shaped slit, the horns sometimes turned in or out. It protrudes conspicuously into the pharynx.

The branchial sac is strong, with thick vessels. The stigmata are short and parastigmatic vessels are rare. The transverse vessels are wide. The meshes are very wide on each side of the endostyle and to the right of the dorsal lamina. There is also a wide mesh, with about 10 stigmata, in the centre of the interspaces; the meshes dorsal and ventral to it have only 6 to 8 stigmata. A moderate-sized (3 cm long) specimen from Queensland (QM GH2198) has internal longitudinal branchial vessels arranged according to the following formula: E0(6)2(8)3(12)4(7)3DL. The branchial folds are long and rather straight, terminating around the posterior border of the oesophageal opening.

The curve of the gut loop is variable: sometimes deep and sometimes an open, shallow curve. The depth of the curve is undoubtedly affected by contraction of the body, since the loop is rather long and extends around the postero-ventral curve of the body. The oesophageal opening is some distance from the posterior end of the branchial sac and the oesophagus extends posteriorly from it. The stomach is very long, occupying about three-quarters of the ascending limb of the gut loop. The gut loop encloses a single, rather elongate, flat-topped endocarp. The rectum is sometimes longer than the gut loop (QM GH2198), but may also be shorter (QM GH2214). The anal border is divided into 5 to 8 lobes, the outside of the border sometimes being undivided.

The gonads vary in number and in the extent to which they are embedded in the body wall, both variations probably a reflection of age and maturity. In contracted specimens, the gonads appear to be forced up into the atrial cavity and to be less deeply embedded. They are usually rather elongate organs, often slightly curved and often crowded and overlapping. They consist of a long ovarian sac and numerous (at least 10) lobed, pyriform male follicles scattered along each side and crowded beneath the ovary, protruding up into its centre. The gonoducts are relatively long and protrude from the body wall into the atrial cavity.

REMARKS: Most previous attempts to resolve the taxonomy of this and related species have been unsuccessful. Michaelsen (1905), working with many of Heller's (1878) specimens from the eastern coast of Australia, believed *Polycarpa radicata* Herdman, 1882 to be synonymous with *P. pedunculata* Heller, 1878 on the basis of paratype material. The holotype of the latter species was not amongst the material he examined. At the same time he described a further species, *P. moebii* Michaelsen, 1905 from Bass Strait (< *P. viridis* Herdman, 1880), separated from the sympatric *P. pedunculata* only by the length of the rectum. Hartmeyer (1909) added *P. viridis* Herdman, 1882 and 1899, from Port Jackson, to the synonyms of *P. pedunculata*. Hartmeyer and Michaelsen (1928) reported *P. pedunculata* and *P. moebii* from Western Australia. They also recognised 3 different forms of *P. pedunculata*, *viz*. f. typica (from NW and eastern Australia); f. viridis (> *P. viridis* Herdman from eastern Australia) and f. chlorotica from SW Australia. The specimens of both f. typica and f. chlorotica from Western Australia referred to by Michaelsen seem to be particularly large (8 cm) and are unlikely to be specimens of *P. pedunculata*, having yellowish grey and dark blue-grey tests respectively.

Polycarpa flava n.sp. is a distinct species, sympatric with *P. pedunculata* in the middle part of the latter's range between South Australia and New South Wales. Like *P. pedunculata*, it is often stalked and sandy. However, living specimens are bright yellow, as are *P. viridis* specimens. In preservative, the test of *P. flava* is blackish and is smooth (again like *P. viridis*), rather than being sharply wrinkled and creased as in the present species.

Polycarpa pedunculata is distinguished from *P. viridis* by its often sandy, wrinkled test; longer gut loop and stomach, longer gonads; long projecting gonoducts; circular dorsal tubercle with an entire slit; and smaller vesicles in the body wall.

The most closely related species to *P. pedunculata*, albeit it has not been confused with it, is *P. contecta*, which has the same long stomach, single endocarp enclosed in the gut loop, minute vesicles embedded in the body wall and a deep, conspicuous opening of the neural gland. *Polycarpa contecta* is distinguished from the present species by its gonads, which are not embedded but are attached to the body wall by a ligament confined to the proximal half of their length.

Polycarpa pigmentata (Herdman, 1906)
(Figs. 89,100e; Pl.IVa)

Styela pigmentata Herdman, 1906, p.318.
Polycarpa picteti Pizon, 1908, p.207; Vasseur, 1967b, p.138.
Polycarpa moebii: ? Michaelsen, 1905, p.104 (part, specimen from Bowen). Vasseur, 1967b, p.136.
Polycarpa cryptocarpa: Hartmeyer 1906, p.17. Tokioka, 1950, p.139; 1961, p.121; 1967a, p.173 (part, not black specimens); 1970, p.95. Kott, 1957, p.145; 1964, p.137. Millar, 1975, p.284 (part, not specimen no. 16 from Kei I. < *Polycarpa stirpes* n.sp.). Nishikawa and Tokioka, 1976, p.394. Nishikawa, 1984, p.133.
Pandocia cryptocarpa: Michaelsen, 1912, p.152.
Polycarpa pedunculata: Hartmeyer, 1919, p.48. Kott, 1981, p.202. Hartmeyer and Michaelsen, 1928, f. typica p.366 (part, specimens from Western Australia).

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, QM G9658). Victoria (Bass Strait, QM GH2792). Queensland (off Moreton Bay, QM GH371: Heron I., QM G9769 G10084 GH354 GH356 GH379 GH1390 GH2189 GH2787 GH2790 GH2793 GH3053; Wistari Reef, GH2193; Tryon I., QM GH1391 GH1412; Swain Reefs, QM GH2786; NW of Bowen, QM GH675; Britomart Reef, QM GH236; Broadhurst Reef, QM GH315, GH2794; Lizard I., QM G9766-8 G9776 GH550 GH2193-4 GH2788-9 GH2791; Martha Ridgeway Reef, QM GH240 GH243 GH259; Murray I., QM G9825-6 G9828 GH237; Tijou Reef, QM G9829; Yorke I., QM G9827; Deltaic Reef, QM GH241 GH257 GH356; Chesterfield Reef, GH239 GH260 GH329; Marion Reef, QM GH238-9 GH258; Lihou Reef, QM GH2478; Flinders Reef, QM GH2190).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919). Queensland (Mackay — Kott 1964; Bowen — Michaelsen 1905). Palau Is (Tokioka 1950 1967a). New Caledonia (Tokioka 1961, Vasseur 1967b). Philippines (Tokioka 1970, Millar 1975). Fiji (QM GH78-9 GH85 Kott 1981). Solomon, Gilbert and Marshall Is (Tokioka 1967a). Truk I. (Nishikawa 1984). Indonesia (Pizon 1908). Japan (Hartmeyer 1906, Michaelsen 1912). Sri Lanka (BM 1907.8.3.16 Herdman 1906). Red Sea (Kott 1957).

The species is one of the largest, most common and conspicuous ascidians in the tropical waters of the Indo-West Pacific. Vast populations occur in shallow water, non-cryptic habitats around coral reefs. Although living specimens are camouflaged by their epibionts, their blue siphon linings are conspicuous.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are laterally flattened, upright and more or less pear-shaped, and rectangular in outline. They are usually sessile fixed by the posterior end of the body, and without a stalk. Living specimens are a brownish colour with deep to pale blue siphon linings. They are beige to brown to blackish brown in preservative; the siphon linings fade to grey. The test is tough and leathery, the surface rough and uneven, usually with epibionts growing on it. It is up to 1 cm thick in some places. The apertures are on very short siphons, wart-like when closed, with 4 naked lobes around each. The branchial aperture is terminal and the atrial is close behind it on the dorsal surface. The body usually narrows in front of the atrial siphon. The branchial aperture is often turned ventrally or dorsally, and the posterior end of the body sometimes turns dorsally, the body being concave along the dorsal surface. Specimens up to 12 cm long are not uncommon.

INTERNAL STRUCTURE: The internal siphons are often long, projecting anteriorly or laterally. There is a outer layer of circular and an internal layer of longitudinal muscles in the external part of the body wall. Internally it is thick, fibrous and opaque. Large spherical, black and sometimes clear vesicles are embedded in the internal layer of body wall. There are about 40 robust branchial tentacles, but often fewer in larger specimens. The dorsal tubercle completely fills the V-shaped peritubercular area. The S-shaped slit in smaller specimens becomes convoluted and interrupted with growth. Larger specimens usually have spongy-looking dorsal tubercles perforated by many small openings.

The branchial sac is robust, as the internal longitudinal vessels are thick. The branchial folds are not very high or flat. Branchial formulae for specimens of 4 cm, 8 cm and 10 cm respectively are: E3(10)3(14)3(14)3(16)3DL; E1(7)7(20)6(24)5(14)5DL; E4(15)7(15)7(15)8(13)5DL. There are 8 to 12 stigmata per mesh.

The gut loop is usually small in relation to the size of the body. It extends across the posterior end of the left side, at right angles to the rectum.

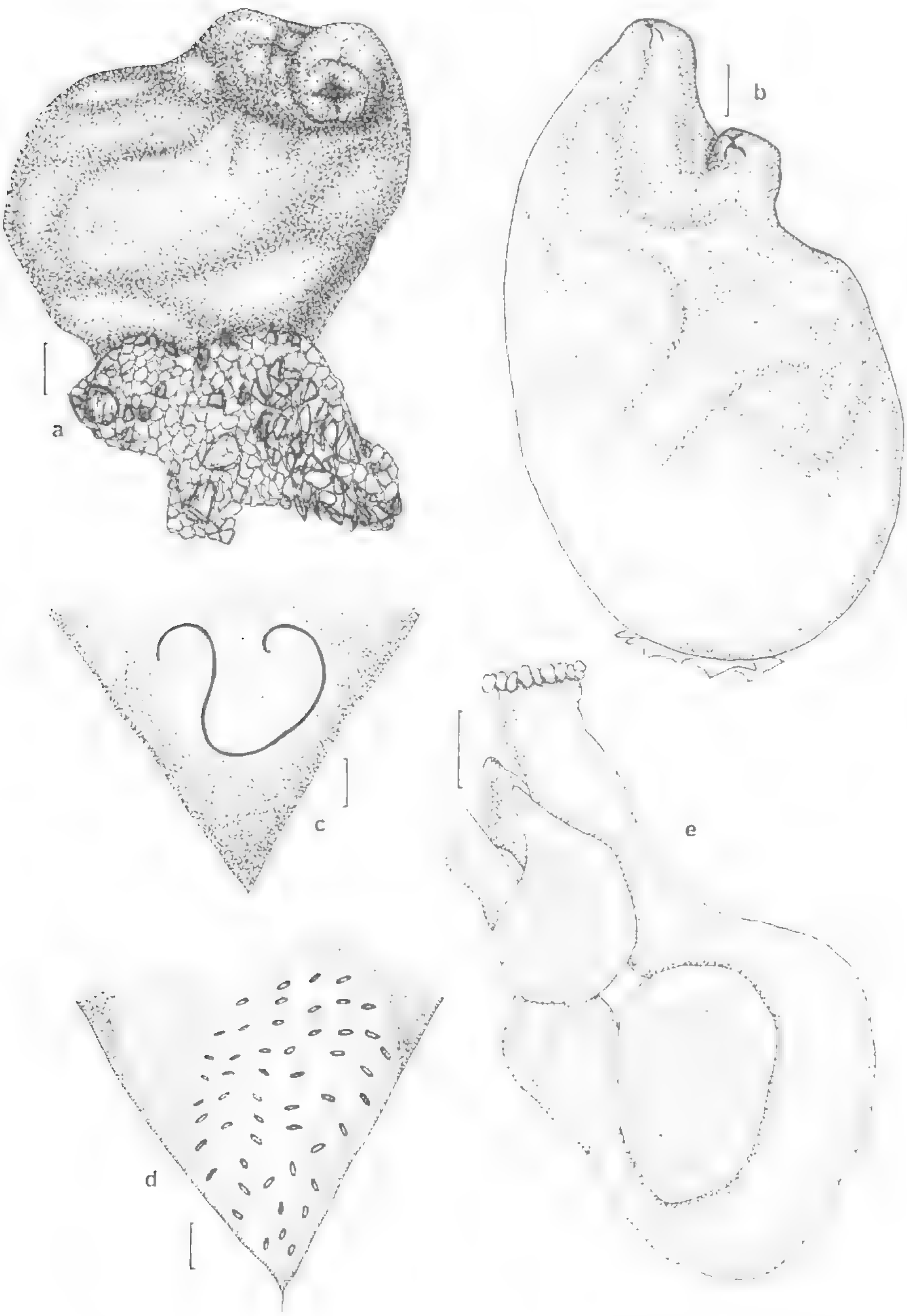


FIG. 89: *Polycarpa pigmentata* — **a, b**, external appearance (QM GH356, G9767); **c, d**, dorsal tubercles (QM GH356, G9827); **e**, gut and endocarps (QM G9658). (Scales: **a, b**, 1.0 cm; **c, d**, 0.5 mm; **e**, 2.0 mm).

A large, flat-topped circular to elongate endocarp is enclosed in the pole of the gut loop. A similar endocarp is enclosed between the proximal part of the rectum and the stomach. The stomach is long and elliptical, with parallel internal longitudinal folds. A gastro-intestinal ligament connects the distal end of the stomach to the intestine and separates the two endocarps enclosed in the gut loop. The rectum is usually at right angles to, and longer than, the gut loop. The anal border is divided into from 12 to 20 rounded lobes.

The gonads are embedded in the tough, opaque inner layer of the body wall. Each consists of a sac-like ovary with pear-shaped, and often very branched, male follicles along each side of the distal half of the ovaries. Sometimes the male follicles project under the ovary and up into it, dividing it into two chambers.

REMARKS: The morphology of this species resembles that of *Polycarpa obscura* (see *Polycarpa pedunculata*: Hartmeyer and Michaelsen, 1928). In addition to a more cylindrical body, posterior stalk, long testis follicles and black test, *P. obscura* has its atrial siphon on the narrow anterior part of the body, while in the present species the laterally flattened body narrows anterior to the atrial siphon. Other differences are discussed under *P. obscura* (Remarks).

The large black *Polycarpa cryptocarpa* Sluiter, 1885, is a synonym of *P. obscura* Heller, 1878. Specimens ascribed to *P. cryptocarpa* by Tokioka (1950, 1961, 1967a and 1970) are characteristic of the present species rather than the large, stalked black individuals of *P. obscura* (see *P. cryptocarpa* Sluiter, 1885, Pl. 2, Fig. 1).

Vasseur's (1967b) specimens from New Caledonia and Pizon's (1908) from Amboina had the same laterally flattened form, black vesicles, short gut loop across the posterior end of the body, and testis follicles beneath and projecting up into the ovary as the present specimens and appear to be conspecific.

Polycarpa molguloides has similar short, branched testis follicles and rounded anal lobes to those of the present species. However, its thin and hairy test distinguish it. The laterally flattened, upright body of *P. pigmentata* is also distinctive. *Pyura pedunculata*, *P. viridis* and *P. flava* n.sp. are smaller species with colourless vesicles in the body and with only a single endocarp in the gut loop.

Other species with an endocarp enclosed in the gut loop and embedded gonads either have long male follicles along the borders of the ovary (*P. decipiens*, *P. nigricans*) or have short testis follicles bordering a circular ovary (*P. argentata*, *P. stirpes* n.sp.).

Hartmeyer and Michaelsen (1928) believed that the specimen from Bowen ascribed by Michaelsen (1905) to *P. moebii* was a specimen of *P. maculata*. However, despite similar dark vesicles being embedded in the body wall, the gonads of the latter species are connected to the body wall by a ligament, rather than being embedded (see Nishikawa and Tokioka 1976). Further, *P. maculata* has a single, circular endocarp in the gut loop rather than the two elongate ones reported by Michaelsen. The Bowen specimen referred to by Michaelsen (1905) was probably a specimen of *P. pigmentata*.

Polycarpa mytiligera Savigny, 1816 from the Red Sea, resembles the present species externally, but its gonads are like those of *P. nigricans* and *P. obscura* with long male follicles along the side of the distal end of the ovary. Kott (1957) distinguished *P. mytiligera* from the present species by the large number of stigmata in each mesh.

Polycarpa irregularis Herdman, 1882 from the Philippines resembles the present species externally, but is distinguished by the numerous endocarps reported to occur on the body wall.

Polycarpa bassi Herdman, 1886 from Bass Strait and *Polycarpa stephenensis* Herdman, 1899 from Port Jackson may be synonyms of *P. pigmentata*.

It is surprising that neither the Challenger (Herdman 1882) nor the Siboga (Sluiter 1904) expeditions took specimens of this large and common species.

Polycarpa plenovata n.sp.
(Fig. 90)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, 38°53.7'S, 147°55.2'E, 71 m shelly sand, Bass Strait Survey, 17.11.81, holotype NMV F51567; 39°01.0'S,143°22.1'E, 84 m, sand, 31.1.81, paratype NMV F51568).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are small and symmetrical, up to 5 mm in diameter and almost spherical, but with opposite ends of the upper surface produced out into rather long, diverging siphons. Basally the body narrows to a very fine stalk that is about the same length as the body. The stalk is completely naked, but the body is covered with a layer of crowded sand grains and shell. The borders of the apertures are gathered rather than lobed. The siphon lining and the test

FIG. 90: *Polycarpa plenovata* n.sp. — **a**, external appearance (NMV H780); **b**, gonads seen through body wall, right side (NMV H379); **c**, inner body wall (NMV H780); **d**, gonad (NMV H780). (Scales: **a**,**c**, 1.0 mm; **b**, 0.5 mm; **d**, 0.25 mm).

immediately around the apertures are slightly greenish and iridescent. However, no scales or spines were detected.

INTERNAL STRUCTURE: The body wall is muscular and opaque. There are about 40 short, fine branchial tentacles. The opening of the neural gland is a simple, transverse slit.

The branchial sac has 4 folds on each side of the body. There are 8 to 10 very crowded internal longitudinal vessels on each fold and one between. Each mesh has 6 short, oval stigmata.

The oesophageal opening is at the posterior end of the dorsal surface, which extends only between the two apertures. The branchial sac is deeply curved ventrally. The gut forms a short, tight and rather straight loop posterior to the branchial sac, the two limbs almost level with one another. The oesophagus is moderately long, curving posteriorly and ventrally. The stomach is large and pyriform, widest at the pyloric end. It occupies most of the ascending limb. The intestine curves to the left and dorsally, lying parallel to, almost level with, and hard up against the stomach, bound firmly to it by membrane. A very short, stout caecum is embedded in the membrane and crowded into the pole of the tight gut loop. The rectum is very short, curving toward the atrial aperture. Its border is divided into 5 shallow lobes.

The gonads are relatively large, sausage-shaped and very conspicuous. They are more or less in 2 rows on each side of the body, with up to 5 in a row. There are 5 to 7 polycarps per side. Each consists of a large, roomy ovary with a single row of about 8 long testis follicles lying transversely across the under surface of the ovary. The very short oviducts are directed toward the atrial aperture. Both gut and gonads are only lightly attached to the body wall. There are no endocarps.

REMARKS: The symmetrical, sandy body; fine naked stalk; short, tight gut loop and large stomach; and the relatively large gonads are the characters by which the species can be distinguished. The species shares certain characters with *Polycarpa sobria*, notably the short gut loop with the stomach occupying much of the ascending loop. *Polycarpa sobria* is distinguishable from the present species by the absence of a stalk, its 3 or 4 (rather than 2) rows of polycarps and the more numerous internal longitudinal vessels in the interspace.

Polycarpa procera (Sluiter, 1885)
(Fig. 91; Pl.IVb)

Styela procera Sluiter, 1885, p.196; 1904, p.59.
Polycarpa procera: Hartmeyer, 1919, p.52. Hartmeyer and Michaelsen, 1928, p.378. Hastings, 1931, p.76. Millar, 1975, p.291.
Polycarpa doderleini Hartmeyer, 1906, p.15. Tokioka, 1960, p.209.
Polycarpa fristedti Michaelsen, 1923, p.46.
Polycarpa tinctor: Kott, 1964, p.134 (part, specimens from Hervey Bay). Kott, 1975, p.13 (part, not U-shaped specimen < *P. lucilla* n.sp.).
Polycarpa rigida: Kott, 1964, p.138.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 927.83). Victoria (Bass Strait, off Ninety Mile Beach, QM G11854; off Warrnambool, NMV F51594) New South Wales (Byron Bay, QM G9390). Queensland (Maroochydore, QM GH1465; Hervey Bay, QM G4946; Gladstone Harbour, QM G9721 G9805; Erskine I., QM G9724; Rockingham Bay, QM GH1372–3; off Innisfail QM GH768).

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Hartmeyer and Michaelsen 1928; Cape Jaubert — Hartmeyer 1919). South Australia (Upper Spencer Gulf — Kott 1975). Queensland (Hervey Bay — Kott 1964). Sri Lanka (Michaelsen 1923). Indonesia (Sluiter 1885 1904, Millar 1975). Singapore (Millar 1975). Japan (Hartmeyer 1919, Tokioka 1960).

DESCRIPTION

EXTERNAL APPEARANCE: The body is usually long and narrow. The largest recorded specimens are 4 cm long and about 3 cm in diameter. Individuals are either oval in outline or elongate, wider anteriorly and narrowing to the posterior end. Specimens are seldom curved. Usually they are laterally flattened, but sometimes they are almost cylindrical or slightly depressed dorso-ventrally, and occasionally individuals have been taken that are rounded in section posteriorly but laterally flattened anteriorly. Often individuals from the one population vary in shape. Hairs or root-like projections of the test are often present around theventral, posterior and postero-dorsal edges of the body; or they extend in a wide band along the ventral surface. Apertures may be sessile or on short siphons. The branchial aperture is terminal; the atrial aperture, which is at the dorsal end of an oblique line across the anterior end of the body, may protrude slightly. The test is always thin, and hard and brittle with embedded sand. The hairs or root-like processes and the orientation of the siphons suggest that specimens either lie on their ventral surface or that much of the ventral border, the posterior end and part of the dorsal border, may be rooted in the substrate so that the anterior end stands up free. They are found crowded together, but not adhering to one another. The test is orange when living.

INTERNAL STRUCTURE: The body wall adheres fairly closely to the glistening white inner surface

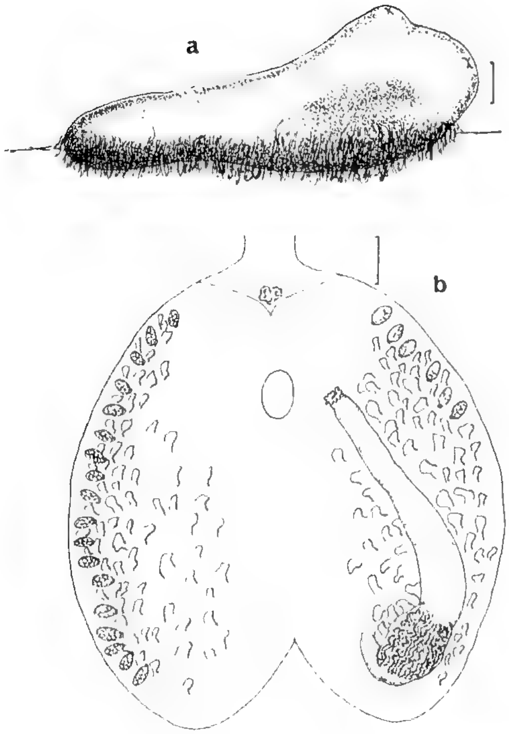


FIG. 91: *Polycarpa procera* — **a**, external appearance (QM GH1377); **b**, gut, gonads and endocarps (QM GH1465). (Scales: **a**, 5.0 mm; **b**, 2.0 mm).

of the test. It is thin, but the musculature is quite well developed, the outer layer of circular muscles being continuous and almost opaque. There are fine internal longitudinal bands. The branchial tentacles are of moderate length and quite crowded. The peritubercular area is very shallow. The dorsal tubercle is large, often inflated and lobed. The slit varies from a simple U with horns turned in or out to several separate oval to elongate, and sometimes curved and coiled, slits. There is a conspicuous atrial velum with small tentacles on its margin.

The branchial folds are narrow and widely separated, with up to 26 crowded internal longitudinal vessels. Six to 10 internal longitudinal vessels are also crowded in the interspace, where there are only 2 or 3 stigmata per mesh. Very occasionally, individuals are found in which the branchial folds are wider and the longitudinal vessels on the folds are closer together. A typical branchial formula for a large (3 cm long) individual is DL(20)11(16)8(17)7(6)12E. Hartmeyer (1919) has recorded specimens with very many internal longitudinal vessels both on (50) and between (40) the folds.

The oesophagus opens at the posterior end of the branchial sac. The gut extends obliquely across the body wall, sometimes forming a smooth, C-shaped curve. The oesophagus is short and the stomach is short and rounded, with undulating longitudinal folds. The anal border is deeply divided into 12 rounded, but occasionally irregular, lobes.

Elongate polycarps extend in a single row along each side of the mid-ventral line, their ducts directed toward the atrial aperture. There are up to 18 polycarps on the right and up to 9 on the left where they are confined to the anterior end of the body in front of the gut. Up to 8 pairs of rather long, club-shaped male follicles lie beneath, and sometimes project up into, the centre of the ovary. Small endocarps are scattered on the body wall between the polycarps.

REMARKS: The brittle, sandy test; general shape of the body; short stomach with undulating folds; and almost straight gut are also characteristic of *Polycarpa chinensis, P. rigida* and *P. tinctor*. However, the present species is distinguished by the large number of internal longitudinal vessels both on and between the folds, by the smaller number of stigmata per mesh, and by the arrangement of its polycarps in a single row along each side of the endostyle.

Polycarpa reniformis (Sluiter, 1904)
(Fig. 92)

Styela reniformis Sluiter, 1904, p.67.
?*Polycarpa reniformis*: Hartmeyer and Michaelsen, 1928, p.360.

DISTRIBUTION

NEW RECORDS: Norfolk I. (QM GH2053). Queensland (Heron I., QM GH920 GH1411 GH2995; Murray I., QM GH2070).

PREVIOUSLY RECORDED: Western Australia (?Cockburn Sound — Hartmeyer and Michaelsen 1928). Indonesia (Sluiter 1904).

The species has been taken under boulders in shallow subtidal waters, and in channels and caves at 10 to 20 m in places of strong surge or current.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens up to 4 cm in length are known. The body is about half as broad as it is long, and only slightly laterally flattened. There is a very slight concavity on the dorsal surface. The body narrows anteriorly to the terminal branchial aperture, which is inclined antero-dorsally. The atrial aperture is from one- to two-thirds of the distance down the dorsal border. Both apertures are sessile and 4-lobed,

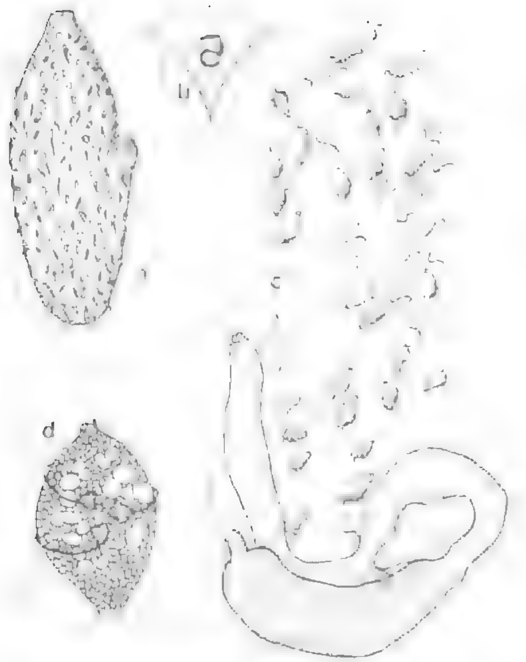


FIG. 92: *Polycarpa reniformis* — a, external appearance (QM GH920); b, dorsal tubercle (QM GH920); c, gut, gonads and endocarps (QM GH1411), d, upright gonad (QM GH920). (Scales: a, 5.0 mm; b, 0.5 mm; c, 1.0 mm; d, 0.25 mm).

although these lobes are obscure when the apertures are withdrawn into the cartilaginous test. Sand particles are sparse and randomly distributed. The test is translucent and cartilaginous, with surface irregularities on larger specimens. Small specimens are smooth. The outer layer of test is packed with bladder cells. Specimens from Western Australia (Michaelsen and Hartmeyer 1928) had a variable encrustation of sand and other particles on tough, fibrous test. Sand is absent from the area around the siphons.

Small (1.5 to 2 cm), living individuals from Heron I. were ochraceous buff (Ridgeway 1886) with darker olive colour around the siphons.

INTERNAL STRUCTURE: The body wall is pale, soft and translucent, with a delicate layer of transverse musculature external to fine, longitudinal bands that break up into a fine mesh at the posterior end of the body. The siphonal lining is delicate and without armature. The branchial tentacles are long, moderately crowded and of variable length. The dorsal tubercle is a large, low cushion completely filling the peritubercular area. It has a conspicuous, inverted S-shaped slit.

The 4 moderately wide branchial folds do not overlap. There are 2 to 5 internal longitudinal vessels in the interspace and up to 13 on the folds, where they are more crowded than in the interspace. There are 6 to 8 long narrow stigmata in the wide branchial meshes. Parastigmatic vessels are often absent. The branchial formula for the 4 cm long specimen from Heron I. (QM GH920) is DL0(10)3(11)2(13)2(8)2E.

The gut forms a closed loop in the postero-ventral corner of the body, enclosing a flat-topped, more or less circular, endocarp. The rectum extends anteriorly to form an obtuse angle with the primary loop. The stomach is long, narrow and cylindrical, with about 16 long, parallel folds. It is sharply cut off from the short oesophagus and narrows to the intestine. The stomach occupies about two-thirds of the ascending limb of the primary gut loop. There is no caecum. The anal border, a short distance from the base of the atrial aperture, is irregularly lobed.

The gonads are upright, short, rounded to spindle-shaped polycarps in 4 or 5 irregular rows in the ventral half of the body wall. They are fixed by only a very small ligament at their proximal end. The oviduct opens on the free end of the gonad. There are 2 asymmetrical rows each of 1 to 3 bi- or tri-lobed male follicles on the dorsal side of each ovary. The long vasa efferentia extend around the ovary in a wide arc and join the short vas deferens on the ventral side at the base of the female opening. There are up to 30 gonads on the right side of the body and about 24 on the left, a few extending down into the secondary gut loop.

With the exception of the one enclosed in the gut loop, endocarps are not present.

REMARKS: The present specimens are the same shape as the type and have identical branchial sacs, dorsal tubercles with inverted S-shaped slits, branchial folds and long, narrow stigmata, as well as being identical in the shape of the gut loop and the distribution, number and form of the gonads.

The specimens from Cockburn Sound (Hartmeyer and Michaelsen 1928) differ in having a leathery test, U-shaped opening of the dorsal tubercle, siphonal armature of overlapping curved spines (0.02 mm long), more longitudinal branchial vessels, especially in the dorsal part of the branchial sac (E9(6)6(18)6(20)7(16)8-12DL) and fewer stigmata in each mesh (3 to 5).

Neither Sluiter (1904) nor Hartmeyer and Michaelsen (1928) record the single endocarp enclosed by the gut loop. Sluiter also overlooked the parallel folds in the lining of the long, narrow stomach. Further material of this relatively rare species will be needed to determine the status of these morphological differences and to establish whether or not Western Australian and Queensland populations are conspecific with those in Indonesian waters.

The species as presently known is readily distinguished by its delicate body wall, numerous and upright gonads, single endocarp and entire opening of the neural gland on its large tubercle.

Polycarpa rigida Herdman, 1881
(Fig. 93)

Polycarpa rigida Herdman, 1881a, p.76; 1882, p.175; 1899, p.47 (part, specimens from Port Jackson). Kott, 1952, p.241; (not: 1964, p.138, < *P. procera*).
Polycarpa longisiphonica Herdman, 1881a, p.77; 1882, p.177; 1899, p.49.
Polycarpa tinctor: Kott, 1972b, p.186.
Polycarpa sluiteri Herdman, 1899, p.46; (not 1906, p.322). Kott, 1952, p.236.
Polycarpa pegasis: Kott, 1954, p.146.

DISTRIBUTION

NEW RECORDS: Tasmania (Thobin Bay, TM D99; Vansittart I., TM D798; NW Tasmania, TM D981; E of Banks Strait, TM D1191; SE of Tasman Head, TM D1189; Port Arthur, TM D768; off Schouten Passage, TM D719 D100; Port Davey, QM GH2011). Victoria (Bass Strait, NMV H451 H459 H461 H476 H518 H760 H918 H951, ZMC 9.9.14; off Cape Howe, ZMC 30.9.14).

PREVIOUSLY RECORDED: South Australia (Waldegrave I. — Kott 1972b). Tasmania (Bass Strait — Herdman 1882; NE Tasmania — AM Y1766 Kott 1954). New South Wales (Port Jackson — AM G2080 Herdman 1899; Kott 1952).

The species is sub-littoral, recorded to 180 m.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are more or less cylindrical, or flattened laterally or slightly dorso-ventrally. The apertures are fairly close together at the antero-dorsal end of the body, both directed dorsally, the atrial aperture usually on a slight conical projection from the dorsal surface. Smaller individuals (up to 5 cm long) sometimes narrow posteriorly. Individuals from 5 to 10 cm are of fairly even diameter throughout, with the rounded posterior end of the body curved up at an angle to form a dorsal concavity. These larger individuals have short siphons, with the branchial siphon often curved to the right, the atrial siphon directed straight upwards. The 4 conspicuous lobes around the apertures are sometimes naked. The remainder of the test is thin, brittle and heavily impregnated with sand. Hairs, roots or stalk are never present in larger specimens, although smaller individuals (1 to 3 cm) have tufts of fine test hairs around the postero-ventral border (ZMC 30.9.14). Individuals apparently usually lie free on the sea floor. Only one specimen has been taken attached (to a scallop shell) by a large part of its right side.

INTERNAL STRUCTURE: The body wall is very delicate indeed and is closely adherent to the test. There is a layer of very fine circular muscles around inner longitudinal bands. The branchial tentacles are stout, but not crowded. The dorsal tubercle is large and inflated; the slit is U-shaped, with the horns turned in, sometimes forming low, spiral cones in larger specimens. The peritubercular area forms a deep V. The dorsal lamina is very long.

Branchial folds are narrow and widely separated. No more than 15 to 22 internal longitudinal vessels are crowded on the folds, with 6 to 8 in the interspace. The 6 to 8 stigmata in each mesh are crossed by parastigmatic vessels, which often divide them. In one senescent specimen (TM D1191), the stigmata are circular to oval perforations in the pharyngeal wall.

The oesophagus opens from the posterior end of the branchial sac. The stomach is short, of only slightly greater diameter than the intestine. The intestine extends anteriorly in a simple curve to the atrial aperture. The anal border is fringed by rounded, sometimes irregular, lobes.

The body wall has small, rounded endocarps and oval to almost spherical polycarps scattered over it. The polycarps are slightly more crowded in the ventral half of the body. They are antero-ventral to the gut on the left. There are numerous eggs in mature ovaries, the largest being just over 0.1 mm in diameter. The oviduct is a short, wide tube directed dorsally. From 4 to 6 pairs of broad, slightly lobed to branched male follicles are present in each polycarp. Many of the larger specimens are senescent and lack gonads and endocarps. In immature gonads, the male follicles are on the body wall slightly distant from the narrow, elongate ovarian tube allowing room for it to expand. Gonads do not appear to be present in specimens less than 2 cm long.

REMARKS: *Polycarpa sluiteri* Herdman, 1899 is the same shape, has the same body musculature and the gut follows the same course as the present species. Its numerous polycarps distinguish it from the sympatric *P. tinctor* and it appears to be a synonym of *P. rigida*.

Individuals of this species grow very much larger than most other species of the *tinctor* group, which it otherwise resembles in its branchial sac, delicate body wall, curved gut and stiff, brittle test. Smaller

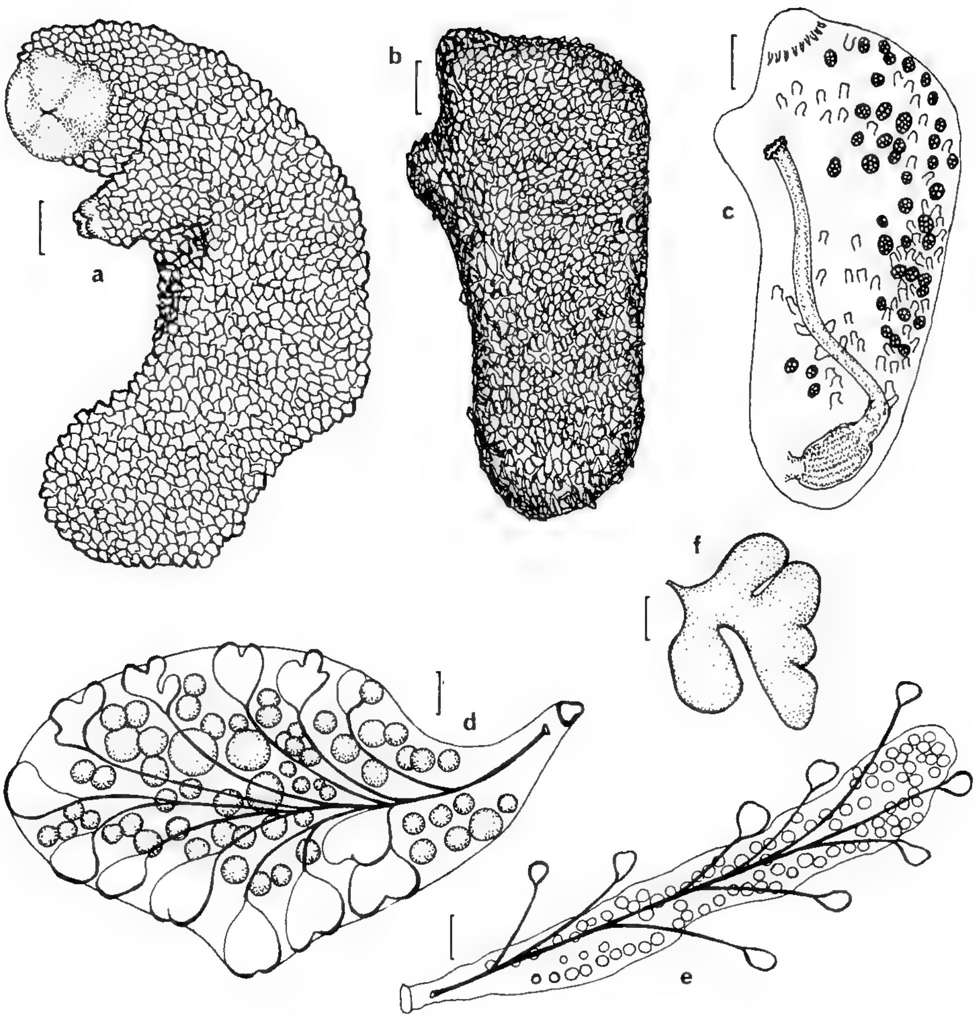


FIG. 93: *Polycarpa rigida* — **a**, **b**, external appearance (TM D1189, D99); **c**, gut, gonads and endocarps on left side of body (TM D99); **d**, **e**, gonads, mature and immature respectively; **f**, male follicle. (Scales: **a**, 1.0 cm; **b**, **c**, 0.5 cm; **d** – **f**, 0.1 mm).

specimens of all the species are very often also the same shape. In *P. rigida*, however, the gonads are scattered over the body wall rather than being confined to a single ventral row. *Polycarpa procera* has more numerous internal longitudinal branchial vessels in the interspace; *P. tinctor* and *P. tinctorella* n.sp. are viviparous, the eggs being larger and more numerous than in *P. rigida*, and the male follicles not lobed or branched. *Polycarpa chinensis* and *P. tinctorella* n.sp. are more conspicuously flattened. Larger specimens of *P. rigida* are also distinguished by the conspicuous siphons, rounded and expanded posterior end and body curvature. Difficulties arise in distinguishing juveniles from other members of the species group (see *Polycarpa tinctorella* n.sp., Remarks).

Kott (1954) mistook this species for the New Zealand species, *Polycarpa pegasis* Michaelsen, 1922, which has a similar arrangement of branchial vessels and gut, test and body form. However, in the New Zealand species, the polycarps are restricted to a narrow band on each side of the endostyle, and endocarps are absent. The New Zealand species is also much smaller. Millar (1982a) infers an viviparous habit for *P. pegasis*. Although such a habit is probable for this species, it appears not to have been recorded. No evidence is available on this aspect of development for the present species.

The present species shares with *Polycarpa pegasis*, the distinction of being the most southerly occurring species of the genus *Polycarpa*.

FIG. 94: *Polycarpa sobria* (WAM 794.83) — inner body wall, left side. (Scale: 1.0 mm).

Polycarpa sobria (Sluiter, 1904)
(Fig. 94)

Styela sobria Sluiter, 1904, p.63.

DISTRIBUTION

NEW RECORDS: Western Australia (Houtman's Abrolhos, WAM 794.83).

PREVIOUSLY RECORDED: Indonesia (ZMA V.TU976.32 Sluiter 1904).

The species is recorded down to 50 m.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are small, almost spherical, and up to 2 cm in diameter. Apertures are almost sessile, separated from one another by about half the body length. The test is sandy, tough and leathery but quite thin. It is very wrinkled and irregular, especially anteriorly.

INTERNAL STRUCTURE: The contracted body wall of the western Australian specimens appears very muscular, although in the lectotype the muscle layers are thinner. Spherical vesicles are present amongst the muscle bands. About 20 fine branchial tentacles alternate with rudimentary ones. The U-shaped slit of the neural gland, which is in a fleshy peritubercular area, is directed to the left. The dorsal lamina is long. Spherical vesicles are also present in the body wall lining the atrial cavity over and between the gonads.

There are 4 low, rounded branchial folds with up to 9 internal longitudinal vessels crowded on the folds and never more than 3 in the interspace. They are arranged according to the following formulae: DL0(8)2(9)2(8)2[illegible] (WAM 794.83); E2(3)3(6)3(8)2(5)3DL (ZMA V.TU976.32). There are 6 to 8 stigmata per mesh.

The gut loop is short, confined to the posterior end of the body, the rectum forming only a slight angle with the loop. The oesophagus is short. Although the round to elliptical, longitudinally folded stomach is not long, it occupies most of the ascending limb of the short gut loop. There is a conspicuous caecum from the distal end of the stomach curving into the gut loop. The anal border is divided into small lobes. The gut is only very lightly attached to the body wall by fine ligments from the inner side of the loop. There is a gastro-intestinal connective between the caecum and the intestine.

Large, flask-shaped polycarps are present in 3 or 4 irregular rows over the body wall on each side of the body, their ducts directed toward the atrial aperture. Gonads were not observed in the lectotype, although Sluiter (1904) reported them to be present.

There are no endocarps on the body wall.

REMARKS: The species is characterised by its short gut loop; small stomach and curved caecum; low, round branchial folds with no more than 9 longitudinal vessels; absence of endocarps; and spherical body with wrinkled, sandy test.

Polycarpa stirpes n.sp.
(Fig. 95)

Pandocia ovata: Van Name, 1918, p.102.
Polycarpa cryptocarpa: Millar, 1975, p.284 (part, specimen no. 16 from the Kei Is.)

DISTRIBUTION

TYPE LOCALITY: Queensland (between Lizard I. and Nymph I., dredged, 18–29 m, coll. E. Newcombe, 12.6.76, holotype QM G9771).

NEW RECORDS: Queensland (Townsville, QM GH2732; off Innisfail, QM GH2733; Green I., QM G11982 G11986; Lizard I., QM GH9770, paratypes QM GH2735; Britomart Reef, QM GH273; off Cape Melville, QM GH2734).

PREVIOUSLY RECORDED: Indonesia (Millar 1975). Philippines (Van Name 1918).

The species is truly tropical, with no records south of Townsville.

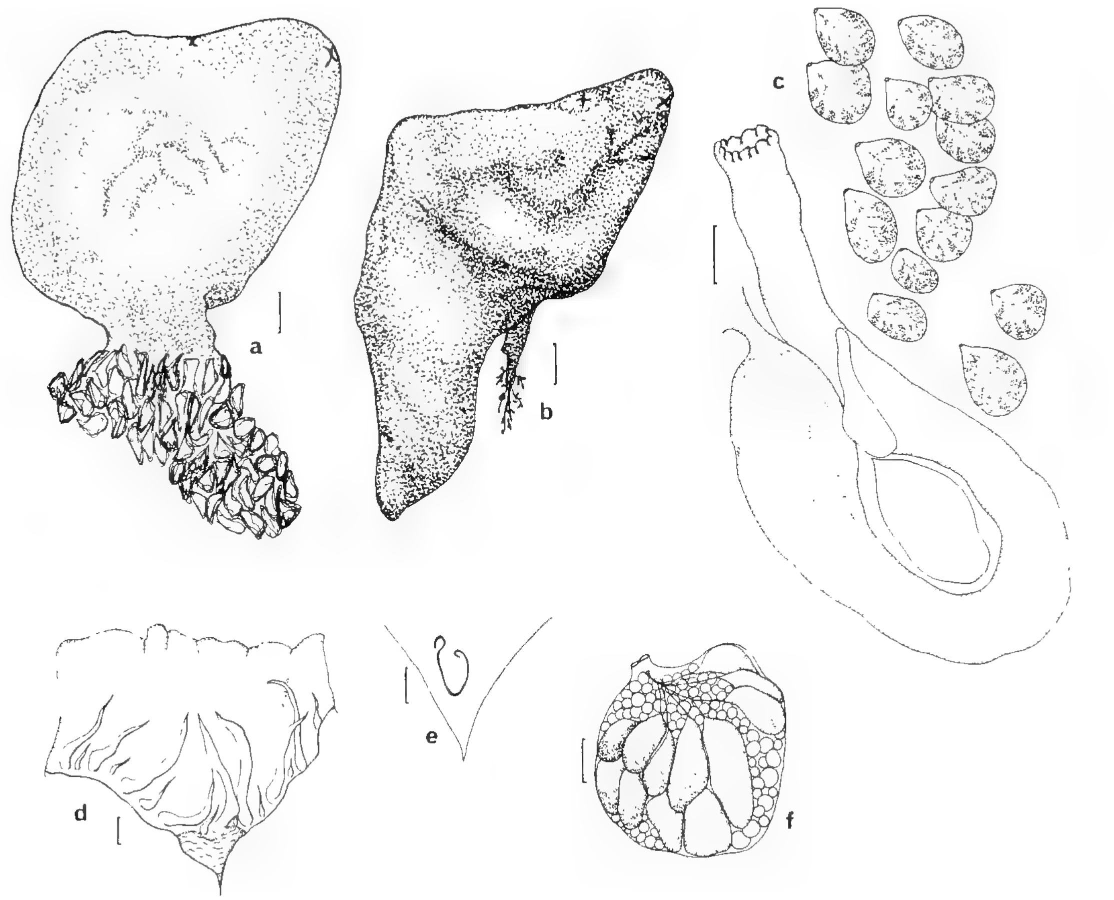


FIG. 95: *Polycarpa stirpes* n.sp. — **a, b**, external appearance (QM G9771, G2735); **c**, gut, gonads and endocarps (QM G9771); **d**, branchial tentacles and complex dorsal tubercle (QM G9771); **e**, simple dorsal tubercle; **f**, gonad. (Scales: **a, b**, 5.0 mm; **c**, 2.0 mm; **d**, 1.0 mm; **e**, 4.0 mm; **f**, 0.5 mm).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are large (up to 5 cm long and 3 cm high), laterally flattened and asymmetrically triangular, with a horizontal upper dorsal surface. The body tapers to the postero-ventral part, which is fixed to the substrate by roots or a short, broad stalk. The branchial aperture is at one end of the body and the atrial aperture is about one-third to half the distance along the upper surface. Both apertures are completely sessile, with inconspicuous lobes. The test is always black in both living and preserved specimens. It is very thin and flexible, with rough external surface to which only a few foreign particles adheres. The siphon linings of living specimens are yellow-orange.

INTERNAL STRUCTURE: The body wall is black and orange in freshly fixed individuals, but becomes black after a time in preservative. Both the ventral and dorsal sinuses are often filled with black blood in preserved specimens. The body wall is thin and flexible, although there is a continuous outer layer of circular muscles and internal longitudinal bands. The internal layer of connective tissue is not thick. The tentacles are few and robust: usually 8 long tentacles alternating with rudimentary ones. Occasionally there are more long tentacles and the rudimentary tentacles are not present in at least the dorsal part of the ring. The dorsal tubercle is a spongy swelling that sometimes completely fills the peritubercular area. Occasionally the peritubercular area extends posterior to the tubercle in a deep, narrow V. The opening of the neural gland varies from a U-shaped slit with the horns turned in or out to a complex opening consisting of numerous short slits.

The branchial sac has 4 well-developed folds with thick internal longitudinal vessels arranged according to the following formula: E3(12)4(15)4(17)6(11)3DL. The meshes are wide, those in the centre of the branchial sac having 12 stigmata. The meshes to the right of the dorsal lamina are very wide indeed. The meshes at the ventral side of each interspace are slightly wider than the others. The gut forms a straight loop projecting postero-ventrally from the oesophageal opening, which is about halfway between the atrial opening and the posterior end of the body. There are two endocarps enclosed in the gut loop, one in the pole and one between the stomach and the distal part of the intestine. The stomach is short and elliptical and occupies about half of the ascending limb of the gut loop. It has internal longitudinal folds. The rectum, which is short, extends anteriorly in line with the gut loop. The anal opening has about 12 rounded lobes.

Gonads are embedded just beneath the surface of the thin, inner, non-muscular layer of the body wall and are quite visible. They consist of a spherical ovary with a very short duct and oval to pear-shaped testis follicles clustered in two layers around the sides of the ovary. The ducts of the follicles curve onto the mesial surface of the ovary to join a short vas deferens on the surface of the oviduct.

REMARKS: The species is characterised by its triangular shape, sessile apertures, lateral flattening, thin test, thin body wall, few branchial tentacles, spherical gonads and relatively short, pear-shaped male follicles around the outside of the ovary. In the rough surface of the black test, spherical gonads just beneath the surface of the body wall and the number of tentacles, the present species resembles *Polycarpa argentata*, which is, however, distinguished mainly by its gonads being confined to a band along each side of the endostyle.

The lateral flattening of the body and the form and arrangement of the gonads, with relatively short male follicles around the border of the more or less circular ovary are identical in the present species and *Pandocia ovata*: Van Name, 1945. However, *Polycarpa ovata* Pizon, 1908 has, unlike the present species, a smooth, egg-shaped body that is not laterally flattened.

The species resembles *P. nigricans* in its colour, branchial tentacles and dorsal tubercle. However, it is larger, has more spherical polycarps less deeply embedded and has sessile apertures.

Millar (1975) has assigned a number of species from Indonesia to *P. cryptocarpa* (< *P. pigmentata*). Gonads of the specimens from the Kei Is are identical with those of the present species, with pear-shaped male follicles around, rather than beneath, the ovarian sac. Further, the laterally flattened triangular body fixed to the substrate by its postero-ventral corner is identical with that of the present species.

The large specimens of *Polycarpa japonica* Michaelsen, 1912 have pear-shaped male follicles separated from the ovary, resembling the gonads of the present specimen from Britomart Reef (QM GH273). However, *P. japonica* is canoe-shaped and not laterally compressed as is the present species.

Polycarpa thelyphanes (Sluiter, 1904)
(Fig. 96)

Styela thelyphanes Sluiter, 1904, p.68.
Polycarpa thelypanes (sic): Kott, 1952, p.238; 1976a, p.76.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 15.75). Victoria (Deal I., NMV H654; Bass Strait, NMV H393).

PREVIOUSLY RECORDED: Western Australia (Albany — Kott 1952). Victoria (Portland Harbour, Western Port Bay — Kott 1976a). Sulu Is (Sluiter 1904).

The species is rarely encountered and its isolated records are puzzling. Its Australian records suggest a temperate range, which is not confirmed by the record from the Sulu Is.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals from 3 to 7 cm are known. The body is rounded posteriorly and narrows to the terminal branchial aperture. The atrial aperture is half to two-thirds of the way along the concave dorsal surface. Both apertures are on short siphons. Particles of sand and shell are embedded in the test and adhere to the surface, which is rough with furrows and wrinkles. The test is moderately thick and firm. Sand is absent from the short siphons, which are longitudinally furrowed.

INTERNAL STRUCTURE: There are strong circular muscles around the siphons, but they become inconspicuous on the rest of the body wall, which is thin and closely adherent to the test. Narrow longitudinal bands radiate from the siphons but fade out halfway down the body. From 12 to 40 rather short branchial tentacles alternate with minute ones. The prebranchial area is very extensive. The dorsal tubercle is a rounded to oval cushion in a relatively large peritubercular area. The slit varies, being an almost closed circle, or U-shaped or S-shaped.

The branchial folds are very narrow, with up to 16 internal longitudinal vessels crowded on them. Six to 10 vessels are present in the interspaces. There are only 2 or 3 stigmata per mesh in smaller specimens. In large (7 cm) specimens (NMV H654), there are 4 to 8 stigmata per mesh. The stigmata are long and oval, although sometimes they can be almost circular when divided into half by parastigmatic vessels (WAM 15.75). The branchial formula for a 7 cm long specimen is E10(14)10(14)10(16)8(14)3DL. The smaller (about 2 cm) specimen from Bass Strait (NMV H393) has the following formula: E5(8)5(11)5(14)6(12)1DL.

The gut forms a simple, straight loop set obliquely across the posterior half of the body. The stomach is short, elliptical and wider than the intestine. It has 6 to 10 longitudinal folds. There are about 16 rounded anal lobes. Gonads are recumbent oval to elongate polycarps in a single, but rather irregular, row on each side of the endostyle. On the left side of the body, the gonads do not extend posterior to the gut loop. Up to 6 pairs of biramous male follicles lie beneath the ovaries. Only rarely are there small, scattered

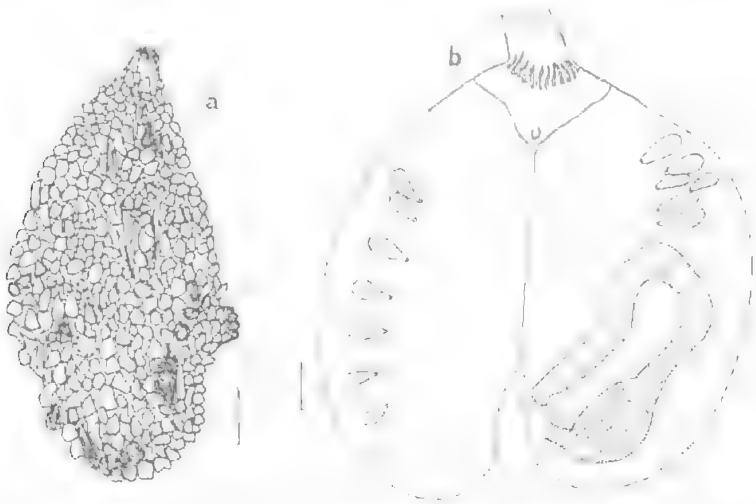


FIG. 96: *Polycarpa thelypanes* (WAM 15.75) — a, external appearance; b, internal structure. (Scales: a, 5.0 mm; b, 2.0 mm).

endocarps on the body wall, but there are none enclosed in the gut loop.

REMARKS: The sandy and rough, hard test; thin body wall adhering closely to the test; narrow branchial folds and wide interspaces; extensive prebranchial area; simple, open gut loop; and the form and arrangement of the gonads are described for all previously recorded specimens. The Philippine specimen (Sluiter 1904, holotype ZMA V.TU976.33) has 10 to 14 longitudinal vessels in the interspace and up to 14 on the folds. Although the 2 dorsal folds are more flattened out than in the Australian specimens, they are otherwise similar.

Polycarpa patens (Sluiter, 1885) has a similar arrangement of internal longitudinal branchial vessels, open gut loop and loosely attached, elongate gonads as the present species. However, the type (ZMA V.TU1042) has a strongly muscular body wall and numerous endocarps on the body wall, which distinguish it from the present species.

Polycarpa tinctor (Quoy and Gaimard, 1834)
(Fig. 97a–c)

Ascidia tinctor Quoy and Gaimard, 1834, p.608.
Polycarpa tinctor: Herdman, 1882, p.170; 1899, p.51. Herdman and Riddell, 1913, p.879. Millar, 1962b, p.399. Kott, 1952, p.234; 1972d, p.254; (not: 1964, p.134, < *P. chinensis* and *P. procera*, 1972b, p.186, < *P. procera*; 1972c, p.242, < *P. chinensis*, 1975, p.13, < *P. lucilla* n.sp and *P. procera*).
Polycarpa rigida. Herdman, 1899, p.47 (part, specimens from Port Stephens).

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: New South Wales (Port Jackson — AM G12235 Herdman 1882; AM G2076 Herdman 1899; Port Stephens — AM G12239 Herdman 1899; Jervis Bay — AM G12222 Herdman and Riddell 1913; Port Hacking — coll. Thetis AM G12215 (test only), Herdman ident. Kott 1952 1972d; Cape Dromedary — Quoy and Gaimard 1834).

The species has a limited range, being recorded only from NSW waters.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are invariably slightly laterally flattened, club-shaped, wide anteriorly and narrowing to the posterior end of the body, which is often almost pointed. The test is impregnated with sand and is rigid, hard and brittle. The branchial aperture is terminal and sessile. The atrial aperture is on a slight prominence from the anterior end of the dorsal surface. The posterior end of the body (behind the atrial aperture) becomes longer with growth. Specimens up to 5 cm in length have been recorded. There are never any hairs, or root-like outgrowths of the test.

INTERNAL STRUCTURE: The body wall is very thin, although there is an almost continuous layer of circular muscles externally, and longitudinal bands are present beneath the circular layer. The dorsal tubercle is large, with a simple U-shaped slit, the horns sometimes coiled in or out.

There are 4 narrow branchial folds separated by wide interspaces. Internal longitudinal vessels (between 10 and 16) are crowded on the folds, with 3 to 6 spaced well apart in the interspace. There are 4 to 6 stigmata per mesh.

The gut extends in a wide arc from the posterior oesophageal opening to the anterior atrial aperture. The oesophagus is short and the stomach short and rounded, with internal longitudinal folds.

Round polycarps are crowded in a single row on each side of the endostyle. Each polycarp consists of up to 6 pairs of undivided male follicles curving around the sides of the rounded ovary. A dorsally directed and rather thick vas deferens lies on the mesial surface of the ovary, but only its terminal part protrudes immediately above the sessile female opening, which is wide with frilled lips. There are only up to 4 large eggs (0.5 mm) in the ovary. Eggs, embryos and juveniles are found free in the peribranchial cavity (AM G12235, G12239). Small, rounded endocarps are scattered on the body wall.

REMARKS: The species is closely related to *Polycarpa tinctorella* n.sp., *P. rigida*, *P. chinensis* and *P. procera*. The species is distinguished from *P. procera* by the relatively small number of internal longitudinal branchial vessels and the greater number of stigmata per mesh that result from the longitudinal vessels being more widely spaced. *Polycarpa chinensis* is distinguished by the marked curvature along its longitudinal axis and by the presence of crowded polycarps along the dorsal border as well as along each side of the endostyle. Direct development and a viviparous habit (Millar 1962b) are further distinctions from most members of the species group except *P. tinctorella* n.sp. Relations with the latter species are discussed below (*P. tinctorella* n.sp, Remarks).

It should be noted that although Herdman records only 8 internal longitudinal vessels, his figure (Herdman 1882, Pl. XII, Fig. 4) shows that number on only one side of the branchial folds. On this, as on other occasions, it appears that Herdman only counted the vessels on one side of the fold.

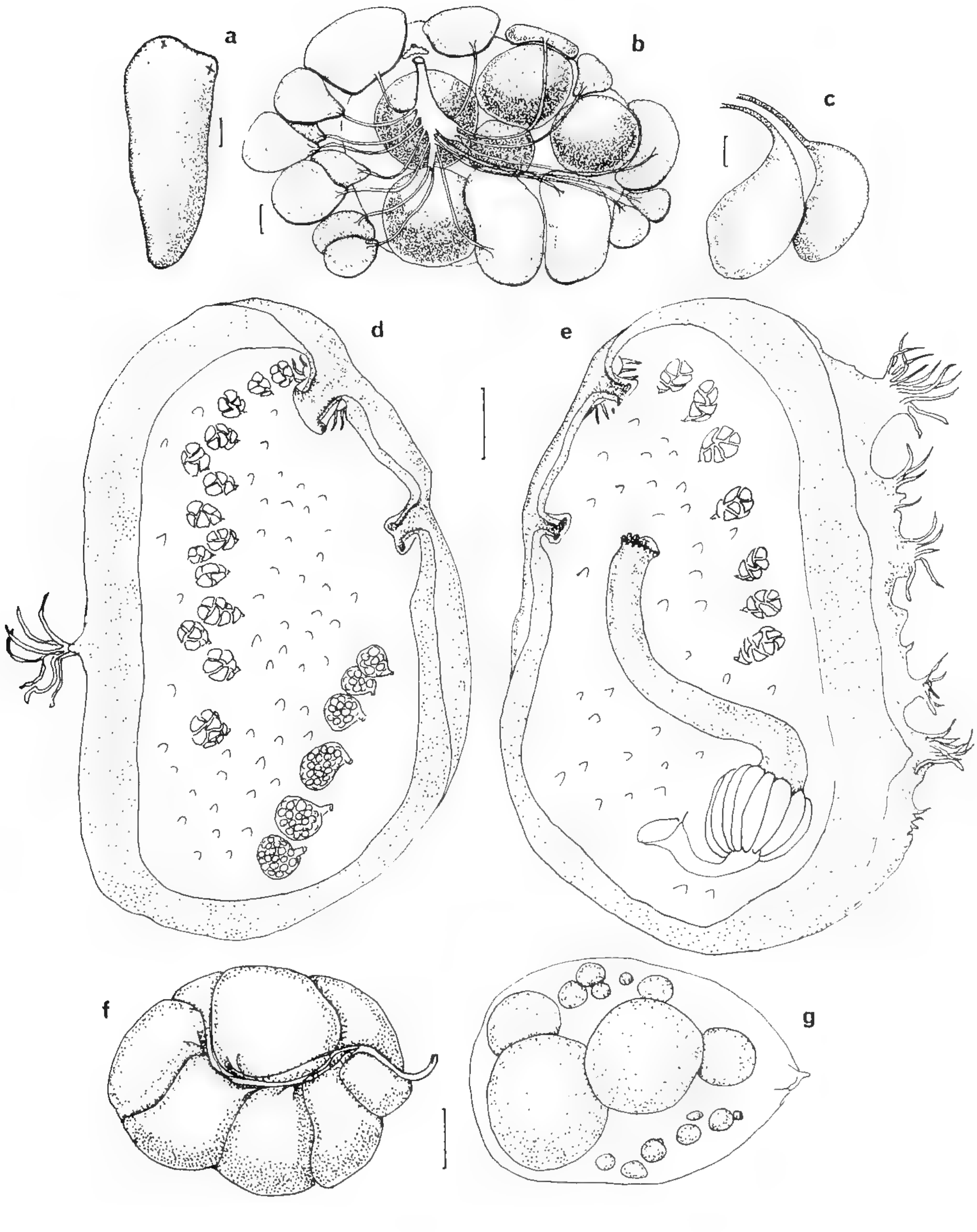


FIG. 97: *Polycarpa tinctor* (AM G12255) — **a**, external appearance; **b**, gonad; **c**, male follicles. *Polycarpa tinctorella* n.sp. (ZMC holotype) — **d, e**, right and left sides of the body showing internal structure, inverted apertures and thick test (which has embedded sand); **f**, testis; **g**, partly expended ovary with mature ova. (Scales: **a**, 5.0 mm; **b**, **c**, 0.1 mm; **d**, **e**, 1.0 mm; **f**, **g**, 0.2 mm).

Polycarpa tinctorella n.sp.
(Fig. 97d–g)

DISTRIBUTION

TYPE LOCALITY: Victoria (Off Cape Howe, 37°05'S 150°05'E, 60–100 m, Dr T. Mortensen's Pacific Expedition, 30.9.14, holotype ZMC, paratypes ZMC 3 lots, juveniles ZMC).

DESCRIPTION

EXTERNAL APPEARANCE: A large number of specimens from 0.5 to 2 cm long were taken. They are all oval, laterally flattened and very hard and sandy. In section they are slightly elliptical, the postero-ventral border narrowing to a sharp knife-edge that is formed by the sand embedded in the test and tangled in the tufts of fine hairs that project from this part of the test. There is a thinner layer of sand on the remainder of the body. The apertures are fairly close together and sessile, the branchial aperture subterminal and the atrial aperture about one-third of the way down the dorsum. In these contracted specimens the apertures are inverted into the body and are concealed in a very fine groove that extends along the narrow but flattened, rather than knife edged, antero-dorsal border. The sandy test is hard rather than brittle.

INTERNAL STRUCTURE: The body wall is very delicate indeed, and adheres closely to the test. The muscles are conspicuous only around the apertures. There are 12 short branchial tentacles. The dorsal tubercle protrudes from a V-shaped peritubercular area, and it has an almost circular slit. The oesophageal opening is at the posterior end of the body and the dorsal lamina is long.

The branchial sac is delicate, with 4 low folds, arranged according to the following formula: E2(6)2(11)2(8)3(5)1DL0(14)1(6)2(8)2(6)2. The dorsal fold on the right tends to flatten out posteriorly and is separated from the dorsal lamina by 1 or 2 internal longitudinal vessels. The most dorsal fold on the left is close to the dorsal lamina and is the widest fold in the branchial sac, while the fold next to it is one of the narrowest. There are 4 to 6 stigmata per mesh, crossed by parastigmatic vessels.

The gut forms a rather open, more or less sinuous curve, the intestine bending dorsally from the distal end of the almost spherical stomach. The stomach wall has parallel glandular folds. The rectum is short and terminates near the atrial aperture. The anal border has about 10 small rounded lobes, mostly on its mesial rim.

There is a row of almost spherical, often crowded, testes along each side of the endostyle. On the left there are up to 12 male glands, the row terminating posteriorly at the gut loop. On the right there are up to 20 testes, the row extending the whole length of the body. Each testis consists of about 10 short, wide, unbranched male follicles crowded together. A duct from each follicle extends toward the dorsal side of the testis where it joins the short vas deferens. The arrangement of the follicles and the course of their ducts appears to be random, depending on the orientation of each follicle in the testis. There is no evidence of a female component in these entirely male organs. An oblique row of about 6 spherical ovaries extends across the postero-dorsal corner of the right side of the body, the short oviducts directed postero-dorsally, not toward the atrial aperture. In most of the individuals examined the ovaries are partly or entirely expended and there are juvenile ascidians and embryos crowded in this postero-dorsal corner of the peribranchial cavity which serves as a brood chamber. Embryos are usually confined to this area dorsal to the ovaries, although sometimes they are also present to the left of the dorsal mid-line. In the holotype the ovaries each contain about 20 relatively large eggs (about 0.1 mm in diameter) andthere are no embryos in the brood chamber. The ovaries appear to be only approaching maturity. Mature eggs are about 0.5 mm in diameter. Incubating embryos appear to be held in place by the connectives between the body wall and the pharynx. It is not clear how they move from their postero-dorsal position to the atrial opening. The delicate body wall adhering closely to the rigid sandy test, does not appear to be capable of the contraction that would force the juveniles toward the excurrent aperture. Individuals from 1.0 cm in length have mature gonads. There are small endocarps scattered over the body wall.

REMARKS: The separation of gonads into male and female components and the absence of female gonads from the left side of the body has not previously been reported for the other species of this genus. The position of the testes and the shape of the follicles resembles the gonads of *Polycarpa tinctor*, however in that species the gonads in rows along each side of the endostyle are hermaphrodite. The mature eggs of this species also resemble the large eggs of *P. tinctor*, however they are more numerous than those of the latter species.

Polycarpa tinctorella appears to reach sexual maturity earlier than other species of the *tinctor* group and mature gonads are present in specimens of 1.0 cm length. However immature specimens (less than 1.0 cm) in which gonads are not developed are not readily distinguished from juveniles of *P. rigida, P. chinensis* and *P. tinctor*; and their ranges overlap. Only *P. procera*, with more internal longitudinal branchial vessels in the interspaces is distinct. They all have the same flat biscuit-like form and, possibly with the exception of *P. tinctor*, they have similar postero-ventral tufts of roots.

Small specimens of *P. rigida* and of the present species were taken together off Cape Howe by the Danish Mortensen expedition (ZMC). The presence of gonads in the larger specimens of both helped to determine the species that were present. Generally the less flattened body and slightly protruding atrial aperture of *P. rigida* individuals of 1.0 cm or more confirmed the distinction. However, there is no character yet identified that can be used to distinguish small (less than 1.0 cm) individuals of these two species and the same is true of *P. chinensis* and *P. tinctor*.

Polycarpa viridis Herdman, 1880
(Fig. 98; Pl.IVc)

Polycarpa viridis Herdman, 1880, p.74; 1882, p.168; 1899, p.47 (part, greenish specimens Pl. Cyn. 18, Fig. 1).

Polycarpa moebii Michaelsen, 1905, p.104 (part, specimen from Bass Strait). Hartmeyer and Michaelsen, 1928, p.372. Kott, 1952, p.244 (part). (Not: Vasseur, 1967b, p.136, < *P. pigmentata*).

Polycarpa pedunculata: Hartmeyer and Michaelsen, 1928, f. viridis p.366. Kott 1972a, p.35 (part, smooth, naked specimens, bright to pale yellow living); 1972b, p.186 (part); 1975, p.13 (part, bright yellow living).

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 30.72 104.72 108.72 121.72 123.72 217.73 227.73 151.74 14.75 90.75 168.75 188.75 195.75 218.82 910–1.83 914.83 934.83 1136.83 1142–3.83 1145.83, QM G9578 G9662). South Australia (Spencer Gulf, QM GH2779 GH2780–1, St Vincent Gulf, QM G9306 G9576). Victoria (Bass Strait, QM G11870 GH11980, NMV H727, ZMC 9.9.14). New South Wales (Cape Jervis, QM GH115).

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound — Hartmeyer and Michaelsen 1928, Kott 1952). South Australia (Great Australian Bight — Kott 1975; Spencer Gulf — Kott 1972b; St Vincent Gulf — Kott 1972a). Victoria (Bass Strait — Michaelsen 1905; BM 1887.2.4.127 Herdman 1882). New South Wales (Port Jackson — BM 1887.2.4.89–92 Herdman 1882, 1899).

DESCRIPTION

EXTERNAL APPEARANCE: The body is either circular, more or less cylindrical, or conical, narrowing to the terminal or subterminal branchial aperture. It is up to 5 cm long and about 2 cm in diameter. There is often a stalk up to 3 cm long from the ventral side of the posterior end of the body. The diameter of the stalk is very variable, increasing where it joins the body. Apertures are sometimes on opposite sides of the anterior end of the body, the branchial aperture directed antero-ventrally and the atrial aperture straight upwards, with a slight prominence dorsal to the branchial aperture. The apertures are often completely sessile, each surrounded by 4 low swellings, or they are on short siphons. The test is thin, tough and smooth or only slightly wrinkled in the preserved specimens. There are no epibionts on the surface. The stalk is sometimes hard and brown in preserved specimens, fading to beige, greenish white or greyish purple on the body. Two specimens from Bass Strait (NMV H727) have a very inflated, balloon-like body.

INTERNAL STRUCTURE: The body wall is greenish brown or slightly purple, with a layer of strong, circular muscles overlying longitudinal bands. Large (0.2 to 1.0 mm diameter) vesicles are crowded in the inner, muscle-free, layer of body wall and also occur between muscle bundles, over the gonads and in the pharyngeal wall. These vesicles often contain particles of green pigment. The conspicuous, protruding dorsal tubercle is heart- or kidney-shaped, often elongate transversely. The aperture of the neural gland is a long, deep slit, following a sinuous course parallel to the outer margin of the tubercle and often interrupted along its length. The dorsal lamina is long.

Up to 15 internal longitudinal vessels are crowded on the low branchial folds, but only 2 or 3 in the interspace. They are arranged according to the following formula: E3(10)3(12)2(14) 2(14)3DL. There are 9 or 10 stigmata per mesh.

The gut loop forms a deep U-shaped loop, the long rectum extending anteriorly almost parallel to the descending limb of the loop. The oesophagus is only of moderate length. The stomach is very long and roomy, extending at least halfway up the ascending limb of the primary loop. It has longitudinal glandular folds that are not visible from the outside of the stomach toward its pyloric end. A large circular or comma-shaped, flat-topped endocarp is enclosed in the primary loop. The rectum extends anterior to the pole of the primary gut loop for up to half its length. The anal border is divided into 7 or 8 lobes around its mesial border, but the outside of the border is usually undivided.

The gonads are broad and oval and embedded in the body wall, although their mesial surface

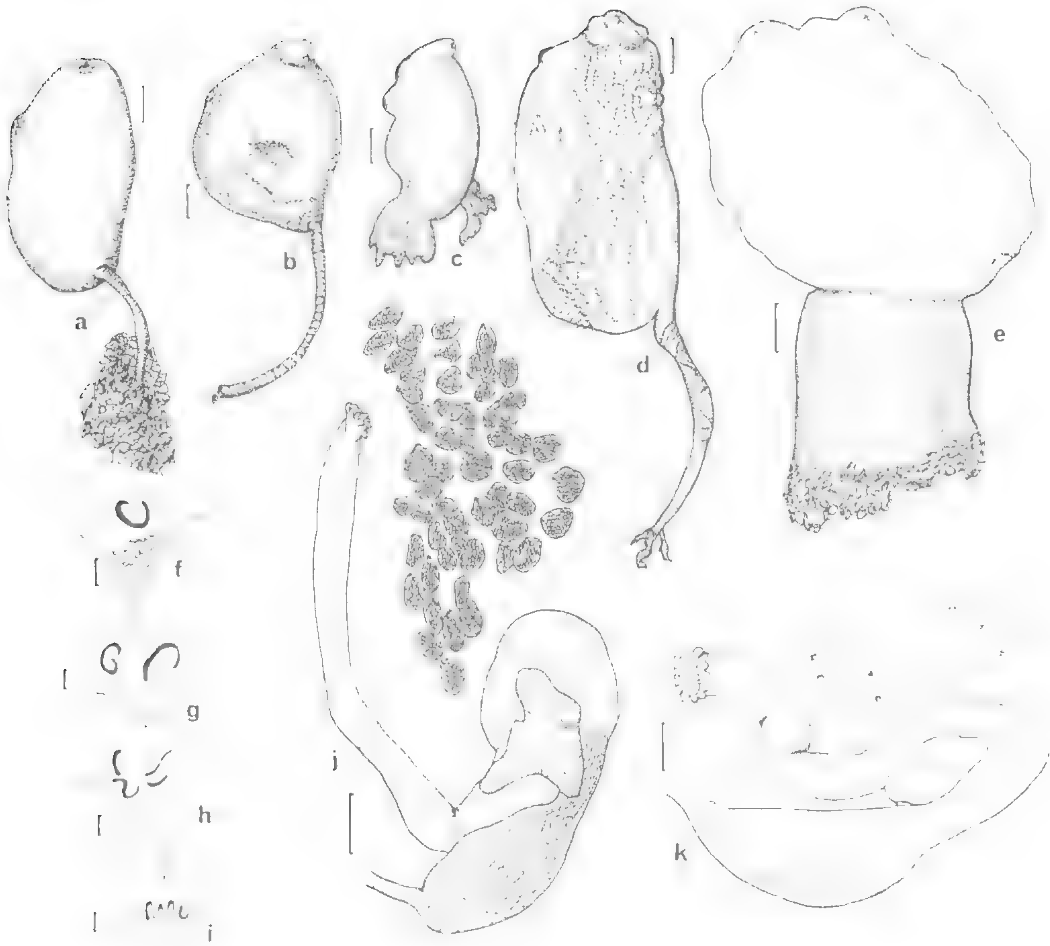


FIG. 98: *Polycarpa viridis* — **a** - **e**, variation in external appearance (WAM 128.75 1144.83 145.83 910.83, NMV H727); **f** - **i**, variation in dorsal tubercles (**f**, NMV H727; **g** - **i**, WAM 1145.83); **j**, **k**, gut, gonads and endocarp (WAM 222.73, NMV H727 also showing large embedded vesicles). (Scales: **a** - **d**, 5.0 mm; **e**, 3.0 mm; **f** - **i**, 0.25 mm; **j**, 4.0 mm; **k**, 2.0 mm).

projects slightly into the atrial cavity in older specimens. They are sometimes crowded and may appear to be arranged in 3 rows on the left anterior to the gut loop and 5 on the right. They consist of a large, sac-like ovary and up to 12 pairs of lobed male follicles beneath and projecting up into the ovary. The ovaries open direct to the atrial cavity and ducts, if present, are very short indeed. The vasa efferentia on each side sometimes join one another or sometimes extend separately around the outer edge of the mesial surface of the ovary to the distal end of the ovary at which point the ducts from each side join before opening into the atrial cavity. There are no endocarps on the body wall apart from the one enclosed by the gut loop.

REMARKS: Although the green pigment by which the species was originally characterised is not always present, other characters distinguish this species from *Polycarpa pedunculata* and *P. ovata*: the regular, broad oval polycarps that do not taper at their distal end; the virtual absence of gonoducts; the large vesicles in the body wall; and the heart- to kidney-shaped dorsal tubercle with its rather complex slit. Its test is invariably naked, as is that of *P. ovata*, which provides a further distinction from *P. pedunculata*. The bright yellow colour of the living specimens is a useful distinguishing feature in the field, although it is less vivid in older specimens with a tough, opaque test. *Polycarpa flava* n.sp. has similar bladder cells and is yellow when alive, but is distinguished by its hard, sandy coating and its black colour in preservative.

The sympatric species *P. pedunculata* and *P. viridis* (> *P. moebii*) have always been confused in the literature (see *P. pedunculata*, Remarks). Confusion arises largely because of variations in body shape, length of rectum, and shape and number of gonads. In *P. viridis* the rectum is always longer than the short rounded gut loop (although it is not always as long as Michaelsen (1905) believed was characteristic) and the vesicles are larger than those of *P. pedunculata*. It is these vesiclesthat form the protrusions Herdman (1899) observed along the vessels and walls of the branchial sac. They sometimes project into the atrial cavity to give it a papillated appearance.

Genus **Monandrocarpa** Michaelsen, 1904

Type species: *Monandrocarpa tritonis* Michaelsen, 1904b.

The genus contains solitary styelids with hermaphrodite gonads that have either a single male follicle or a single pair. Zooids are small, seldom being more than 1 cm in length. There are 3 or 4 branchial folds. Relatively few internal longitudinal branchial vessels are present on the folds, and they are seldom present in the interspace. There is a long, curved gastric caecum.

Although Michaelsen (1904b) provisionally regarded the genus as a member of the subfamily Polyzoinae, there is no trace of vegetative reproduction in any of the 3 known species. The small zooids of the present genus do, however, share many characters with the colonial zooids of the polyzoinid genus *Eusynstyela* (see below).

One of the two species known from the western Pacific, *Monandrocarpa incubita* (Sluiter, 1904), is not recorded from Australia. The type species was taken from off South Africa.

The small individuals of species of the genus have been taken on sandy sediments. This habitat has not been well sampled, which may account for the discontinuity of the records.

Monandrocarpa plana (Kott, 1972)
(Fig. 99)

Monoandrocarpa plana Kott, 1972d, p. 250.
Polycarpa simplicigona Millar, 1975, p. 286.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: New South Wales (Cronulla — holotype AM Y852, paratypes Y853 Kott 1972d). Philippines (Millar 1975).

The Philippines specimen was taken at 457 m depth; the specimen from Cronulla at 160 m. It is possible that the species has a wide range in the interstitial habitat for which it appears well adapted.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are oval, dorso-ventrally flattened and about 1.5 cm long, including the sandy covering. The apertures are sessile on the upper surface, about one-third to half of the body length apart. There are long test hairs around the meridian of the body, to which sand adheres. Sand also adheres to other parts of the test, although sometimes a longitudinal area along the dorsal mid-line that includes the apertures is free of sand.

INTERNAL STRUCTURE: The body wall is thin, with delicate muscles everywhere except around the apertures where they are more conspicuous. There are about 40 crowded tentacles. The dorsal tubercle is small, with a C-shaped opening. The dorsal lamina is very long, the oesophageal opening being at the posterior end of the branchial sac.

The 4 straight branchial folds have the following formulae: DL0(6)0(4)0(8)0(5)E (AM Y853);

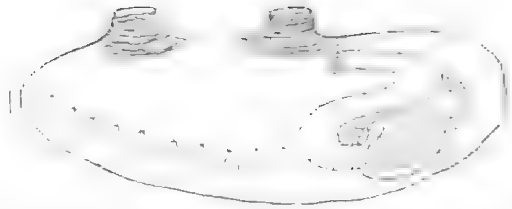


FIG. 99: *Monandrocarpa plana* — left side of body (after Kott 1972d). (Scale: 1.0 mm).

DL0(5)0(2)0(4)1(3)0E (Millar 1975). There are about 5 oval stigmata per mesh.

The gut forms a short and compact loop in the posterior third of the body, the pole of the loop not projecting further forward than a point level with the atrial aperture. The oesophagus curves forward to the short, rounded stomach with 12 longitudinal glandular folds. The long, curved gastric caecum in the gut loop sometimes has a kink. The intestine is wide but very short. The rectum curves sharply around onto the dorsal surface to open at the base of the atrial aperture. The anal border is deeply divided into narrow lobes.

The gonads are in a row on each side of the body a little distance from the endostyle. There are only 4 polycarps on each side in the specimen from the Philippines, but in the Australian specimens the gonads are more crowded, with up to 16 on the right and 13 on the left. They are identical, with a small, rounded ovary containing numerous eggs, and a single large male follicle beneath the ovary. A single, short male duct curves around the anterior side of the ovary to open just above the very short oviduct. Gonoducts are directed dorsally.

REMARKS: The species is distinguished from *M. incubita* (Sluiter, 1904) from Indonesia and the Marianas Is (Tokioka 1967a) by its test hairs, single male follicle (instead of the 2 present in *M. incubita*) and its very short stomach and gut loop.

Monandrocarpa tritonis Michaelsen, 1904b, from South Africa, closely resembles the present species, with similar numbers of internal longitudinal branchial vessels and only a single testis follicle in each hermaphrodite gonad.

Subfamily POLYZOINAE Hartmeyer, 1903

Vegetatively reproducing members of the family Styelidae that form colonies, but in which zooids open separately to the exterior and never form colonial systems. Zooids are usually either joined to one another by basal stolons formed by extensions of the body wall and external test, or they are embedded in common test. The mesenchymal septum (present in Perophoridae) is absent from the basal stolon although there is a mesenchymal reticulum and haemocoel. Vegetative zooids are produced from the ectoderm and mesodermal tissue of the parietal body wall (Berrill 1935b, 1938, 1948; Newberry 1965). Zooids are always small, only occasionally being more than 1 cm in length.

Progressive size reduction and simplification of the zooids is an evolutionary phenomenon associated with all vegetatively reproducing ascidians and convergent adaptations can be observed. In the Polyzoinae, the branchial sac tends to become simplified, the branchial folds suppressed and the internal longitudinal vessels reduced in number. Progressive simplification of the gonads is reflected through the subfamily, from the characteristic styelid or polycarpid gonads (present in *Polyandrocarpa* and *Oculinaria*) in which large ovarian tubes or sacs are associated with numerous male follicles, to small hermaphrodite gonads with 2- or 3-egg ovaries and single or paired male follicles (*Eusynstyela*, *Polyzoa* and *Symplegma*). In other genera, male follicles are always large and single, and some occur without associated female glands. Further, although hermaphrodite organs persist on the right side of the body there is a tendency for the female components of the gonads to be lost completely from the left (*Stolonica*, *Theodorella*). In yet other genera, hermaphrodite gonads are never present, and separate male and female organs are present on both sides of the body (*Metandrocarpa*) or on opposite sides (*Alloeocarpa*). Sometimes the male glands are very numerous, scattered and small (*Distomus*, *Amphicarpa* and *Oligocarpa*).

Simplification of the branchial sac is a secondary adaptation, associated with size reduction and its condition does not always afford a reliable indicator of phylogeny (e.g., *Metandrocarpa*). Similarly, stages in the progressive loss of female components of hermaphrodite gonads from one or the other side of the body can result in confusion if applied too rigorously to the definition of taxa at generic level. The type of gonads, especially the size and shape of their male and female components and their numbers and position on the body wall, constitute more reliable indicators of generic relationships. These characters, together with considerations of the condition of the branchial sac and progressive

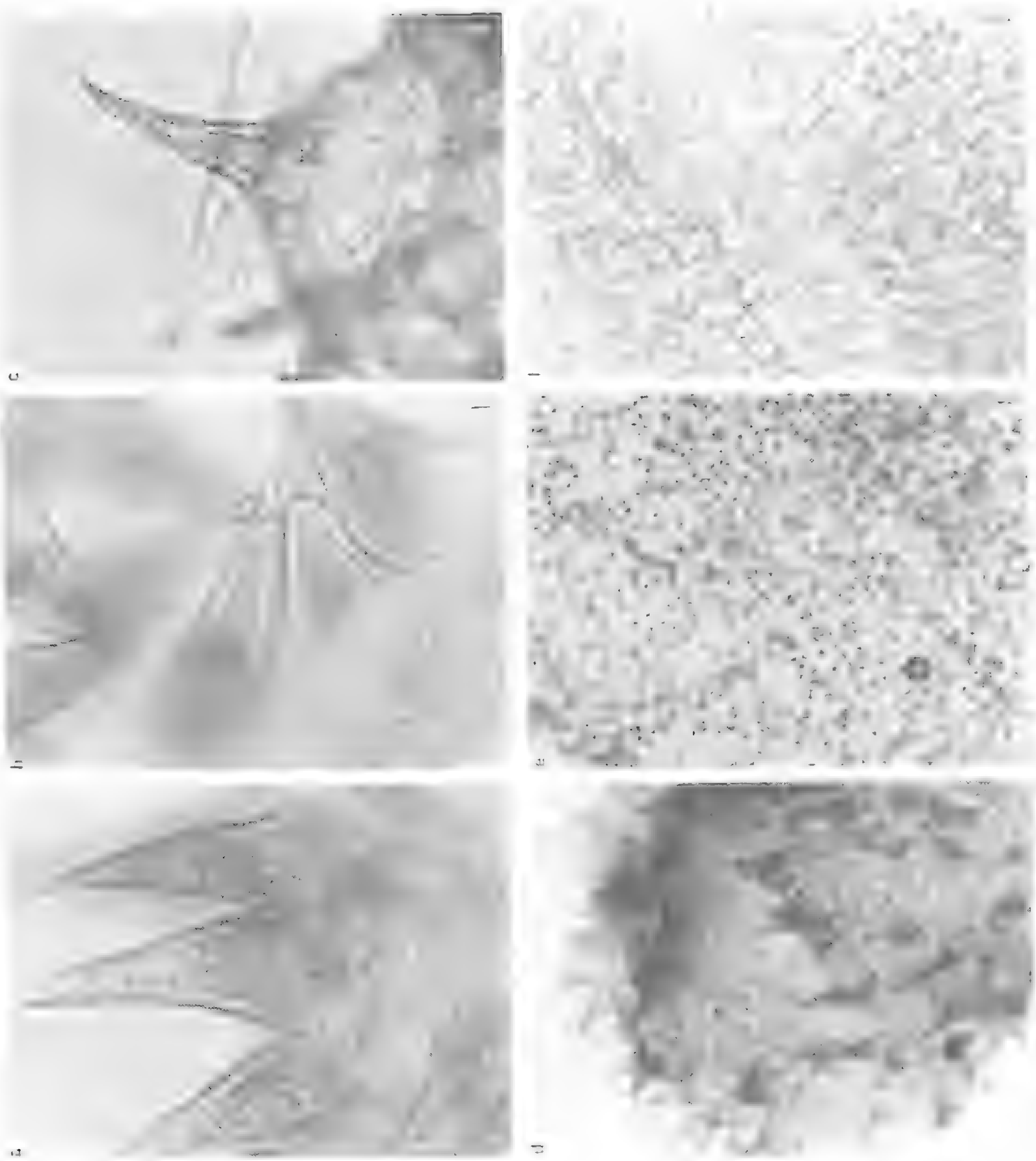


FIG. 100: *Polycarpa olitoria* — **a**, test spines around apertures; **b**, siphonal spines (NMV H478); **c**, siphonal spines (WAM 182.75); **d**, siphonal spines (WAM 182.75). *Polycarpa pigmentata* — **e**, pigment particles and bladder cells in body wall. *Amphicarpa diptycha* — **f**, siphonal scales. (Scales: a – c, f, 0.01 mm; d, e, 0.1 mm).

changes in the association of female with male gonads, can be used to determine species identity.

Seriocarpa Diehl, a styelid genus in which vegetative reproduction has been shown to occur by horizontal division of zooids to produce solitary rather than colonial individuals, is possibly not phylogenetically related to other genera of the Polyzoinae. It resembles the genus *Eusynstyela* in some characteristics that are discussed below (*Eusynstyela*), but the resemblance may be due to convergence, rather than an indication of affinity.

Genera of the Polyzoinae are viviparous, fertilisation being internal, and larvae are occasionally found in the peribranchial cavity. Their unstalked adhesive organs have a triradial arrangement, as in other stolidobranch larvae. However, polyzoinid larvae bear certain resemblances to those of other viviparous colonial groups (Botryllinae, Perophoridae and Aplousobranchia): they are large, with a mass of yolk; there is a circle of finger shaped ectodermal ampullae at the anterior end of the trunk; and larval sense organs are well developed. The larval ocellus (lost in *Polycarpa*) is not present, but secondarily acquired light sensitive elements are added to the gravity sensitive otolith to form a photolith, as in Botryllinae (Grave 1932, Berrill 1950). The life history of south-western Pacific species is not known. Berrill (1935a) reports the free swimming life of larvae of this subfamily to be from 3 to 30 hours — a relatively long time when compared with aplousobranch larvae. Nevertheless, larvae are strong swimmers and that, combined with their capacity for site-selection, presumably ensures maintenance of populations. This view is supported by the large number of indigenous species of this subfamily in Australian waters (18 of the 24 species recorded).

Of the 22 genera known in this subfamily, the 13 set out below have not been recorded from Australia (see Huus 1937):

Gynandrocarpa Michaelsen, 1900 (monotypic), from Africa (Millar 1962a); *Syncarpa* Redikorzev, 1913 (monotypic), Okotsek Sea; *Seriocarpa* Diehl, 1969 (polytypic), Atlantic and western Pacific (Millar 1975); *Kukenthalia* Hartmeyer, 1903 (monotypic), Arctic; *Arnbackia* Brewin, 1950b (monotypic), New Zealand; *Oligocarpa* Hartmeyer, 1911 (monotypic), sub-Antarctic; *Distomus* Gaertner, 1774 (polytypic), Atlantic and western Pacific; *Protostyela* Millar, 1954 (monotypic), Scotland; *Botryllocarpa* Hartmeyer, 1909 (monotypic), Indonesia; *Berrillia* Brewin, 1952a (monotypic), New Zealand; *Theodorella* Michaelsen, 1922 (polytypic), New Zealand; *Alloeocarpa* Michaelsen, 1900 (polytypic), Antarctic.

Distomus malayensis Sluiter, 1915 from Indonesia has embedded zooids, 3 internal longitudinal branchial vessels on each side, a few ovarian sacs on the right and a row of male follicles on the left. This genus has not been recorded from Australian waters.

Similarly, *Seriocarpa* has not yet been recorded from Australia, but is represented in waters to the north by *S. littoralis* Millar, 1975. *Botryllocarpa viridis* (Pizon, 1908) closely resembles *Symplegma* and may be synonymous (see *S. pizoni* Tokioka, 1972).

KEY TO THE GENERA OF POLYZOINAE
(* not recorded from Australia)

1. Gonads always monoecius; each with more than a single pair of male follicles 2
   Gonads dioecious or monoecious; each with no more than a single pair of male follicles 5
2. Gonads present on both sides of body .... *Polyandrocarpa*
   Gonads not present on both sides of body .. 3
3. Branchial sac with 4 folds; numerous gonads .... *Oculinaria*
   Branchial sac with less than 4 folds; single gonad 4
4. Branchial sac with 3 folds .. *Gynandrocarpa* *
   Branchial sac with 1 fold .... *Syncarpa* *
5. Gonads in usual position in body wall lining atrial cavity 7
   Gonads not in usual position in body wall lining atrial cavity 6
6. Numerous gonads in a row beneath endostyle embedded in test .... *Seriocarpa* *
   Single gonad in a pouch projecting from left body wall .... *Kukenthalia* *
7. Gonads all hermaphrodite 8
   Gonads not all hermaphrodite 11
8. Branchial sac with folds .... *Eusynstyela*
   Branchial sac without folds 9
9. A single gonad on each side 10
   Numerous gonads on each side .... *Polyzoa*
10. Branchial sac with 4 internal longitudinal vessels .... *Symplegma*
    Branchial sac with 3 internal longitudinal vessels .... *Botryllocarpa* *
11. Gonads on left only; only protostigmata in branchial sac .... *Berrillia* *
    Gonads on both sides; not only protostigmata in branchial sac 12
12. Male gonads on both sides; female gonads on one or both sides 13

Male gonads on one side only; female gonads on side opposite to male 17
13. Male and hermaphrodite gonads present ...14
Male and female gonads present ....*Metandrocarpa*
14. Branchial folds present..........................15
Branchial folds not present 16
15. Gonads confined to a row each side of endostyle .... *Stolonica*
Gonads not confined to a row each side of endostyle .... *Amphicarpa*
16. Protostigmata persist; not more than 3 gonads per side........................... *Protostyela* *
Protostigmata do not persist; more than 3 gonads per side.................*Theodorella* *
17. Branchial folds present..........................18
Branchial folds not present 20
18. Male gonads on left, female on right 19
Male gonads on right, female on left ....*Arnbackia* *
19. Ovaries few and long .... *Oligocarpa* *
Ovaries numerous and rounded... *Distomus* *
20. More than a single gonad on each side .... *Alloeocarpa* *
Not more than a single gonad on each side .... *Chorizocarpa*

Genus **Polyandrocarpa** Michaelsen, 1904

Type species: *Goodsiria lapidosa* Herdman, 1898

Vegetatively reproducing species with 4 branchial folds and numerous gonads consisting of short flask-shaped ovaries and paired rows of male follicles beneath the ovaries.

Polyandrocarpa spp. differ from *Polycarpa* spp. in those characters that are associated with their vegetative reproduction *viz.*, colonial habit, small-sized zooids and viviparous larvae. Many species (e.g., *P. simulans*, *P. sparsa* n.sp.) have a closer relationship with species of *Polycarpa* than they do with one another. It is probable that the genus is polyphyletic, demonstrating convergent evolution from a number of different ancestors in the Styelinae. At least one species (*P. triggiensis*) has long ovaries reminiscent of *Cnemidocarpa*, while others have gonads clearly related to those of *Polycarpa*. Further, *P. sagamiensis* and the related species *P. lapidosa* and *P. watsonia* n.sp. have different colony form and zooid morphology from other smaller species that occur in Australia, and it is probable that the mechanism of vegetative reproduction in these two groups of species is different. These differences may justify their separation from other species of the genus. However, the morphology of all these species fits well the present definition of *Polyandrocarpa*; accurate resolution of their taxonomy must await information on the processes of vegetative reproduction, which may indicate their true phylogeny.

Oculinaria is a closely related genus distinguished only by the absence of gonads on the left side of the body. In *Eusynstyela* Michaelsen, 1904a, the form of the colony, with prostrate zooids embedded in tough test, resembles that of some species of *Polyandrocarpa*. However, zooid and gonad reduction has proceeded a stage further and male follicles are reduced to 1 or 2 in each gonad. *Eusynstyela* was formerly regarded as a subgenus of the *Polyandrocarpa*, but the difference in the gonads justifies their separate generic status.

Polyandrocarpa is well represented in Australian waters, although the colonies (which generally are not small) are sandy and consequently inconspicuous and may be overlooked by collectors. Half of the species are reported from tropical and temperate locations, but the others have a more restricted range. Only one species (*P. sagamiensis*) has a wide recorded range in the Indo-West Pacific, the others being indigenous Australian species. *Polyandrocarpa lapidosa* and *P. watsonia* n.sp. have affinities with the sub-Antarctic *P. placentela* (Herdman), while *P. abjornseni*, *P. australiensis* and *P. triggiensis* may have affinities with tropical fauna.

Key to Species of *Polyandrocarpa* Recorded from Australia

1. Compact colony; zooids embedded 2
Colony not compact; zooids connected by stolons 6
2. Zooids completely embedded...................3
Zooids only partially embedded ....*P. sagamiensis*
3. Zooids embedded in parallel longitudinal compartments in test 4
Zooids not embedded in parallel longitudinal compartments in test 5
4. Atrial apertures at anterior end of body .... *P. lapidosa*
Atrial apertures at posterior end of body ....*P. watsonia* n.sp.
5. Gonads numerous; scattered over body wall .... *P. simulans*
Gonads not numerous; not scattered over body wall ....*P. abjornseni*
6. Gut does not form a loop ..... *P. sparsa* n.sp.
Gut forms a loop 7
7. Gonads short and flask-shaped; in a row each side of endostyle.............*P. australiensis*

Gonads long and cylindrical; in dorsal half of body ....*P. triggiensis*

The following species, recorded from adjacent areas, are not recorded from Australia:

Polyandrocarpa colligata Sluiter, 1913 from Aru I. has colonies with embedded zooids lying on their ventral surface in the common test. The gonads are elongate and confined to a row along each side of the endostyle as in the temperate species *P. lapidosa*.

Polyandrocarpa maxima (Sluiter, 1904), from Indonesia, is a compact species with embedded zooids lying on their ventral surface and 4 branchial folds on each side of the endostyle. Its small gonads are smaller than those of *P. colligata*, although they are in a row on each side of the endostyle. The long stomach and short gut loop also resemble those of *E. latericius*, although they appear to be orientated across the posterior end of the body, rather than parallel to its longitudinal axis. The number of testis follicles may not exceed the number characteristic of *Eusynstyela* and the species may be a species of the latter genus.

Polyandrocarpa maxima: Van Name 1918, 1945, from the Philippines and from the eastern Atlantic has scattered gonads each with numerous testis follicles in two rows beneath each ovary. However, the gonads are scattered rather than in rows, and the species is clearly not a synonym of *P. maxima* Sluiter. The gonads are lightly attached to the body wall (Van Name 1945). The specimens may be conspecific with specimens of an undescribed species of this genus from the Philippines (QM GH2081) with a rounded endocarp in the gut loop and scattered gonads standing upright (fixed to the body wall by a ligament at their proximal end. With the exception of their colonial habit, these zooids resemble individuals of *Polycarpa reniformis*, supporting the hypothesis that *Polyandrocarpa* is polphyletic.

Polyandrocarpa robusta Sluiter, 1915 from Indonesia resembles *P. colligata* with its embedded zooids, elongate gonads in a row each side of the endostyle, and a curved gut loop and gastric caecum.

Polyandrocarpa abjornseni (Hartmeyer Mand Michaelsen, 1928)

Polycarpa abjornseni Hartmeyer and Michaelsen, 1928, p.374.
?*Polycarpa obscura* (juv?) Heller, 1878, p.22.
?*Polycarpa* aff. *obscura*: Hartmeyer, 1919, p.44.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound — Hartmeyer and Michaelsen 1928; ? Cape Jaubert — Hartmeyer 1919)

DESCRIPTION (after Michaelsen and Hartmeyer 1928)

EXTERNAL APPEARANCE: The colonies are irregular, the zooids in tight, irregular aggregates, separated from one another by partitions of the tough test, their anterior ends projecting from the surface of the colony. The test is smoke-grey to dark brown, almost black. There is some sand encrusting the external test, but no test hairs. The apertures are sessile and inconspicuous, about half the body length apart. The test is moderately thick, flexible, white in section, the inner surface with an iridescent sheen.

INTERNAL STRUCTURE: The body is almost spherical, about 1 cm in diameter. The body wall, which does not adhere closely to the test, contains numerous black vesicles. The dorsal tubercle is a diagonal, oval cushion with an S-shaped slit. There are more than 40 crowded branchial tentacles.

The 4 thick, but not wide, branchial folds have 6 to 8 internal longitudinal vessels on the folds and 1 in the interspace. There are 7 to 10 long oval to rectangular stigmata per mesh in the wide interspaces.

The gut loop is confined to the posterior end of the body and encloses a shield-shaped endocarp in the pole. The stomach is elliptical, wider at the cardiac end and tapering toward the intestine. It has 14 distinct folds and a small caecum curved in the loop of the gut. The rectum curves anteriorly, forming an obtuse angle with the descending limb of the gut loop.

There are 2 large, flat, oval gonads on each side of the body. They are in the ventral part of the body, each side of the endostyle. Each gonad consists of a flask-shaped ovary and up to 6 pairs of pyriform male follicles beneath the ovary, with the male ducts curving around each side to join a common opening on the surface of the short oviduct.

REMARKS: The colonies of the present species resemble those of the possibly colonial species *Polycarpa nigricans*, although the latter species has numerous scattered gonads. Species of the *pedunculata* group of the genus *Polycarpa* resemble the present species in having dark vesicles embedded in the body wall, a similar flat-topped endocarp enclosed in the pole of the gut loop, and a dark body wall.

TABLE VIII — SUMMARY OF CHARACTERS OF SPECIES *POLYANDROCARPA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Zooid organisation	Gut loop	Stomach caecum	Endocarps: in gut loop; elsewhere	Gonads arrangement per side	Additional features
P. simulans	—	SA	embedded	curved	absent	1:0	scattered	black test and body wall; massive leathery colony
P. abjornseni	—	Cape Jaubert – Cockburn Sd	″	″	present	″	2 only	black test and body wall; massive leathery colony
P. australiensis	—	Gladstone – Cockburn Sd	stolons	″	″	1; +	single row	flexible sometimes sandy test, dark body wall; zooids less than 1 cm long
P. triggiensis	—	Cockburn Sd	″	″	″	0; +	3 only, long	flexible, sandy test; zooids less than 1 cm long
P. sparsa n.sp.	—	N. Solitary I.	″	none	absent	″	single row	sandy brittle test
P. lapidosa	—	SA – NSW	embedded	″	″	0;0	″	preserved body purple; massive sandy colony
P. watsonia n.sp.	—	Bass Strait	″	straight	″	″	″	atrial apertures posterior; massive sandy colony
P. sagamiensis	IWP	Gladstone – Townsville	posteriorly embedded	straight, vertical	″	″	2–3 rows	flexible sometimes sandy test

[1]IWP, Indo-West Pacific. [2]Range given anti-clockwise around the continent.

Polyandrocarpa australiensis Kott, 1952
(Fig. 101)

Polyandrocarpa australiensis Kott, 1952, p.249.

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, WAM 1233.83; Cockburn Sound, WAM 922.83). Queensland (Gladstone Harbour, QM G9484 G12710–1 GH208; Abbot Point, QM GH684; Townsville, QM GH1845).

PREVIOUSLY RECORDED: Western Australia (Triggs I., Cockburn Sound — Kott 1952).

The species is most often recorded at shallow depths where collecting has been assiduous. It has been recorded at 15 m about 24 km off Dongara (WA). It very likely has a wider range around the coast of Australia, although it appears not to be present on the Great Barrier Reef and may be found to favour mainland locations.

DESCRIPTION

EXTERNAL APPEARANCE: Small zooids 0.5 to 1 cm high are joined by basal stolons and are sometimes joined together along their length by test hairs and sand. The zooids are longer than they are wide, and narrow posteriorly to a stalk of varying thickness. The posterior stalk is sometimes thick and wedge-shaped or resembles a tap root, with secondary stolons branching off it; in other specimens it is a narrow, stem-like structure. The stalk is often as long as, or longer than, the zooid. There are irregular hairs and 'tag-like' processes, less crowded but longer posteriorly, projecting from the test through the sand-coating in some of the Queensland specimens (QM G9484). The apertures are sessile, on opposite sides of the upper surface. The test around the apertures is free of sand and wrinkled, with some very fine, short test hairs projecting from it. The test, when the sand is removed from it, is a thin, translucent membrane through which the blackish grey body wall shows. Small specimens appear as blackish blisters joined by basal stolons attached to the substrate. Buds develop in the basal stolons. The terminal branches of test vessels are slightly expanded into ampullae, which are scattered rather sparsely in the surface. They often contain darkly pigmented particles.

INTERNAL STRUCTURE: The body wall has a thin mesh of circular muscles around some fine longitudinal bands that fade out posteriorly. There are about 30 simple, crowded branchial tentacles. The dorsal tubercle is small, with a transverse slit. The dorsal lamina is long, the oesophagus opening at the posterior end of the body.

There are 4 branchial folds on each side of the body, although these are low and rounded and tend to flatten out posteriorly. Sometimes there are only 3 folds on the left. The internal longitudinal vessels in the interspaces are especially delicate and often irregular and branching. Branchial formulae for several zooids are: E0(3) 0(5)1(8)1(8)1DL; E0(4)1(5)1(6)1(5)1DL; DL2(7) 2(7)3(8)2(5)2E. There are 2 to 5 small, oval stigmata per mesh. Delicate parastigmatic vessels are often present.

The gut forms a wide round (almost circular) loop in the posterior end of the body, with the rectum extending anteriorly at a sharp angle to it. As the zooid lengthens with age, the gut loop tends to extend obliquely backwards from the oesophageal opening and the angle of the rectum to the loop becomes obtuse. The oesophagus is of moderate length. The stomach is short, narrow at the cardiac end and very wide at the pyloric end, with 8 to 12 broad, shallow folds. A caecum from the distal end of the gastric suture line curves into the gut loop. A gastro-intestinal connective extends from the base of the caecum to the intestine, enclosing a circular, flat-topped endocarp in the pole of the gut loop. The anal border is divided into about 12 round lobes. The gut is attached to the body wall by an almost continuous membrane that extends along the inner curve of the loop. There is also a strong ligament from the postero-ventral end of the stomach.

The gonads are spherical to oval. They are arranged in a row on each side of the endostyle, 5 to 7 on the right and 2 to 4 on the left, with the short gonoducts directed dorsally. Each gonad consists of a short, wide, flask-shaped ovary with up to 6 pairs of pyriform male follicles arranged in 2 rows beneath the ovary, the vasa efferentia passing around each side to meet at the base of the common male opening on the surface of the short, wide oviduct or on the top of the ovary. The species is viviparous, and large-tailed larvae are present in the peribranchial cavity of some specimens.

There are a few small endocarps scattered amongst the polycarps, in addition to the one enclosed in the gut loop.

REMARKS: The species resembles other species of *Polyandrocarpa* in its *Polycarpa* characters. Of other species of the genus that have a single row of gonads on each side of the endostyle, it least resembles *P. lapidosa* and *P. watsonia*, whose long zooids lying parallel to each other, form compact colonies. *Polyandrocarpa abjornseni* and *P. simulans* resemble the present species in their internal structure, but are distinguished by their compact colonies. *Polycarpa triggiensis* has similar colonies, but its long styelid-type gonads suggest a different phylogeny from that of the present species.

FIG. 101: *Polyandrocarpa australiensis* — **a**, **b**, external appearance (QM G9484); **c**, stomach (QM GH684); **d**, internal body wall (QM GH684); **e**, gonad; **f**, anal border. (Scales: **a**, **b**, 2.0 mm; **c**, 0.25 mm; **d**, 1.0 mm; **e**, **f**, 0.1 mm).

Polyandrocarpa lapidosa (Herdman, 1891)
(Fig. 102; Pl.IVd,e)

Goodsiria lapidosa Herdman, 1891, p 637; 1899, p.90.
Polyandrocarpa lapidosa: Kott, 1952, p.250; 1972b, p.184; 1976a, p.76; (not: 1964, p.134, < *P. sagamiensis*). Millar, 1963, p.730.

DISTRIBUTION

NEW RECORDS: South Australia (St Vincent Gulf, QM G9318; Pearson I., QM GH1315; E Great Australian Bight, QM GH2381). Victoria (Bass Strait, QM GH 2197, NMV H637; Wilson's Promontory, QM G12721; Portland Harbour, QM GH35, NMV F51595). New South Wales (Port Jackson, NMV F51725; Port Kembla, QM G9601).

PREVIOUSLY RECORDED: South Australia (Investigator Strait — Kott 1972b). Victoria (Port Phillip Bay, Western Port — Millar 1963, Kott 1976a). New South Wales (Port Jackson — Herdman 1899, Kott 1952).

The species is found on hard, sometimes vertical, surfaces where water currents are strong. It has been recorded down to 25 m.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are massive and rounded, either potato-shaped, like thick plates, or hemispherical, and up to at least 9 cm in diameter and 2 to 5 cm thick. The test is white and cartilaginous but usually has embedded and adherent sand. Zooids are arranged parallel to one another in long compartments separated by thin partitions of usually sandy, and often brittle, test. The upper surface is interrupted by zooid apertures and is sometimes raised into swellings over the anterior ends of the zooids. Colonies are usually fixed to the substrate by their basal surface, although occasionally a thick colony is apparently not fixed, as zooids open all around the surface.

In the living colonies, the brown-orange colour of the zooids can be seen through the evenly spaced pairs of open apertures on the upper surface. In preservative, the zooids are always a red-purple or cyclamen colour.

The vegetative process in this species is not yet understood. Small zooids are found at the top of the colony amongst the anterior ends of the larger zooids (see Millar 1963).

INTERNAL STRUCTURE: The individual zooids are up to 3 cm long and relatively narrow. They have long, cylindrical terminal branchial siphons. The long atrial siphons projecting forward from about the middle of the dorsal surface open level with the branchial aperture. The rim of each aperture is divided into 4 not very conspicuous lobes. The small dorsal tubercle has a simple U-shaped or oblique longitudinal opening. The body wall adheres closely to the sandy, brittle test partitions within the colony, and the musculature is delicate. There are up to about 40 simple tentacles at the base of the branchial siphon, a wide prebranchial area, and a long neural ganglion that stretches to the base of the atrial siphon.

The 4 narrow folds on each side of the branchial sac have up to 7 internal longitudinal vessels on the folds and 1 to 3 in the interspaces. The

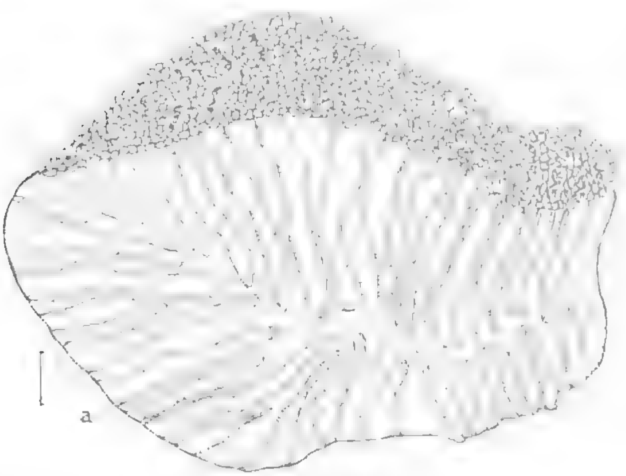


FIG. 102: *Polyandrocarpa lapidosa* (QM G12721) — a, section through colony showing position of zooids; b, internal body wall, left side. (Scales: a, 5.0 mm; b, 2.5 mm).

longitudinal vessels in zooids from two colonies are arranged according to the following formulae: DL0(4)1(3)2(5)3(3)2E; DL0(10)1(3)1(7)1(4)1E. The second and fourth folds are often only rounded ridges. The stigmata are short, only sometimes with parastigmatic vessels, and there are 5 per mesh.

The gut forms a simple arc from the posterior oesophageal opening, curving up the left side of the long body into the proximal part of the atrial aperture. The oesophagus is short. The stomach is short and rounded, with 12 to 18 internal glandular folds. The anal border has 10 to 20 small, rounded lobes.

There are 6 to 9 sac-like to elongate gonads in a row on each side of the endostyle.

There are no endocarps on the body wall.

REMARKS: The species is distinguished by its large, compact colonies; thin test partitions between the zooids; long zooids; short, almost spherical, stomach; and the very characteristic colour of the zooids. It appears to be closely related to *Polyandocarpa watsonia* n.sp., differing primarily in the position of the atrial siphon, length of gut loop and length of stomach.

Millar (1963) has discussed the relationship between this species and *P. anguinea* (Sluiter) from South Africa. His conclusion that the species can be distinguished by the longer stomach of the South African species is confirmed here.

Polyandrocarpa sagamiensis Tokioka, 1953 (Fig. 103)

Polyandrocarpa sagamiensis Tokioka, 1953a, p.246.
Polyandrocarpa rollandi Tokioka, 1961, p.116.
Polyandrocarpa lapidosa: Kott, 1964, p.134
Polyandrocarpa anguinea: Vasseur, 1967a, p.113.

DISTRIBUTION

NEW RECORDS: Queensland (Hervey Bay, QM GH9603; Yeppoon, QM GH2227; Mackay, QM G9594).

PREVIOUSLY RECORDED: Queensland (Tannum Sands — QM G4949, Kott 1964; Townsville — Kott 1964). New Caledonia (Tokioka 1961). Japan (Sagami Bay — Tokioka 1953a). Indian Ocean (Vasseur 1967a).

The species was taken intertidally at Australian locations and at 15 m in Sagami Bay.

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are upright and parallel to one another in the colony, free at their anterior ends but compact basally. Apertures are on long, conical siphons that protrude from the upper surface of the colony. The branchial aperture is terminal and the atrial aperture originates from about halfway down the dorsal surface. Zooids are about 2 cm long. The test is thin and flexible. The colony from Yeppoon has a layer of sand embedded in it. There are thin partitions of test between the embedded zooids in the basal half of the colony.

INTERNAL STRUCTURE: The body wall is very thin and translucent, with an outer layer of fine, circular fibres. The internal longitudinal bands are inconspicuous and irregular. The tentacles are very fine and are not crowded. There is a deep peritubercular V and a small tubercle with a C-shaped slit. The dorsal lamina is short, only half the length of the branchial sac.

There are 4 narrow branchial folds. Posteriorly they curve dorsally to open around the oesophageal opening, which is about halfway down the branchial sac. Internal longitudinal vessels are arranged according to the following formula: E6(12)5(12)4(13) 4(9)3DL. There are 2 or 3 rather short stigmata per mesh and only very occasional parastigmatic vessels.

The gut is covered by a fleshy layer of body wall, but is only very lightly attached by a few short ligaments. It forms a simple, vertical loop, but tends to be rather mobile and flexible. The oesophagus is of moderate length. The stomach occupies half of the ascending limb of the loop and is spherical to pear-shaped, with narrow, parallel longitudinal folds. It narrows at the cardiac end. Tokioka (1953a) refers to a minute stomach caecum, but this was not detected in the present specimens. The anal border is divided into short, rounded lobes.

The gonads are elongate and 14 to 25 are crowded in 3 rather irregular rows over the whole of the right side of the body, with 9 to 14 in 1 or 2 rows anterior to the gut loop on the left. Paired rows of irregularly lobed male follicles are present under the long ovarian tube. The gonads are oriented toward the atrial opening, and are lightly attached to the body wall with ligaments along their length

There are no endocarps on the body wall.

REMARKS: The form of the colony, with the zooids separate at their anterior ends; the long siphons; the lightly attached gut loop; the short stomach; and the gonads that occur all over rather than being limited to the ventral part of the body wall, are all distinctive characters.

Tokioka (1961) believed *P. rollandi* to be distinct from *P. sagamiensis*; however, the gut loop, the position of the atrial aperture and the number of gonads are all variable within a single colony and do not indicate an interspecific difference.

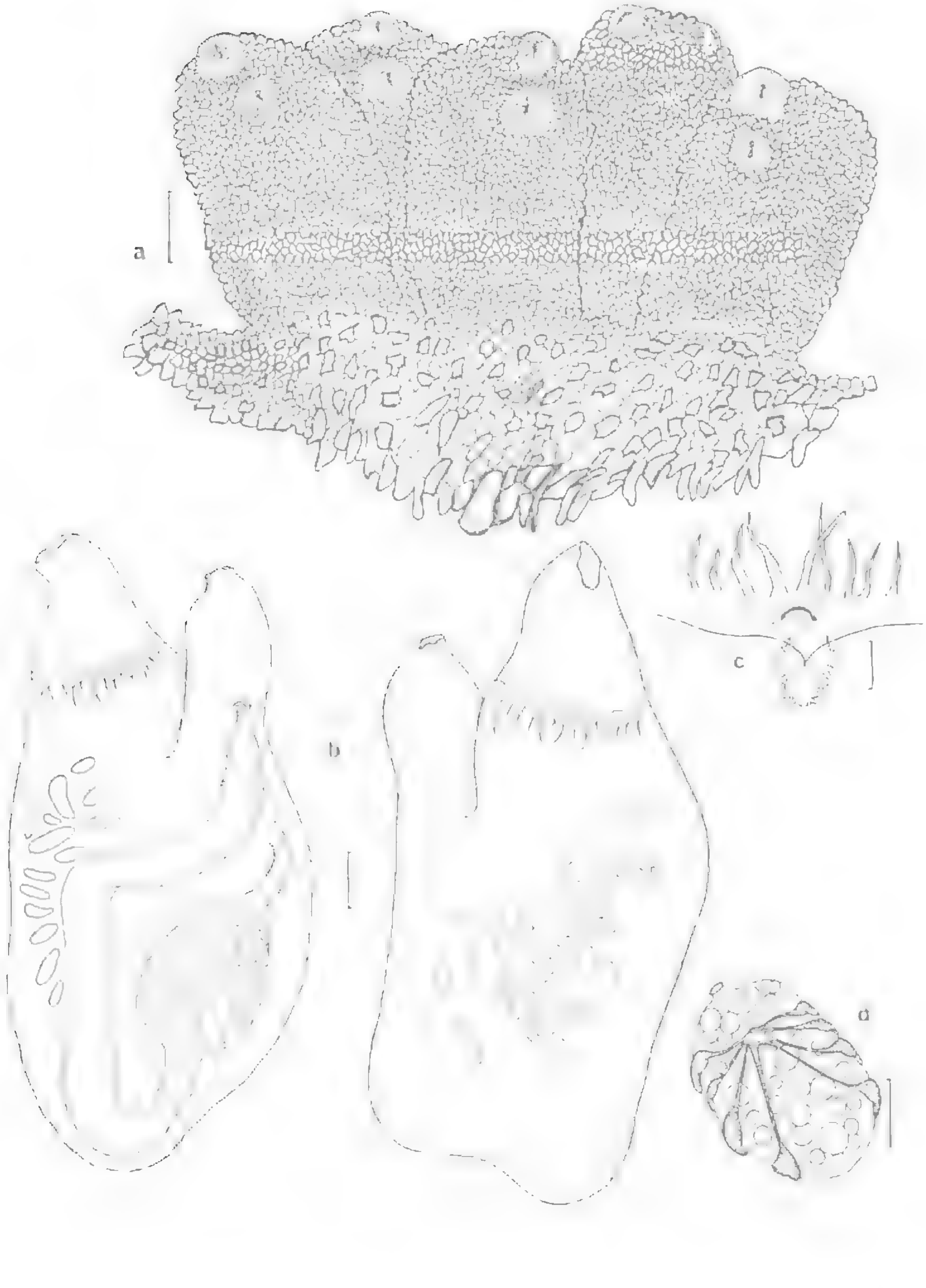


FIG. 103: *Polyandrocarpa sagamiensis* (QM GH2227) — **a**, colony; **b**, left and right sides of body; **c**, dorsal tubercle; **d**, gonad. (Scales: **a**, 5.0 mm; **b**, 2.0 mm; **c**, **d**, 0.25 mm).

Polyandrocarpa colligata Sluiter, 1913 and *P. robusta* Sluiter, 1915 have gonads confined to a single row each side of the endostyle, and their zooids are more deeply embedded than are those of the present species.

Polyandrocarpa simulans Kott, 1972
(Fig. 104)

Polyandrocarpa simulans Kott, 1972b, p.184.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: South Australia (Great Australian Bight, Investigator Strait — Kott 1972b).

DESCRIPTION

EXTERNAL APPEARANCE (after Kott 1972b): The colonies are compact, the zooids, embedded in the thick, tough common test, protruding only very slightly from the surface. Each individual is more or less spherical, about 1.0 cm diameter. The apertures are on low rounded swellings on the upper surface of the body, separated by about one-third of its length. There is a slight encrustation of sand on the surface of the colony. Living specimens are reddish brown tipped with black. Preserved specimens are black.

INTERNAL STRUCTURE: The body wall is very muscular, with almost continuous layers of longitudinal and outer circular muscles that are especially crowded around the apertures. The dorsal tubercle is large and circular with a reverse C-shaped slit.

The branchial sac is very tough with 4 low folds, each crowded with thick internal longitudinal vessels arranged according to the following formula: E1(6)1(9)1(8)1(9)ODL.

The gut forms a closed loop in the posterior end of the body and the rectum extends anteriorly, forming an angle with the descending limb of the loop. The gut loop encloses a flat-topped endocarp. The stomach is short (about half the length of the ascending limb of the gut loop) and has internal glandular folds. The anal border has about 4 wide, shallow and sometimes indented lobes.

Up to 5, scattered, flask-shaped gonads are embedded in the body wall on the left. There are up to 9 on the right. They open by short ducts into the atrial cavity. Beneath the ovaries are 5 or 6 pairs of testis follicles.

There are no endocarps on the body wall outside the gut loop.

REMARKS: The species is closely related to *Polycarpa nigricans* in most characters except its better developed colonial habit, associated small size and sessile apertures. Its tough, compact colonies contrast with those of *Polyandrocarpa australiensis* in which the zooids are connected by stolons. The colony resembles that of *P. abjornseni*, but *P. simulans* is distinguished by its scattered and more numerous gonads and the absence of a stomach caecum, more numerous internal longitudinal vessels (especially in the interspace) and the presence of external siphons.

FIG. 104: *Polyandrocarpa simulans*, colony. (Scale: 2.5 mm).

Polyandrocarpa sparsa n.sp.
(Fig. 105)

DISTRIBUTION

TYPE LOCALITY: New South Wales (North Solitary I., 6 m, coll. P. Frederickson, 1976, holotype QM G9591).

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of sandy, upright zooids connected to one another by common basal stolons. Accessory root-like projections at the posterior end of each zooid contribute to their adhesion to the substrate and help keep the zooids in an upright position. Each zooid also adheres to it neighbours along the sides of its body to form a loose, rather than compact, colony. The branchial aperture is terminal, protruding slightly. The atrial aperture is antero-

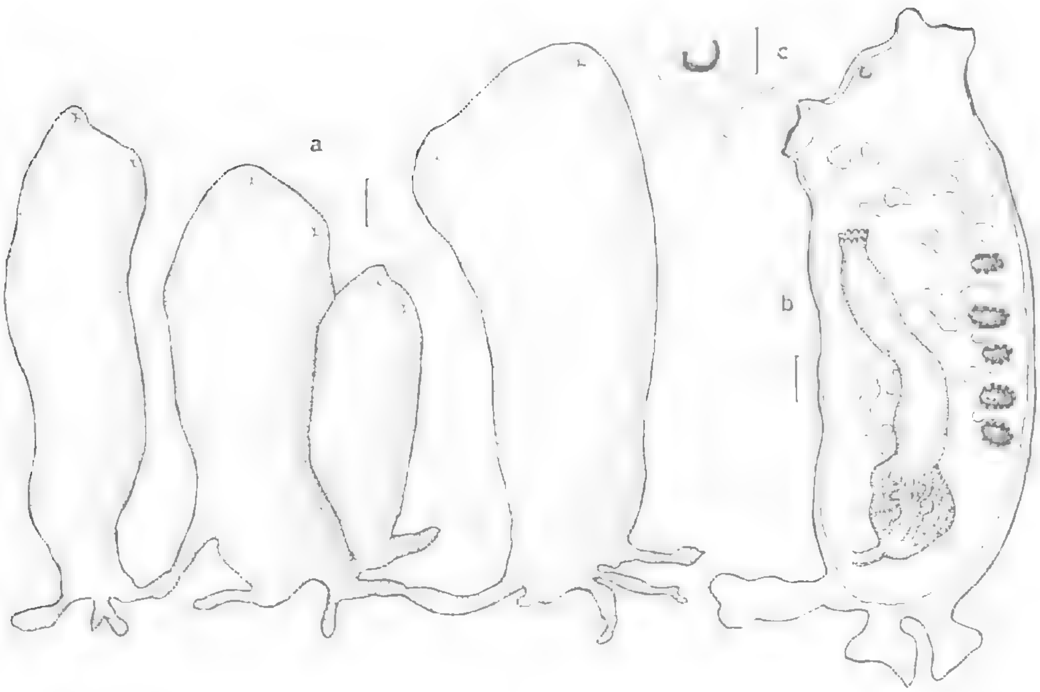


FIG. 105: *Polyandrocarpa sparsa* n.sp. (QM G9591) — a, colony; b, left side of zooid; c, dorsal tubercle. (Scales: a, 1.5 mm; b, 1.0 mm; c, 0.25 mm).

dorsal at the widest part of the laterally flattened, wedge-shaped body, which narrows slightly toward the posterior end. The test is very thin, and brittle with embedded sand.

INTERNAL STRUCTURE: The body wall is extremely thin and colourless and is very closely adherent to the test. There is a thin outer layer of circular musculature and some fine inner longitudinal bands. Circular muscles around the siphons are more conspicuous than on other parts of the body. There are 40 simple, curved branchial tentacles. The dorsal tubercle is a rounded cushion with a shallow, sickle-shaped slit and there is a long dorsal ganglion. The dorsal lamina is long and straight.

The branchial folds are low and rounded, with crowded internal longitudinal vessels. The longitudinal vessels are further apart in the interspaces; nevertheless, there are only 1 or 2 stigmata per mesh in the centre of the branchial sac. The internal longitudinal vessels are arranged according to the following formula: E8(11)7(12)5(12)5(11)7DL0(9)6(12)4(12)4(7)7E. Parastigmatic vessels cross the stigmata. There is a wide space between the dorsal lamina and the first fold on the right; on the left, the dorsal lamina is close to the dorsal fold.

The gut is not looped, but extends forward in a simple curve from the oesophageal opening at the posterior end of the branchial sac. The stomach is short and almost spherical. It has about 18 deep, longitudinal glandular folds that extend its whole length on the mesial side, but on the parietal side, about 5 folds originate along each side of the suture line and extend obliquely to the distal end of the stomach. The stomach folds are sometimes branched, and from the outside of the stomach, appear to be corrugated and interrupted. There is no caecum. There are about 9 small, rounded lobes on the rim of the anal aperture.

The gonads are elongate polycarps lying parallel to one another in a row along each side of the endostyle. Small rounded endocarps are present on the body wall, more crowded along each side of the endostyle than on the dorsal half of the body wall.

REMARKS: The shape of the zooids, and the body wall, branchial sac and gut loop are all exactly as in *Polycarpa procera*. The zooids are very much smaller than those of *P. procera*.

however, and are colonial rather than solitary. The shape and course of the gut loop also resembles that of *Polyandrocarpa lapidosa*, but the compact, solid colony of the latter species, with its embedded purple-coloured zooids, is quite different from the rather loose colony of the present species. A further characteristic of *P. sparsa* is the small number of stigmata per mesh, which also distinguishes it from *P. lapidosa* with its approximately 5 stigmata per mesh.

The characteristics that this species shares with *Polycarpa procera* are so striking that it is probable that its phylogenetic relationships with that species are closer than those with other *Polyandrocarpa* spp., thus supporting the view that the genus is a polyphyletic group.

Polyandrocarpa triggiensis Kott, 1952
(Fig. 106)

Polyandrocarpa triggiensis Kott, 1952, p.248.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (Triggs I. — holotype AM Y1574, paratypes AM Y1575 Kott 1952).

DESCRIPTION

EXTERNAL APPEARANCE: Zooids are delicate and upright, about 4 mm long. They are joined by basal stolons. The branchial aperture is terminal and the atrial aperture is about one-third of the body length along the dorsal surface. The apertures are on small protruberances. The test is thin, and brittle with encrusted sand.

INTERNAL STRUCTURE: The body wall is moderately muscular, and whitish pink in preservative. The branchial tentacles are crowded. The dorsal tubercle is a small cushion with a simple transverse slit. The dorsal lamina is moderately long, the oesophagus opening about two-thirds of the distance down the dorsal surface.

In the branchial sac are 4 rounded folds with very crowded internal longitudinal vessels. The second dorsal fold on each side is less well developed than the others. Internal longitudinal vessels are arranged according to the following formulae: DL0(12)0(4)0(8)1(6)0E. They are so crowded that there are only 2 or 3 stigmata in each mesh, crossed by parastigmatic vessels.

The gut forms a straight, simple loop, oriented across the posterior end of the body. The long rectum curves anteriorly almost in line with the loop, which tends to project posterior to the branchial sac. The stomach is pyriform, widest at the pyloric end. It has 17 glandular folds. The caecum is very long, extending forwards from the gastric suture and spiralling one and a half times in the gut loop. The anal border is smooth and bilabiate.

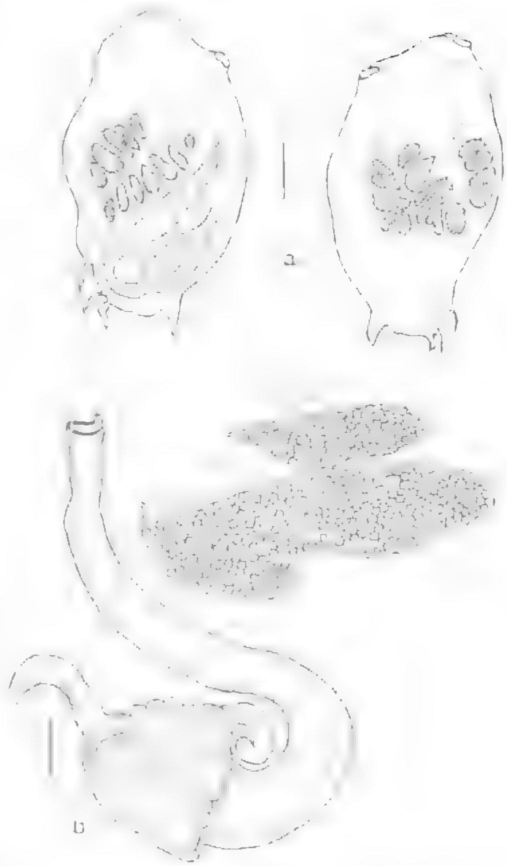


FIG. 106: *Polyandrocarpa triggiensis* (AM Y1574) — a, left and right sides of body from outside, single row of testis follicles seen beneath ovaries; b, gut, gonads and endocarp on left side of body. (Scales: a, 1.0 mm; b, 0.5 mm).

The gonads are long, each consisting of a long tubular ovary and one row of about 6 long male follicles set transversely beneath the ovary. There are 1 or 2 gonads on the left and 3 or 4 on the right. On the left, they are anterior and parallel to the gut loop. On the right, they are arranged around the postero-ventral corner of the body and extend up toward the atrial aperture. The vas deferens extends along the mesial surface of the ovary to open with the oviduct at the distal end.

Large endocarps are present between the gonads, but not in the gut loop.

REMARKS: The species is distinguished from other species of this genus by its relatively long and few gonads, reminiscent of cnemidocarp- rather than polycarp-type organs.

Polyandrocarpa watsonia n.sp.
(Fig. 107)

DISTRIBUTION

TYPE LOCALITY: Victoria (Rams Head, 28 km S of Mallacoota Inlet, 6m, coll. J.E. Watson, holotype NMV H170).

DESCRIPTION

EXTERNAL APPEARANCE: The colony forms a thick, curved upright lamella, slightly convex on one side and concave on the other, with a long, curved upper outer border and a shorter basal edge by which it is fixed. The colony is 6 cm long and 4 cm high, with a maximum thickness of 3 cm in the middle of the colony. The convex side is continuous with the upper surface. Both are sandy, and marked with slightly rounded prominences on which there are inconspicuous atrial openings. The upper surface of the lamella overlaps the less sandy concave side from which naked branchial apertures protrude. Closely packed, parallel zooids extend obliquely from the concave surface (with branchial openings) through to the upper and convex surfaces (with the atrial openings). A single layer of sand impregnated test is present between adjacent zooids.

The vegetative process is not understood. The form of the colony suggests that new zooids may develop between the branchial and atrial siphons of the parent individuals. Millar's (1963) observation that smaller zooids were present at the surface of colonies of *P. lapidosa* would not be at variance with this hypothesis.

INTERNAL STRUCTURE: The zooids are very long, especially in the centre of the colony, although they are shorter toward the upper border. The branchial aperture is terminal; the posteriorly directed atrial aperture is on a short siphon at the postero-dorsal corner of the individual. The body musculature is inconspicuous except around the apertures, where there are circular muscles. The body wall adheres closely to the test. The prebranchial area is extensive and there is a large V-shaped peritubercular area with a circular dorsal tubercle at the base of the V. The opening on the dorsal tubercle is a simple, slightly curved, longitudinal slit. The very long dorsal ganglion has a median dorsal nerve extending from its posterior end to fan out in 3 branches anterior to the base of the atrial siphon. From the anterior end of the ganglion, about 8 branches extend across the peritubercular and prebranchial areas. There is a ring of simple tentacles at the base of the branchial siphon. The dorsal lamina is a long, plain-edged membrane.

There are 4 branchial folds on each side of the body, with 4 or 5 longitudinal vessels on each fold and 2 or 3 vessels between the folds. There are 3 stigmata per mesh between the folds. Parastigmatic vessels are present. The stigmata are particularly long and rectangular.

The gut forms a simple, horizontal loop across the posterior end of the body. The oesophagus is fairly long, and the stomach is of only slightly greater diameter than the intestine. It has regular, longitudinal glandular folds. The intestine forms the anterior limb of the gut loop and extends dorsally and slightly posteriorly to open in a 2-lipped anus at the base of the atrial siphon, adjacent to the opening of the oesophagus.

Oval to elongate gonads lie in a row on each side of the endostyle, 9 on the right and 6 on the left. The short gonoducts open from the dorsal end of each gonad. The gonads are the usual polycarp-type with a double row of male follicles beneath each ovary.

REMARKS: This species closely resembles *Polyandrocarpa lapidosa* (Herdman, 1899) and *P. anguinea* (Sluiter, 1898a) (see Millar 1963). *Polyandrocarpa watsonia* is distinguished from those species and others of this genus mainly by the position of the atrial siphon at the postero-dorsal corner of the body and the fact that the atrial apertures are on the opposite side of the colony to the branchial openings. The course of the gut is a consequence of the position of the atrial aperture. Thus, in *P. lapidosa*, there is no gut loop and the intestine and rectum extend in a gentle arc to the anteriorly positioned excurrent aperture. In the present species, there is a simple, straight gut loop, the anus opening near the oesophageal opening at the base of the posteriorly positioned atrial siphon. The orientation of the zooids, with their anterior ends towards the substrate and posterior ends extending obliquely upwards, is a further consequence of the posteriorly positioned atrial aperture.

Other characters distinguishing the present species also appear to be consequent upon the position of the atrial siphon. The dorsal ganglion, which in *P. lapidosa* and *P. anguinea* is relatively short, in *P. watsonia* is about half the length of the long dorsal surface, accommodating the greater part of the distance between the two siphons.

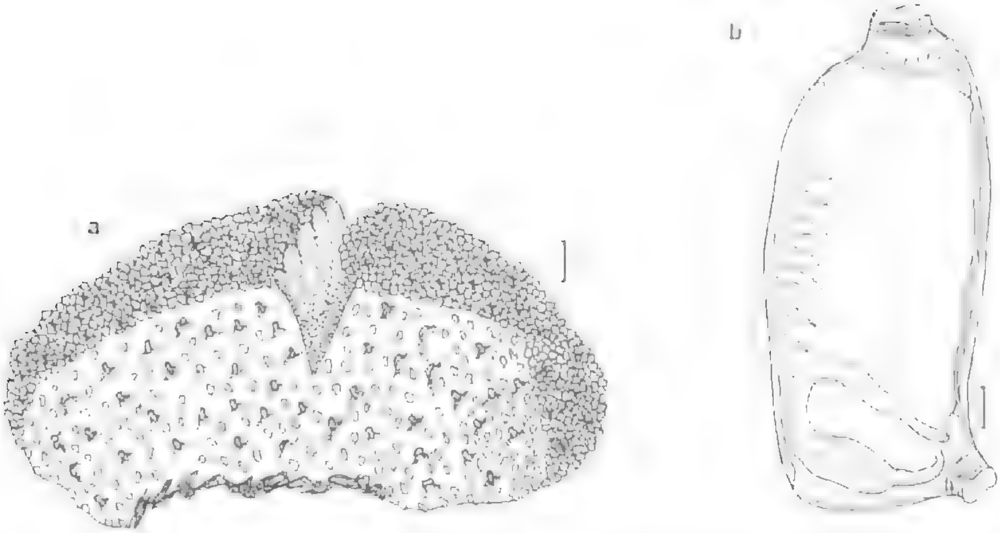


FIG. 107: *Polyandrocarpa watsonia* n.sp. (NMV H170) — **a**, colony with wedge removed to show position of zooids, with conspicuous branchial openings on the concave side of the colony and atrial openings obscured by sand on upper surface and convex side; **b**, single zooid. (Scales: **a**, 2.5 mm; **b**, 2.0 mm).

It is possible that the characteristics of this species are a response to an environment where an adaptation to a unidirectional current flow is an advantage, the concave side, with branchial apertures possibly being directed towards the oncoming current.

Genus **Oculinaria** Gray, 1868

Type species: *Oculinaria australis* Gray, 1868

The genus is monotypic and indigenous to temperate waters of Australia. It closely resembles *Polyandrocarpa*, differing only in the absence of gonads from the right side of the body.

Oculinaria australis Gray, 1868
(Fig. 108)

Oculinaria australis Gray, 1868, p.564. Herdman, 1886, p.323; 1891, p.638. Michaelsen, 1904a, p.18. Hartmeyer, 1909, p.1377; 1918, p.385. Hartmeyer and Michaelsen, 1928, p.346. Kott, 1952, p.251; 1972a, p.29; 1972b, p.184; 1975, p.11. Millar, 1963, p.734; 1966, p.369.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 581-2.31 1227.83; Wonnerup, WAM 171.75; Dongara, WAM 1228.83). Tasmania (Stanley, TM D710). Victoria (Rams Head, QM G9592; off Lakes Entrance, QM G11857). New South Wales (Port Jackson, attached to *Chorizocormus leucophaeus* Herdman, 1899 < *Chorizocarpa sydneyensis* AM U284).

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound to Albany — Gray 1868, Hartmeyer and Michaelsen 1928, Kott 1952, Millar 1963). South Australia (Great Australian Bight — Kott 1972b 1975; West I., Wright I. — Kott 1972a). Victoria (Port Phillip Bay — Millar 1966).

The species is taken in water down to 44 m, growing around stems of weed etc.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are massive rounded or cylindrical clumps. Zooids are crowded, embedded for most of their length but with their anterior ends sometimes projecting from the surface of the colony. The apertures, close together on the upper free surface of the zooid, are usually depressed into the surface so that the surrounding test stands up around them in rounded ridges, which are opaque and usually sand-free. In the test partitions within the colony, there is often no or very little sand, but elsewhere the test is completely impregnated with sand and is accordingly rigid and brittle.

Nothing is known of the vegetative process.

INTERNAL STRUCTURE: The body is more or less spherical. The body wall is thin, with delicate musculature except around each siphon, which has conspicuous circular muscles and short longitudinal bands terminating at its base. The longitudinal muscles on the atrial siphon are sometimes more conspicuous than those on the

FIG. 108: *Oculinaria australis* — a, part of a colony (QM G11857); b, zooid removed from test (WAM 581/2.31); c, gut (QM G9592). (Scales: a, 2.0 mm; b, 0.5 mm; c, 0.25 mm).

branchial siphon. There are 32 branchial tentacles of various lengths. The dorsal tubercle is a circular cushion lying in a small peritubercular area, with a symmetrical, posteriorly directed U-shaped slit, with both horns turned out. The dorsal lamina is very short and the branchial sac is deeply curved.

There are 4 to 10 internal longitudinal vessels on each of the 4 branchial folds and 2 to 4 in the interspace. A branchial formula is: E0(4)4(8)4(8)4(8)0DL1(10)2(8)4(8)4(6)5E. There are 2 or 3 short stigmata per mesh.

The gut loop is variable, depending on the length of the zooid. In short, spherical zooids it forms a simple, straight and rather open loop (WAM 171.75). In larger zooids, the rectum turns anteriorly to form an acute angle with the gut loop; or the gut follows a slightly sinuous S-shaped course anteriorly to the atrial aperture (Kott 1952). The stomach is short and elliptical, with up to 18 oblique folds that meet the suture line on its anterior edge. There is no caecum. The anal border has small serrations. A gastro-intestinal duct crosses from the distal end of the stomach to the intestine. It is expanded into an elongate gastric reservoir about halfway along its length.

To the right of the endostyle is a single row of up to 9 long, more or less parallel gonads, each oriented toward the atrial aperture. Testis follicles are in a paired row beneath each ovary.

REMARKS: The species is distinguished principally by its colony form, and by the single row of gonads on the right side of the endostyle.

Genus **Eusynstyela** Michaelsen, 1904a

Type species: *Michaelsenia tincta* Van Name, 1902

The genus has vegetatively reproducing species with the usual styelid complement of 4 branchial folds. The hermaphrodite gonads are reduced and, although there are flask-shaped ovaries with numerous eggs, only one or two male follicles are associated with each ovary. The zooids are small, usually embedded in the test. The apertures are not conspicuously lobed.

The zooids resemble individuals of *Monandrocarpa*, the genera being separated only by the colonial habit of *Eusynstyela*. The gonads of the genus *Polyzoa* resemble those of the present genus, but *Polyzoa* has a further reduction of the branchial sac, with almost complete loss of branchial folds, and a very much smaller ovary. *Eusynstyela* is also related to *Amphicarpa* and *Stolonica*, in which there are some branchial folds, though their number is reduced. However, there is a tendency for the gonads to separate into male and female components in the last two genera.

The genus is not diverse, and there are few interspecific morphological differences. This may possibly be the result of convergence in these small, simplified organisms. Only a single species of the genus has been recorded from Australian waters.

Eusynstyela tincta (Van Name, 1902), *E. gravei* Van Name, 1931 and *E. floridana* (Van Name, 1921) are related species from the western Atlantic. *Eusynstyela tincta* and *E. gravei* resemble *E. latericius* in most characters, although they have a greater number of stigmata in each mesh. The zooids of *E. floridana* are joined by stolons rather than being embedded in the common test (see Van Name 1945). *Polyandrocarpa maxima* (Sluiter, 1904), from Indonesia, may be a species of *Eusynstyela* (see *Polyandrocarpa*, above)

In his description of *E. tincta*, Van Name (1945) has drawn attention to the way the gonads project into the test beyond the general surface of the ventral region in small knob-like evaginations of the body wall, which are constricted at their base. This tendency for the gonads to be associated with the test is reminiscent of species of *Seriocarpa* Diehl, 1969 in which the gonads are embedded in a rod of test that projects into the body along the mid-ventral line of the body. The possibility of a relationship between *Seriocarpa* Diehl and *Eusynstyela* is further supported by their very similar morphology, including the form of the gonads and their position in a simple row on each side of the endostyle. However, *Seriocarpa rhizoides* Diehl, 1969 reproduces vegetatively by division of the body rather than the parietal budding of *Eusynstyela* and other Polyzoinae (Berrill 1935b) and the morphological resemblance between *Seriocarpa* and *Eusynstyela* may be the result of convergence. *Seriocarpa rhizoides* Diehl, *S. cristata* Millar and *S. littoralis* Millar have all been recorded from the tropical western Pacific (Millar 1975). *S. littoralis* has also been taken from Indonesia (ZMA V.TU1019.6).

Eusynstyela latericius (Sluiter, 1904)
(Fig. 109; Pl.IVf,g)

Gynandrocarpa latericius Sluiter, 1904, p.94.
Eusynstyela latericius: Van Name, 1918, p.105.
Polyandrocarpa (Eusynstyela) latericius: Tokioka, 1952, p.115; 1955a, p.213; 1967b, p.400. Millar, 1963, p.732; 1975, p.275. Kott, 1964, p.133.
Gynandrocarpa imthurni Herdman, 1906, p.330.
Polyandrocarpa tincta: Vasseur, 1967a, p.114.

DISTRIBUTION

NEW RECORDS: Western Australia (Cape Preston, WAM 1208.83; Port Hedland, WAM 1207.83 1210.83; Dampier Archipelago, WAM 1206.83 1209.83; Kendrew Archipelago, WAM 182.75). Queensland (Moreton Bay, QM GH345; Tallebudgera Creek, QM GH2237; Heron I., QM G9424 G10086 GH2047–8 GH2714–6 GH3099; Wistari Reef, QM GH1394 GH2080; Yeppoon, QM GH2236; Townsville; Murray I., QM GH306; Lizard I., QM GH2076–85).

PREVIOUSLY RECORDED: Western Australia (NE Port Hedland — Millar 1963). Queensland (Moreton Bay, Bowen — Kott 1964). Arafura Sea (Tokioka 1952). Indonesia (Sluiter 1904). Philippines (Van Name 1918, Millar 1975). Vietnam (Tokioka 1967b). Gulf of Siam (Millar 1975). Indian Ocean (Vasseur 1967a). Sri Lanka (BM 1907.8.30.26 Herdman 1906). Japan (Tokioka 1955a).

The species has a wide Indo-West Pacific range, down to 82 m depth. It is often found as an epibiont on other stolidobranch ascidians.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies form rather flat mats or sheets up to 3 mm thick, with zooids opening on the upper surface; or thick, flat lobes with zooids opening around the outer surface. These lobes narrow basally, where they are fixed to the substrate. In the thin, sheet-like investing colonies, the dorso-ventrally flattened zooids show as oval swellings in the thin common test, with the apertures at opposite ends of the upper surface of each individual . In thicker colonies, the crowded zooids tend to be laterally flattened and zooids may either be completely embedded with only their apertures protruding on cones or the whole dorsal surface of each zooid may project (QM GH3099). Thin colonies have a quite transparent test and body wall, through which the body organs can be seen from the flat base of the colony. Thicker colonies are completely opaque. The test is always tough and naked. In preservative, it is white and/or pinkish white or carmine. Living specimens are a purple, red or raspberry colour. The pigmentation is more intense around the apertures. A pale strip along each side of the mid-line between the apertures, sometimes creates a symmetrical pattern on the surface.

INTERNAL STRUCTURE: The zooids are about 1 cm long. They are rounded in section in the thicker, free-standing lobes, but in the thin, sheet-like colonies they are more or less dorso-ventrally flattened, around a plane that on the right is closer to the endostyle, and on the left is closer to the dorsal lamina. The body wall is thin, sometimes closely adhering to the test. The musculature is very delicate and is conspicuous only around the apertures. There are 24 short branchial tentacles. The dorsal tubercle is a simple, vertical slit in a V-shaped peritubercular area. The dorsal lamina is long, the oesophageal opening being at the posterior end of the pharynx.

The branchial folds are low and rounded, consisting of crowded internal longitudinal vessels along slight internal elevations of the pharyngeal wall. The branchial folds are straight. Branchial formulae are: E0(4)2(9)1(4)1(12)0DL; E0(5)1(12)0(5)0(10)0DL0(6)1(4)1(12)0(8)0E. There are about 3 long stigmata per mesh and about 25 rows of stigmata. The second dorsal fold is often represented only by a group of crowded longitudinal vessels.

The gut loop is simple, extending from one half to two-thirds of the length of the branchial sac. In the flattened zooids, the gut loop is mainly on the under surface; only the distal part of the rectum curves dorsally around the meridian of the flattened body to the atrial aperture. The oesophagus is short and curved. The cylindrical

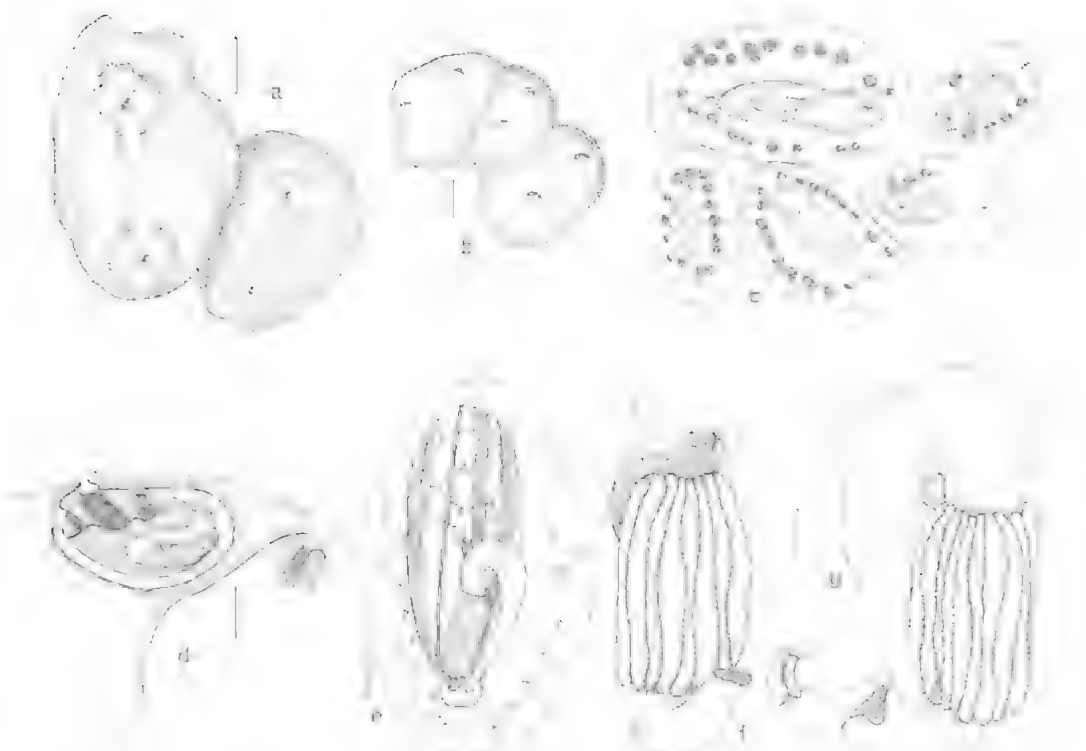


FIG. 109: *Eusynstyela latericius* — **a**, **b**, colonies from above (QM GH306, WAM 182.75); **c**, juvenile colony, transparent (Townsville); **d**, section through large, opaque colony, showing zooids in position (Townsville); **e**, zooid from ventral surface (from **d**); **f**, stomach with gastric caecum (from **d**); **g**, gut loop (from **d**). (Scales: **a**, **d**, **e**, 1.0 mm; **b**, **c**, 2.0 mm; **f**, **g**, 0.25 mm).

stomach has about 12 longitudinal folds. It is half to three-quarters of the length of the ascending limb of the loop, and is of only slightly greater diameter than the voluminous intestine. A short gastric caecum projects into the pole of the gut loop. The terminal part of the caecum is curved or straight and is usually bulbous. The anal border is smooth and bilabiate. There is a gastro-intestinal connective between the base of the caecum and the intestine.

In flattened zooids, a single row of up to 12 hermaphrodite gonads on each side of the body is arranged around the meridian or just ventral to it. The gonads of cylindrical zooids are closer to the endostyle, although the posterior part of the left row often extends dorsally in front of the gut loop. The gonads consist of a flask-shaped ovary with a very short oviduct, and 2 long, comma-shaped male follicles, both sometimes deeply divided into two. They are usually found side by side beneath the ovary, although fully developed male follicles may be aligned in tandem beneath the ovary. The male ducts curve around opposite sides of the ovary and meet to form a short common duct on the top of the oviduct.

REMARKS: The species is readily distinguished by its tough, naked test, straight gut loop, cylindrical stomach, bulbous gastric caecum, and the arrangement of its gonads.

Eusynstyela monotestis Tokioka, 1953a, from Japan and Hsia-men (Tokioka 1967a), is the only other species of this genus recorded from the western Pacific. Its colony resembles that of *E. latericius*, but it is readily distinguishable by the single, rod-shaped male follicle associated with each tubular ovary. From the Red Sea and the Gulf of Suez, *E. hartmeyeri* Michaelsen, 1904a also resembles the present species, although gonads are not present on the right side of the endostyle.

TABLE IX — SUMMARY OF CHARACTERS OF SPECIES OF *STOLONICA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Zooids	Apertures	Branchial tentacles	Dorsal tubercle slit	Number of branchial folds	Number of stomach folds	Stomach: length; shape	Maximum number of eggs/ ovary	♂ follicles shape	on left
S. reducta	WP	Coral Sea – Cockburn Sd	stolons; naked	sessile	24	longi-tudinal	3-3	20	long; expanded	7	fan-shaped -flask	absent
S. aluta n.sp.	—	Dongara	"	wart-like siphons	20	"	"	17	short; spurred	"	flask-circular not lobed	"
S. vesicularis	WP	SA	"	sessile	48	transverse	3-2	18	"	4	circular, lobed	"
S. truncata	—	Cockburn Sd - SA	stolons; sandy	recessed in transverse slit	50	"	3-3	36	"	3	elongate, lobed	"
S. agnata n.sp.	—	Cockburn Sd, Bowen	stolons; some sand	sessile	60	longi-tudinal	4-4	12	moderate; cylindrical	"	flask	present
S. australis	—	Albany – Tas.	stolons; sandy	wart-like siphons	48	"	2-2	18	short; pyriform	"	circular	"
S. carnosa	—	Cockburn Sd – Bass St	embedded; little sand	"	"	"	"	15	"	"	flask, not lobed	"

[1]WP, western Pacific. [2]Range given anti-clockwise around the continent.

Genus **Stolonica** Lacaze-Duthiers and Délage, 1892

Type species: *Stolonica australis* Hartmeyer, 1903.

The genus contains polyzoinid species usually with less than 4, often reduced branchial folds; and gonads, consisting of large, single testis follicles, some of which are associated with a small sac-like ovary, arranged in two rows, one on each side of the endostyle. The morphology of the species of this genus is strongly affected by the small size of the zooids, and characteristics of the genus are those associated with size reduction and simplification. With only one exception (*S. carnosa*), the small zooids are joined by stolons rather than being embedded. There are from 2 to 4 branchial folds on each side, although at least one of these may be vestigial, and they are often represented by crowded vessels on otherwise flat expanses of branchial wall. Folds that are well developed anteriorly often flatten out toward the posterior end of the body. There are usually only 12 to 15 rows of stigmata in the branchial sac, although one species (*S. aluta* n.sp.) has 20. The stigmata are very long.

The body wall musculature is usually a thin layer of delicate circular and longitudinal fibres, which form a continuous mesh over the body. The wide longitudinal bands that are conspicuous in most Styelidae are only rarely present (e.g., *S. truncata*). The gut loop is only very lightly attached to the body wall by delicate ligaments, and the gastric caecum is large and well-developed in all species except *S. australis*. Endocarps are present in the gut loop in a few species, but they usually occur on other parts of the body wall, dorsal to the gonads.

Several species have a remarkable spur-like extension of the stomach projecting into the gut loop. A similar structure is found in certain species of the genus *Metandrocarpa*. This spur-like extension is an expansion of the anterior side of the pyloric end of the stomach to accommodate extra short glandular folds. These folds, which lie parallel to the other stomach folds, extend along each side of the spur, originating from both sides of the gastric suture line, which runs along the outside of the spur. When the spur is present, the pyloric caecum from the distal end of its suture line is carried forward into the centre of the space enclosed by the gut loop, rather than being close against its inner curve.

Expansion of the stomach at its pyloric end also occurs in species that do not have a spur. In these cases, the expansion accommodates extra interstitial gastric folds that do not extend the whole length of the stomach. Some folds on the parietal side of the stomach tend to run obliquely and terminate against the suture line, rather than extending to the cardiac end of the stomach. Folds on the mesial side of the suture line run parallel to it, however.

The male follicles are sometimes oval or egg-shaped, but can be elongate or wide proximally, narrowing to a short vas deferens, or flat and almost circular, with the vas deferens projecting into the peribranchial cavity from the centre of the upper surface of the follicle. Mature male follicles are often lobed around their periphery or at their proximal end. The ovaries are small and sac-like, with a maximum of 7 eggs in each. They lie toward the dorsal or distal end of the mesial surface of some of the male follicles (usually of those on the right side of the body). When well-developed, they slip to the side of the male gland and lie on the body wall in line with, but apparently independent of the male follicles.

Distinctions between *Amphicarpa* and *Stolonica* on the basis of the separate female gonads or on the number of hermaphrodite gonads, are not reliable, since the separation of male and female components of the hermaphrodite gonads in the latter genus is variable and dependent on their maturity. Male and female components of the gonads do not develop simultaneously, and ovaries are often very few and small. Sometimes only testis follicles are present. The occurrence of ovaries on only the right side of the body is common, although not universal. Their position may be an adaptation to ensure that the large viviparous embryos are retained in the right peribranchial cavity (where they are usually found) to avoid crowding the voluminous and loosely attached gut loop, which occupies a large part of the left peribranchial cavity.

The morphology of species of the genus *Amphicarpa* is, like *Stolonica*, affected by the small size of the zooids and has resulted in adaptations convergent with those in *Stolonica*. The single row of relatively few large male follicles arranged on each side of the endostyle distinguishes *Stolonica* from *Amphicarpa*.

The genus *Stolonica* is diverse in Australian waters, particularly in southern Australia where several indigenous species and a western Pacific species (*S. vesicularis*) have been recorded. The discontinuity in the recorded range of many of the species suggests that these small ascidians may often be overlooked. The genus has not been recorded from the Antarctic, nor from the eastern Pacific and western Atlantic, although *S. socialis*

Hartmeyer, 1903 is known from the eastern Atlantic.

KEY TO THE SPECIES OF *STOLONICA* RECORDED FROM AUSTRALIA

1. Stomach wall produced into spur-like extension in gut loop 2
   Stomach wall not produced into spur-like extension in gut loop 4
2. Sandy test; stomach folds 36 ...... *S. truncata*
   Naked test; stomach folds less than 36 3
3. 2 branchial folds on left .... *S. vesicularis*
   3 branchial folds on left .... *S. aluta* n.sp.
4. Branchial folds 2 per side........................ 5
   Branchial folds more than 2 per side 6
5. Zooids embedded...................... *S. carnosa*
   Zooids connected by stolons....... *S. australis*
6. Branchial folds 4 per side...... *S. agnata* n.sp.
   Branchial folds 3 per side............ *S. reducta*

Stolonica agnata n.sp.
(Fig. 110)

DISTRIBUTION

TYPE LOCALITY: Queensland (Abbot Point, off mouth of Don River, 15 m, coarse sand with mud, coll. C. Roberts and L. Hammond, Ockleman Sledge, 19.3.18, holotype QM GH723).

FURTHER RECORDS: Western Australia (Cockburn Sound, QM G9669 GH2007). Queensland (NW Bowen, paratypes QM GH2228-9; Deltaic Reef, QM GH2796).

DESCRIPTION

EXTERNAL APPEARANCE: Sessile, upright or spherical zooids, up to 5 mm high, are joined by thick basal stolons. The zooids are often close together, their bases almost confluent. The branchial aperture is terminal, the atrial aperture from one-third to half of the distance down the dorsal surface. The apertures are almost completely sessile, on very slightly protruding conical siphons, which are free of sand. The remainder of the moderately thick and cartilaginous but translucent test sometimes has adherent sand or mud, and occasionally has epiphytic growths, but is often naked and wrinkled or with parallel longitudinal creases.

INTERNAL STRUCTURE: Very fine circular and longitudinal muscle fibres form a close meshwork in the translucent grey-brown body wall. There are approximately 60 crowded branchial tentacles. The neural gland is long and elliptical, opening directly into the pharynx by a simple longitudinal opening. The dorsal ganglion, slightly posterior and dorsal to it, is large and spherical. The dorsal lamina is long and narrow, the oesophageal opening being at the posterior end of the branchial sac.

There are 4 branchial folds on each side of the body. Dark pigment cells are present in the robust, internal longitudinal vessels on the folds, but are absent from the very delicate and inconspicuous longitudinal vessels in the interspaces. The last are often the same diameter as the bars between the long stigmata and can be confused with them. Between the folds, there are 2 stigmata per mesh, crossed by parastigmatic vessels. Stigmata are sometimes more numerous between the dorsal lamina and the first fold. The internal longitudinal vessels are arranged according to the following formulae: E0(3)4(8)4(6)4(8)0DL0(10)5(1)5(8)5(3)0E; E5(4)5(10)6(10)4(12)2DL3(11)3(3)4(8)5(3)0E. The second fold on the left is reduced to a few longitudinal vessels, made conspicuous in relation to the vessels of the interspaces by their greater diameter and contained pigment cells. There are 13 rows of stigmata.

The gut forms a simple loop in the posterior curve of the body. The stomach is wide and cylindrical, with about 12 longitudinal folds. It

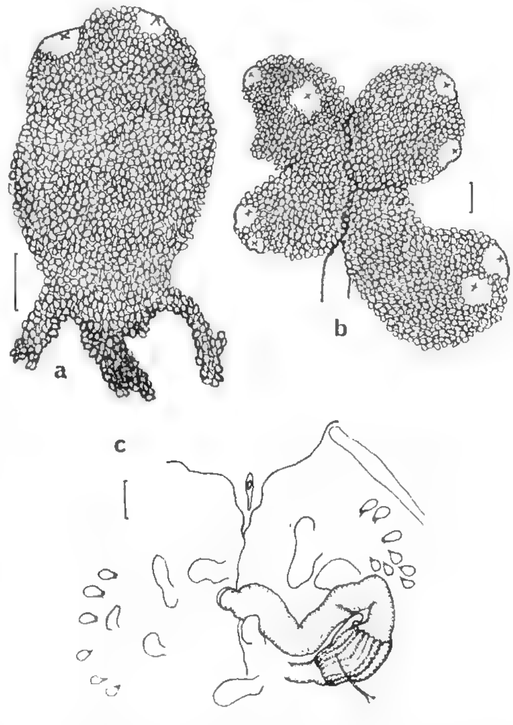


FIG. 110: *Stolonica agnata* n.sp. — **a**, single zooid (QM GH723); **b**, colony (QM G9669); **c**, internal body wall (QM G9669). (Scales; **a**, **b**, 1.0 mm; **c**, 0.5 mm).

occupies about half of the ascending limb of the loop and is covered by darkly pigmented body wall. There is a short, straight caecum in the pole of the loop and a gastro-intestinal connective. No endocarps are present in the gut loop. The rectum extends forward to the atrial aperture, forming a right to obtuse angle with the gut loop. Evenly spaced, delicate ligaments along the whole length of the inner curve of the gut attach it to the body wall.

Up to 8 gonads are present more or less in a row along each side of the endostyle. About half are hermaphrodite gonads, consisting of a small, flask-shaped ovary containing 2 or 3 eggs, and a single, almost spherical, male follicle beneath each ovary. Posterior to the hermaphrodite gonads are male follicles without associated ovaries, 3 on the right and 5 on the left. Those on the left are clumped together just anterior to the pole of the gut loop. A large larva is often present in the peribranchial cavity on the right or left side of the body (larval trunk 1 mm long, tail 1.2 mm long). Larvae have the usual circle of ampullae around the anterior adhesive organs.

Several long, flat-topped endocarps are present on each side dorsal to the gonads.

REMARKS: The species is distinguished from others in this genus by its 4 branchial folds, the second fold on the left being very reduced. The unlobed, flask-shaped testis follicles resemble those of *S. carnosa*, which it also resembles in the longitudinal rather than transverse slit of the dorsal turbercle and in the presence of hermaphrodite as well as male gonads on the left side of the body. However, the present species does not have endocarps enclosed in the gut loop, and has a cylindrical rather than pyriform stomach.

Stolonica aluta n.sp.
(Fig. 111)

DISTRIBUTION

TYPE LOCALITY: Western Australia (82 km W of Dongara, 29°14'S, 114°04'E to 29°14.8'S, 114°5.1'E, 164 m, small stones and sand with sponges, coll. L. Marsh on M.V. Sprightly, triangular dredge, 17.2.76, holotype WAM 968.83, paratype WAM 40.84; 69 km W of Cliff Head, 126 m, paratypes WAM 969.83).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright (about 0.1 to 1.0 cm high) rather narrow and top-shaped, with a rounded upper surface, narrowing to a posterior stalk. The test is hard and very wrinkled and the surface is raised into conspicuous rounded swellings, especially around the apertures. Each aperture, which is on a small, wart-like siphon, is surrounded by four conspicuous, swollen lobes. The branchial siphon is terminal; the atrial siphon is from one-third to half the distance down the dorsal side of the body. The extremely irregular surface of the test is partly a result of the contracted condition of these specimens. The short, narrow stalk expands into a flat basal plate adhering to the substrate. Narrow basal stolons connect the zooids.

INTERNAL STRUCTURE: The body wall is muscular, with an external layer of circular muscles and internal longitudinal bands. There are about 20 rather flat branchial tentacles. The large, oval dorsal tubercle with a simple longitudinal slit is present in a V-shaped peritubercular area. The neural ganglion is large and postero-dorsal to the dorsal tubercle. The oesophageal opening is near the posterior end of the branchial sac. The dorsal lamina is long and narrow.

The branchial sac has 3 low, rounded folds on each side of the body. Internal longitudinal vessels are robust and ribbon-like. They are crowded on and between the folds, and are arranged according to the following formula: E6(8)8(11)6(12)6DL3(12)7(13)7(10)7E. There are 20 rows of stigmata with about 3 in each mesh, crossed by fine parastigmatic vessels.

The oesophagus is short. The stomach is short but very wide at its pyloric end, its inner side with the suture line being produced out into a spur that curves into the gut loop and terminates in a large, curved caecum. There are 17 moderately wide longitudinal gastric folds, of which 4 extend from each side of the suture line to the expanded pyloric end of the stomach to form the spur-like extension. The rectum is rather long, curving anteriorly to the base of the atrial aperture and terminating in a smooth-rimmed anus. There are 2 or 3 lobed endocarps in the gut loop. The gut is only lightly attached to the body wall by ligaments, 1 around the stomach, 1 from the pole of the gut loop to the body wall and to the small endocarp enclosed by the gut loop, 3 where the intestine curves anteriorly to the rectum, and 1 near the anus.

There are about 12 crowded, circular or flasked-shaped male follicles on each side of the posterior end of the endostyle, those on the left arranged in an arc that curves around the postero-ventral aspect of the gut loop. Each follicle has a narrow vas deferens directed dorsally from either the dorsal border or the mesial surface of the follicle. On the right side of the body, sac-like ovaries are crowded in amongst the male follicles.

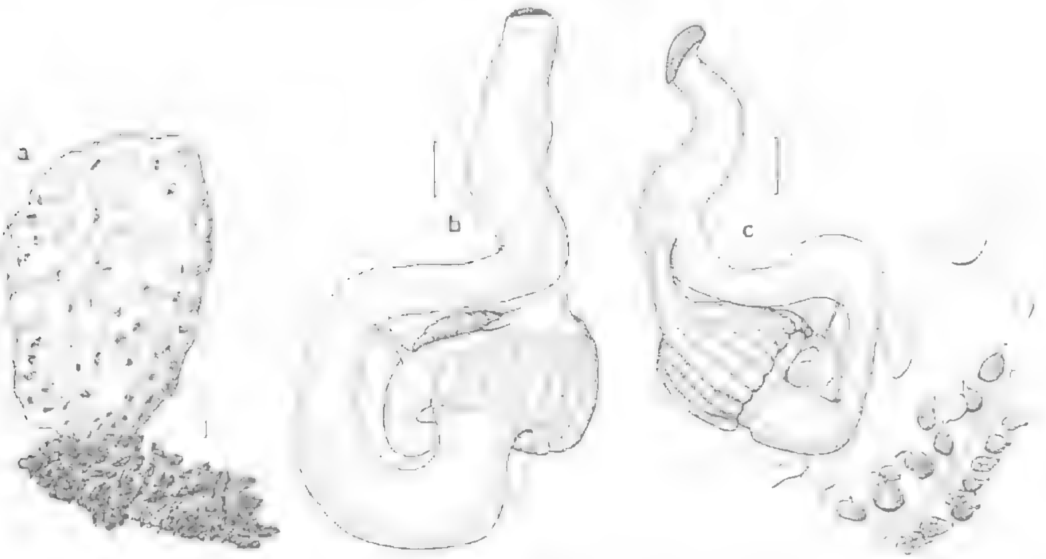


FIG. 111: *Stolonica aluta* n.sp.: a, single zooid (WAM 968.83); b, gut loop from outside surface (WAM 969.83); c, gut loop and gonads from inside body wall (WAM 968.83). (Scales: a, 1.0 mm; b, 0.25 mm; c, 0.5 mm).

Two large larvae are present in the peribranchial cavity. They have larval trunks about 1.7 mm long and narrow tails of about the same length.

Large oblong endocarps (4 or 5) are scattered on the body wall, others between the gonads.

REMARKS: In the width and number of folds on the stomach, the spur-like gastric extension and the position and shape of the gonads, this species most resembles *S. vesicularis*. However, it is distinguished from the latter by its male follicles (which do not appear to be lobed), its ovaries with more numerous eggs, its longer stomach folds, its hard, leathery and wrinkled test and its very large larvae.

The species is especially robust, its opaque body wall and thick internal longitudinal branchial vessels contrasting with the delicate structures of other species of this genus. Its very large larvae with relatively short tails suggests that their free-swimming life may be short and the species' range restricted to a relatively small area off the western Australian coast.

Stolonica australis Michaelsen, 1927
(Fig. 112)

Stolonica australis Michaelsen, 1927, p.202. Hartmeyer and Michaelsen, 1928, p.352. (Not: Kott 1952, p.253; 1972a, p.28; 1972b, p.183. < *Amphicarpa meridiana* n.sp.).

Stolonica carnosa: Kott, 1975, p. 11.

DISTRIBUTION

NEW RECORDS: Tasmania (Port Davey, QM GH2024).

PREVIOUSLY RECORDED: Western Australia (Albany — Hartmeyer and Michaelsen 1928). South Australia (Investigator Strait — Kott 1975)

DESCRIPTION

EXTERNAL APPEARANCE: Separate oval, sandy and slightly laterally flattened individuals up to 7 mm high are joined by stolons. The zooids are often crowded together. The apertures are close together on the upper surface on short, wart-like siphons. The openings are not conspicuously lobed. The test is very thin, embedded with sand and often brittle, with a slightly pearly inner surface.

INTERNAL STRUCTURE: The body wall is fleshy and closely adherent to the test. It has strong muscles only on the siphons. There are about 48 slender branchial tentacles. The dorsal tubercle is a long, oval cushion with a simple longitudinal slit. The neural ganglion is large and rounded.

The dorsal border of the branchial sac is only slightly shorter than the ventral border. The branchial folds are relatively straight, with longitudinal vessels arranged according to the following formula: DL0(12)3(9)6E7(9)6(9)0DL. There are 6 or 7 long, narrow stigmata in each long mesh, but more in the long meshes near the endostyle. Each mesh is crossed by a parastigmatic vessel.

FIG. 112: *Stolonica australis* (QM GH2024) — **a**, inner body wall, left side; **b**, stomach from outside surface. (Scales: **a**, 0.25 mm; **b**, 0.1 mm).

The gut loop is in the posterior end of the body and the rectum extends anteriorly almost at right angles to the gut loop. The stomach is short and pear-shaped, very wide at the pyloric end, but narrowing to the oesophagus at the cardiac end. It has 18 parallel longitudinal folds extending the whole length of the stomach on the parietal side, but on the mesial side, about 5 of the folds terminate against the suture line. The stomach caecum is short and curved. The anal border is smooth and bilabiate. A gastro-intestinal connective from the curve of the caecum breaks into branches over the intestine. The stomach is covered by a fairly thick layer of body wall that sometimes obscures the stomach folds. A row of ligaments beneath the gut attaches it to the body wall.

There are up to 15 flat, circular testis follicles with lobed borders on the right and up to 11 on the left. Each has a short vas deferens projecting from its surface. Very small sac-like ovaries containing up to 3 eggs are present on some of the male follicles on both sides of the body.

A few irregular endocarps of varying size are present on the body wall outside the gut loop. Two others are enclosed by the gut loop: one in the pole and one dorsal to the gastro-intestinal ligament.

REMARKS: The species appears to be related to *S. carnosa*, with its wart-like external siphons, similar numbers of branchial tentacles, longitudinal slit on the dorsal tubercle, and only 2 branchial folds on each side. However, the zooids of the present species are not embedded as they are in *S. carnosa*, and the flat, circular, lobed male follicles more closely resemble those of *S. vesicularis* and *S. reducta*, from which the present species is distinguished by its reduced branchial sac, wart-like external siphons, sandy test and endocarps in the gut loop.

Stolonica carnosa Millar, 1963
(Fig. 113)

Stolonica carnosa Millar, 1963, p. 735. Kott, 1972a, p. 28.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV 752).

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound — BM 1962.1.12.25 Millar 1963). South Australia (Spencer Gulf — Kott 1972a).

The species is taken to 6 m depth.

DESCRIPTION

EXTERNAL APPEARANCE: All the known specimens form compact colonies growing around the thin stems of plants. The zooids are up to 6 mm long, with their anterior ends projecting slightly from the surface as rounded swellings. The apertures are both present on the upper surface on short, wart-like protruberances. The test is very tough and cartilaginous, with only a small amount of sand externally. Sometimes the surface of the colonies is subdivided into lobes, each with about 10 zooids, but usually it is even and compact.

INTERNAL STRUCTURE: The body, when removed from the test, is almost spherical. The body wall is closely adherent to the test, with a regular network of very delicate and fine longitudinal and transverse muscles. There are up to 48 crowded and rather stout branchial tentacles. The dorsal tubercle is simple, with a narrow longitudinal slit.

There are 2 branchial folds on each side of the body. Previously recorded specimens had up to 7

FIG. 113: *Stolonica carnosa* (NMV H1752) — a, single zooid, removed from test; b, gut, endocarps and gonads on left side of body. (Scales: 0.5 mm).

internal longitudinal vessels on each fold. A typical branchial formula is: DL0(6)2(5)1E5(5)2(5). In the newly recorded specimen from Bass Strait, there appear to be up to 12 internal longitudinal vessels on each fold, although these were very crowded and difficult to count, the pharynx being very contracted. There are 12 to 15 rows of fairly short, oval stigmata, 3 to 5 per mesh. Parastigmatic vessels are present.

The stomach is short and wide with 16 longitudinal folds, which are conspicuous in the South Australian specimens, but not in the type material (Millar 1963), where the stomach is coveredby a relatively thick layer of body wall. The long, curved gastric caecum sometimes forms a complete circle in the gut loop. A connective from the caecum extends across the loop and divides into branches along the intestine. The gut forms a simple loop extending posteriorly from the oesophageal opening, which is halfway down the branchial sac. Sometimes the rectum extends forwards to the atrial aperture more or less in line with the gut loop, although in smaller or contracted specimens it forms an angle with the gut loop. The anal border is smooth and bilabiate. A series of ligaments along the parietal side of the gut attach it firmly to the body wall.

Gonads are present in a row along each side of the endostyle. Ovaries contain 1 to 3 eggs of different sizes. The testes are simple, undivided, elongate, flask-shaped follicles with a short narrow duct directed dorsally. Initially each ovary is associated with a single male follicle to form hermaphrodite gonads; only when mature do they separate, male and female gonads alternating.

Endocarps are scattered over the body wall. The gut loop encloses one on each side of the gastro-intestinal connective. These endocarps, which vary in size, are sometimes quite large and flat-topped.

REMARKS: *Stolonica carnosa* is unusual in this genus in that its zooids are embedded in common test, rather than joined by stolons.

It resembles *Stolonica australis* in having only 2 branchial folds on each side, a pyriform stomach, and two endocarps enclosed in the gut loop. It is distinguished from *S. australis* by its embedded zooids, the absence of sand in the test, its fewer internal longitudinal branchial vessels and flask-shaped, rather than circular, testis follicles. Its flask-shaped male glands resemble those of *S. agnata*; its relationship with that species is discussed under *S. agnata*.

Stolonica reducta (Sluiter, 1904)
(Fig. 114)

Styela reducta Sluiter, 1904, p.72.
Amphicarpa elongata Kott, 1952, p. 255.

DISTRIBUTION

NEW RECORDS: Coral Sea (Lihou Reef, QM GH252; Marion Reef, QM GH248–50).

PREVIOUSLY RECORDED: Western Australia (Trigg I. — AM Y1597 Y1599 Kott 1952). Indonesia (ZMA V.TU1050 Sluiter 1904).

The Queensland specimens were taken from channel faces, epizooic on *Polycarpa longiformis*, and on rubble.

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of sessile, hemispherical to spherical, stalked zooids joined by basal stolons. The stolons extend out over the substrate either from around the periphery of the basal surface of sessile individuals, or from the short posterior stalk. Both apertures are present, quite close together, on the

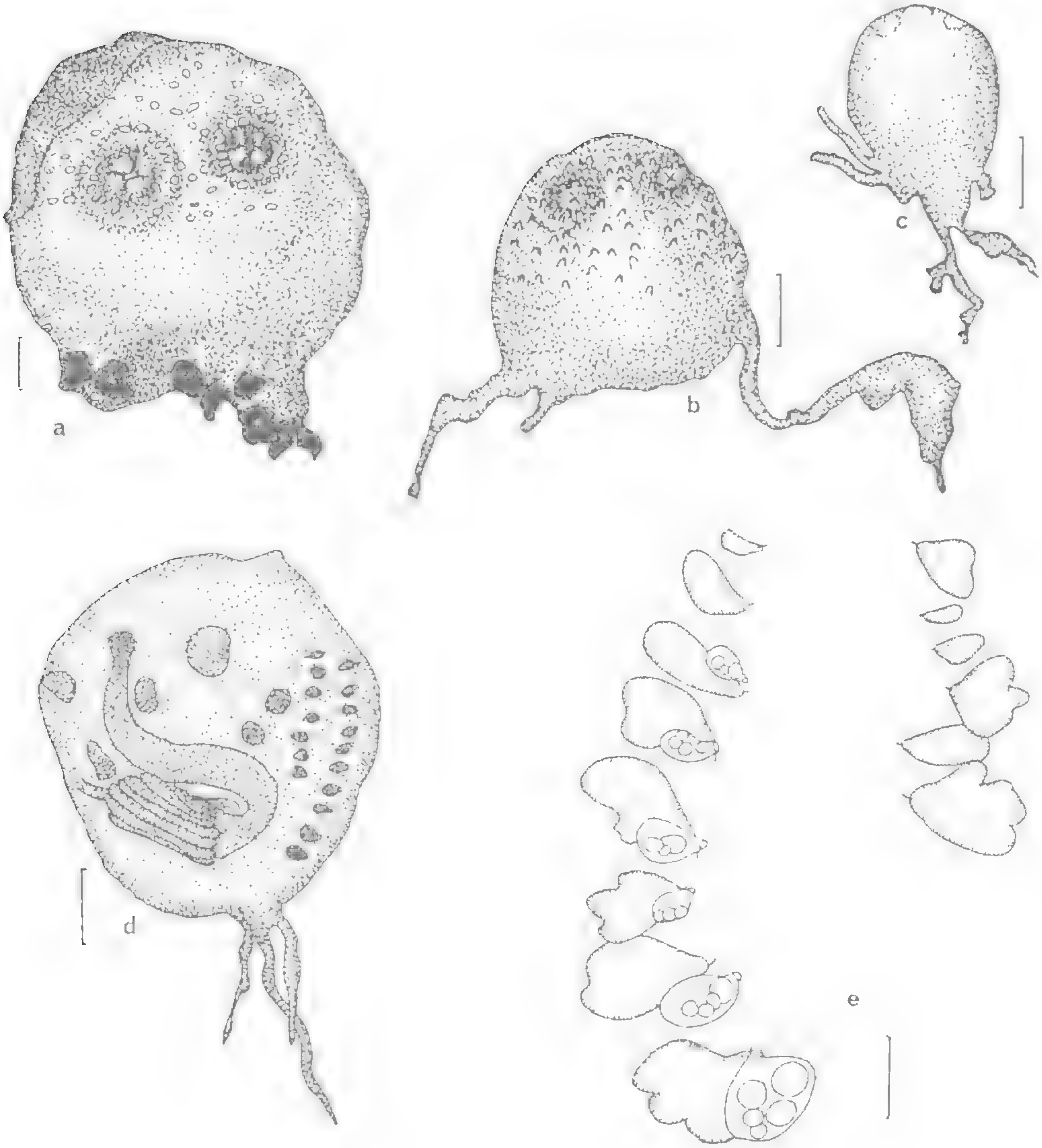


FIG. 114: *Stolonica reducta* — **a–c**, external appearance (QM GH248); **d**, body organs seen through right side of body wall (QM GH248); **e**, gonads on right and left sides of the body respectively (QM GH252). (Scales: **a**, 0.5 mm; **b**, **d**, 1.0 mm; **c**, 2.0 mm; **e**, 0.25 mm).

upper rounded surface. Each aperture is slightly depressed into the upper surface, and the surrounding test has minute, crowded papillae. These are also present over the whole surface of the body, becoming progressively less crowded away from the apertures. The test is thin and translucent but appears brown or red-brown in living specimens, largely because the dark body wall is visible through the translucent test.

INTERNAL STRUCTURE: The zooids are only about 4 mm in diameter. The body wall is very delicate and closely adherent to the test, with a fine coat of parallel circular bands and very fine longitudinal fibres. There are 12 robust, sometimes long, simple, pointed branchial tentacles alternating with rudimentary ones. The prebranchial area is quite wide and the peritubercular area very shallow. The dorsal tubercle has a simple, circular to longitudinal opening directed forwards. The dorsal lamina is only moderately long, the oesophageal opening being halfway along the length of the branchial sac.

There are 3 branchial folds on each side of the body. The 2 ventral folds on each side are represented by crowded vessels, which tend to spread out posteriorly. The branchial formula from Marion Reef specimens is: E3(6)3(9)4(11)3DL0(9)4(10)3(8)3E. The stigmata are long and slender, arranged in 12 rows along the pharynx. There are very slender and inconspicuous parastigmatic vessels. Each mesh has 2 stigmata.

The gut forms a simple loop, and the rectum curves anteriorly, forming a wide angle with the gut loop. The oesophagus is short. The stomach is long, occupying almost the whole of the ascending limb of the loop. It has about 20 folds and is wider at the pyloric than at the cardiac end. Most of the folds extend the whole length of the stomach, although 4 of them extend obliquely from the anterior side of the suture line and 2 or 3 short, interstitial folds are accommodated in the generally increased diameter of the distal end of the stomach. There is a long curved caecum in the pole of the gut loop, and a gastro-intestinal connective between the base of the caecum and the intestine. The anal border is bilabiate and is turned back. Fine, branching ligaments cross the space enclosed by the pole of the loop to connect it to the body wall. The gut is attached to the body wall only very lightly by 4 very fine ligaments, one at each end of the rectum, one at the postero-ventral corner of the stomach, and one from the pole of the loop.

The gonads are arranged in a single row along each side of the endostyle. They are only either male or hermaphrodite. The ovaries are flask-shaped, with up to 7 eggs. The testes are single, broad, flask- to fan-shaped follicles, often lobed around their proximal or ventral border. In hermaphrodite gonads, the testis follicle may lie beneath the ovary, but when mature, they tend to lie on the body wall beside the ovary, rather than beneath it. The oviduct has a wide opening, and the testis narrows dorsally to a thin, short vas deferens. There are up to 10 male and hermaphrodite gonads on the right and up to 7 male gonads on the left. Female glands are always absent from the left side of the body.

There are numerous large, circular or elongate endocarps scattered over the body wall dorsal to the gonads, but none in the gut loop.

REMARKS: The small, upright zooids with long stomach, slightly depressed apertures, and thin, naked, papillated test are distinctive.

Stolonica truncata Kott, 1972
(Fig. 115)

Stolonica truncata Kott, 1972b, p.183.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 67.72 875.83, QM GH2119).

PREVIOUSLY RECORDED: South Australia (Waldegrave I. — Kott 1972b).

The species is recorded on a rocky bottom with sand patches from 3 to 25 m depth.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of upright to rounded, sandy individuals, either sessile or narrowing to a posterior stalk. They are up to 1 cm high. Zooids are joined by basal stolons. There are also numerous accessory root-like projections from the posterior end of the body, heavily encrusted with sand. The small, 4-lobed, sessile apertures are on the upper surface, about one-fifth of the circumference of the body apart from each other. Each is in a transverse strip of naked, blackish test. The remainder of the body is encrusted with sand. The apertures can be withdrawn into the body, with sand strengthened test dorsal and ventral to each opening meeting in a transverse line across the top of the opening.

INTERNAL STRUCTURE: The body wall is thin, but moderately muscular. Longitudinal band radiate from each siphon and extend down the length of the body. Circular fibres are present around each aperture, around the anterior part of the body, and around the posterior third of the

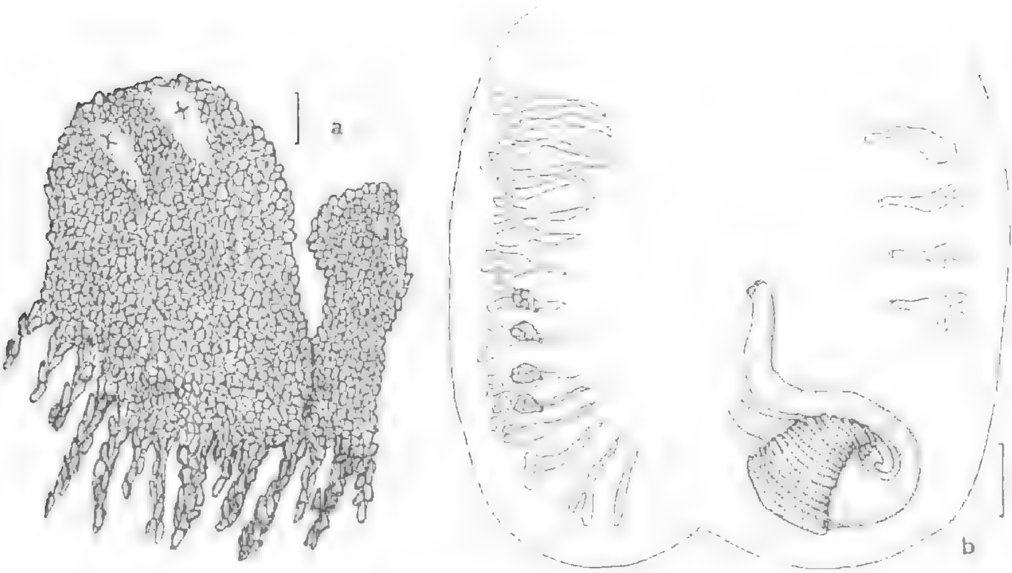


FIG. 115: *Stolonica truncata* (QM GH2119 — part, WAM 875.83) — a, external appearance; b, inner body wall. (Scales: 1.0 mm).

body, leaving a section of the body without conspicuous circular muscles. There are about 50 rather robust branchial tentacles, very variable in length and quite crowded. The dorsal tubercle, which is in a very shallow peritubercular area, has a transverse slit.

The 3 rounded branchial folds on each side tend to fade out posteriorly. Internal longitudinal vessels are arranged according to the following formula: DL0(10)5(9)5(6)6E. There are about 2 stigmata per mesh, angled slightly obliquely to the longitudinal vessels.

The gut forms a simple, circular loop in the posterior part of the body, and the short rectum turns anteriorly to the base of the atrial aperture. The stomach is short and very wide. Its anterior side is produced into a pointed spur that projects up into the loop of the gut and curves around in it, terminating in a curved caecum. There are 36 narrow longitudinal folds on the stomach and on the spur, becoming shorter along the spur where their proximal ends meet the suture line along its dorsal or outside edge. The anal border is smooth and bilabiate. The gut loop is attached to the body wall by two ligaments: one around the stomach, and one from the pole of the loop attaching it to the body wall and to a very small endocarp in the gut loop. The rectum is more firmly attached by a continuous membrane along its length.

Gonads are present in a single row on each side of the endostyle. There are 16 long, narrow testis follicles on the right and 5 on the left, anterior to the gut loop. They lie at right angles to the endostyle, lobed at their proximal ends and tapering dorsally to a short vas deferens. Small 3-egg ovaries are present on the distal end of the male follicles on the right. Ovaries are not present on the left. Some endocarps are scattered on the body wall.

Up to 12 larvae, at different stages of development, are crowded in the right peribranchial cavity. They have triradially arranged papillae and resemble the larvae of other Polyzoinae (Millar 1960). The larval trunk is 1.0 mm long and the tail 1.5 mm.

REMARKS: The species has the characteristic features of the genus, as well as many special characters. Apertures in a transverse strip of sand-free test have not been observed in other Ascidians. A similar adaptation in which the apertures are drawn into a single median depression (rather than the separate transverse depressions that occur in the present species) occurs in *Symplegma arenosa* and in other families (e.g., Agnesiidae and Molgulidae). The peculiar spur-like prolongation of the stomach into the gut loop is found, but to a lesser extent, in *Stolonica vesicularis* and *Metandrocarpa indica*.

The testis follicles are unusually long and narrow. The species is distinguished from *S. vesicularis* by its sandy test, narrower and more numerous stomach folds and long, rather than circular, male follicles.

Stolonica vesicularis Van Name, 1918
(Fig. 116)

Stolonica vesicularis Van Name, 1918, p.109. Millar, 1975, p.279.

DISTRIBUTION

NEW RECORDS: South Australia (Ward I., QM GH1308-10; Top Gallant I., QM GH2309).

PREVIOUSLY RECORDED: Philippines (Van Name 1918, Millar 1975).

In South Australia, the species was found at 1 to 5 m depth amongst colonies of *Podoclavella molluccensis* and *Pycnoclavella diminuta*. It is recorded down to 46 m in the Philippines.

DESCRIPTION

EXTERNAL APPEARANCE: Dome-shaped to upright individuals from 3 to 6 mm high are joined by stolons that radiate from around the perimeter of the flat basal surface. The apertures, which are completely sessile, are close together on the upper surface. The test is thin, only slightly translucent, and of a brownish colour. It is wrinkled around the apertures in these contracted specimens. It is free of encrusting sand.

INTERNAL STRUCTURE: The body wall adheres closely to the test. The musculature is delicate over most of the body. There are fine fibres in the outer layer of fine circular muscles. The inner longitudinal bands radiate from the siphonal region, where they are most conspicuous. About 20 stout branchial tentacles of varying sizes alternate with rudimentary ones. The dorsal tubercle is small, with a simple transverse slit. There is a long, wide dorsal lamina. The branchial folds are straight, with a retropharyngeal band at the posterior end the body.

There are 3 branchial folds on the right side of the body, but only 2 on the left. The only well-formed folds are the most dorsal on the right and the second on the left. The other folds are represented by crowded vessels on a flat expanse of branchial sac. They are arranged according to the following formula: E4(4)4(4)4(9)5DL0(7) 3(9)7E. The stigmata are in 11 rows, 2 or 3 per mesh. Some of the long, narrow stigmata are subdivided by parastigmatic vessels.

The gut forms a short, tight loop at the posterior end of the body, and the stomach is very short and very wide, with about 14 broad longitudinal folds. Its anterior border projects into the gut loop as a short appendix or spur that curves into the pole of the gut loop. The suture line on the inside of the stomach extends out along the outside of this projection away from the longitudinal axis of the stomach. The longitudinal folds gradually reduce along the projecting spur. Their proximal ends meet the suture line. The long caecum from the tip of the stomach spur is continuous with the suture line. The caecum curves around in the pole of the gut loop. The rectum extends forwards to the atrial aperture, forming an obtuse angle with it. The anal border is smooth. There is a gastro-intestinal connective between the gastric caecum and the intestine. The gut is only very lightly attached to the body wall by 3 very fine ligaments, one from the gastro-intestinal connective in the gut loop, one from each end of the rectum and one from the postero-ventral end of the stomach.

There are up to 9 large, flat male follicles in a single short row in the postero-ventral curve of the body to the right of the endostyle, but only 3 on the left just ventral to the gut loop. They are divided into rounded lobes, especially around their wide ventral border. Each follicle has a short duct from the upper surface (when an ovary is present) or from the narrowing dorsal border (when there is no ovary). The ovaries are small, with up to 4 eggs. They are present on the right side of the body only, on some or all of the male follicles just to the side of the male duct, which crosses over the short, wide oviduct to open. When the male gland is mature, the vas deferens is very long and conspicuous, projecting into the atrial cavity. There are 3 to 7 endocarps scattered over each side of the body wall.

A single larva, with trunk about 0.9 mm long, is sometimes present in the right peribranchial cavity. It has 3 adhesive organs arranged in a triangle, and a circle of numerous, short, ectodermal ampullae.

REMARKS: The species is characterised primarily by its very short, broad stomach projecting into the pole of the gut loop. This stomach closely resembles that of *Stolonica truncata* Kott, from which it is distinguished by its naked test, circular male follicles and sessile apertures. The stomach is similar to that of *Metandrocarpa indica* Kott.

The species resembles *S. reducta* in the form of its gonads and the absence of sand on the surface test. It is distinguished by having a shorter stomach that is produced into a distinctive spur-like extension in the loop of the gut.

The stomach of the Philippine specimens may not be quite as short as that of the Australian

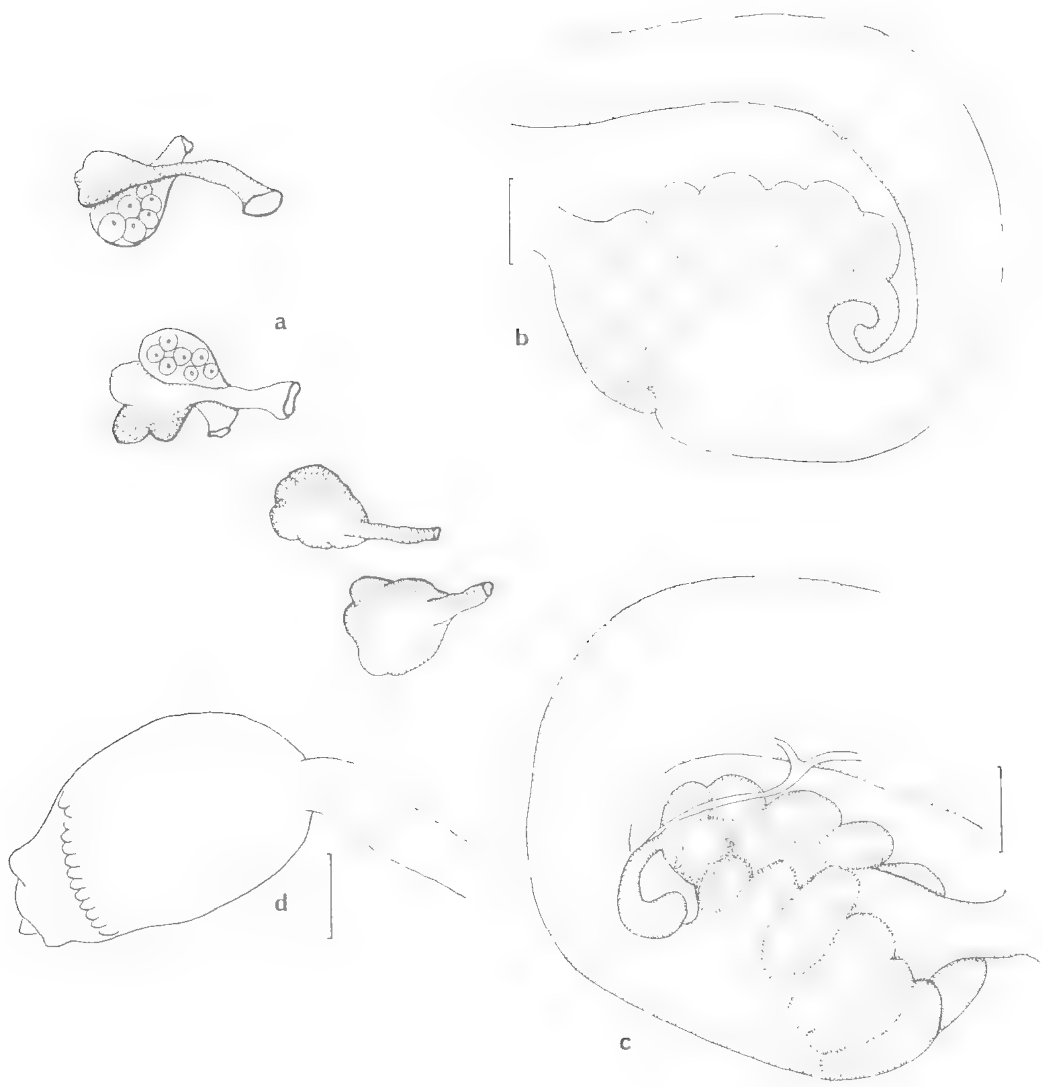


FIG. 116: *Stolonica vesicularis* — **a**, gonads, showing long male duct crossing neck of oviduct (QM GH2309); **b**, mesial side of stomach (QM GH1308); **c**, parietal side of stomach (QM GH1308); **d**, larva (QM GH1308). (Scales: 0.25 mm).

specimens, but its suture line appears to diverge away from the longitudinal axis of the stomach in exactly the same way. There are also more numerous gonads in the Philippine specimens; however their number varies in both Australian and Philippine populations. All other characters, including the distinctive lobed male follicles and the transverse slit of the dorsal tubercle, appear to be identical.

Genus **Amphicarpa** Michaelsen, 1922

Type species: *Stolonica prolifera* Sluiter, 1905a

The genus contains polyzoinid species with no more than 3 branchial folds per side; numerous small, undivided male follicles scattered over the body wall; and hermaphrodite gonads in a row each side of the endostyle. There are no solitary female gonads. The hermaphrodite gonads each consist of a single male follicle and a small ovary. In most species, immature ovaries have been observed to contain 2 or 3 ova although only one matures at a time. Only in *A. duploplicata* do the ovaries appear to produce a single egg. The zooids usually are joined by stolons rather than being embedded in common test.

The branchial sac of species of this genus usually has a similar number of rows of stigmata (15 to 20) to *Stolonica* spp. Only in *A. duploplicata* is the pharynx especially long with up to 28 rows of stigmata.

The related genus *Stolonica* is distinguished from *Amphicarpa* by its usually hermaphrodite gonads; large and often lobed the male follicles; and the single line of gonads on each side of the endostyle.

Like other genera of the Polyzoinae (e.g. *Polyandrocarpa*), *Amphicarpa* is probably polyphyletic. In one species (*A. diptycha*), the presence of siphonal scales, similar to those found in *Styela* spp. and *Cnemidocarpa* spp., suggests a relationship with those genera rather than *Polycarpa*.

Species of *Amphicarpa* are difficult to distinguish from one another, with their simplified bodies, very similar body organs. The problem is amplified by the ephemeral nature of the gonads, which are necessary to determine the genus.

The genus is well represented in Australian waters. Three of the four species are indigenous, and only the western Pacific *A. duploplicata* extends outside the Australian waters. All the known species are viviparous.

TABLE X — SUMMARY OF CHARACTERS OF SPECIES OF *AMPHICARPA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range	Zooid shape	Siphon lining	Branchial folds	Rows of stigmata	Gastric caecum	♀ on left
A. nodula n.sp.	—	Bowen	round	—	3–3	15	small, straight	absent
A. diptycha	—	Port Hedland - Albany	"	iridescent scales	2–2	15–19	long, curved	present
A. meridiana n.sp.	—	SA - NSW	"	—	"	15	variable, curved	"
A. duploplicata	WP	Arafura Sea - Dampier Arch.	elongate	black	"	28–30	absent	"

[1]WP, western Pacific. [2]Range given anti-clockwise around the continent.

KEY TO THE SPECIES OF *AMPHICARPA* RECORDED FROM AUSTRALIA

1. Siphonal scales present .... *A. diptycha*
   Siphonal scales absent 2
2. 2 branchial folds on each side 3
   3 branchial folds on each side ....
   .... *A. nodula* n.sp.
3. Zooids with black siphon linings; no gastric caecum .... *A. duploplicata*
   Zooids without black siphon linings; with gastric caecum .... *A. meridiana* n.sp.

Amphicarpa sigma (Tokioka, 1952), from the Arafura Sea, resembles *A. duploplicata*. However, it has smaller zooids, fewer stomach folds, and a much longer gut loop.

Amphicarpa diptycha (Hartmeyer, 1919)
(Figs 100f, 117)

Distomus diptychos Hartmeyer, 1919, p.87.
Amphicarpa diptycha: Michaelsen, 1922, p.457. Hartmeyer and Michaelsen, 1928, p.357. (Not: Kott, 1952, p.254; 1975, p.11; 1976a, p.74, < *A. meridiana* n.sp. Millar, 1960b, p.99; 1963, p.734, < *A. meridiana* n.sp.).

DISTRIBUTION

NEW RECORDS: Western Australia (N and NE Port Hedland, WAM 1230.83 1234.83; Abrolhos, WAM 1232.83; Albany, WAM 1231.83).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Shark Bay, Albany — Michaelsen and Hartmeyer 1928).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are almost spherical, up to 2 cm long. They sometimes narrow to a posterior stalk or they are sessile, joined to stolons that often form a tangled basal mass. Sometimes the zooids are crowded, adhering to one another along their sides to form compact colonies. The apertures are fairly close together on the upper surface, with the test forming a rounded ridge around and often between them. The siphonal lining has irridescent blue bands formed by overlapping curved scales with rounded borders, which resemble the scales that line the siphons of species of the genera *Cnemidocarpa* and *Styela*. The test is tough, sometimes leathery, usually with some sand adhering to the surface.

INTERNAL STRUCTURE: The body wall is a dark purple-brown. It is very muscular, with an almost continuous external layer of circular muscles and inner longitudinal bands. Particularly strong circular muscles surround each siphn and the anterior part of the body behind the siphonal muscles. There is a muscular velum at the base of each siphon. There are up to 100 crowded branchial tentacles. The dorsal tubercle is a rounded cushion with a simple, oval slit. The dorsal lamina is broad and ribbed, but is quite short, the branchial folds being deeply curved.

There are 2 well-developed but rounded folds on each side of the body, with up to 6 internal longitudinal vessels between the folds and up to 16 on the folds. The dorsal fold on each side is larger than the ventral one. Typical branchial formulae are: E7(8)4(12)3DL; DL3(12)5(10)6E; DL0(16)6(11)8E7(11)5(12)2. The stigmata are in 15 rows, 4 to 6 per mesh. The flat branchial wall between the endostyle and the ventral fold on each side is wider than that between the dorsal lamina and the dorsal folds.

The gut forms a short loop across the posterior end of the body, with the rectum continuing anteriorly at right angles to the loop. The stomach is rather short and is expanded distally. Most of the 18 stomach folds extend the full length of the stomach, but some on the inner side of the stomach extend between the gastric suture line and the distal end of the stomach. The curved gastric caecum is of variable length. It continues from the suture line, closely applied to the parietal side of the gut. A strong gastro-intestinal connective extends from the proximal part of the outer border of the caecum to branch along the wall of the intestine. It encloses a flat-topped endocarp in the pole of the loop. A similar endocarp is enclosed in the proximal part of the gut loop. The anal border is smooth and bilabiate. The gut loop is attached to the body wall by a series of strong, regularly spaced ligaments around the outside of the loop. The posterior border of the stomach is firmly anchored by a strong ligament that extends across the surface of the stomach.

Hermaphrodite gonads consist of a single male follicle beneath a 3-egg ovary. Only a single egg develops at a time, and the mature ovaries appear to contain only one large egg. The oviduct is very short, with an almost completely sessile opening. The hermaphrodite gonads are sometimes in a row an each side of the body, but not always near the endostyle. On the left, they are often also in an arc across the top of the gut loop and occasionally they are found in groups rather than in a strictly linear arrangement. Varying numbers of small male follicles are present in patches around the ends of the rows of hermaphrodite gonads or ventral to them. Larvae are found in the peribranchial cavity on both sides of the body. The larval trunk is 1 mm long and the tail 2.5 mm.

Endocarps are usually present on the body wall outside the gut loop, in addition to those enclosed in it.

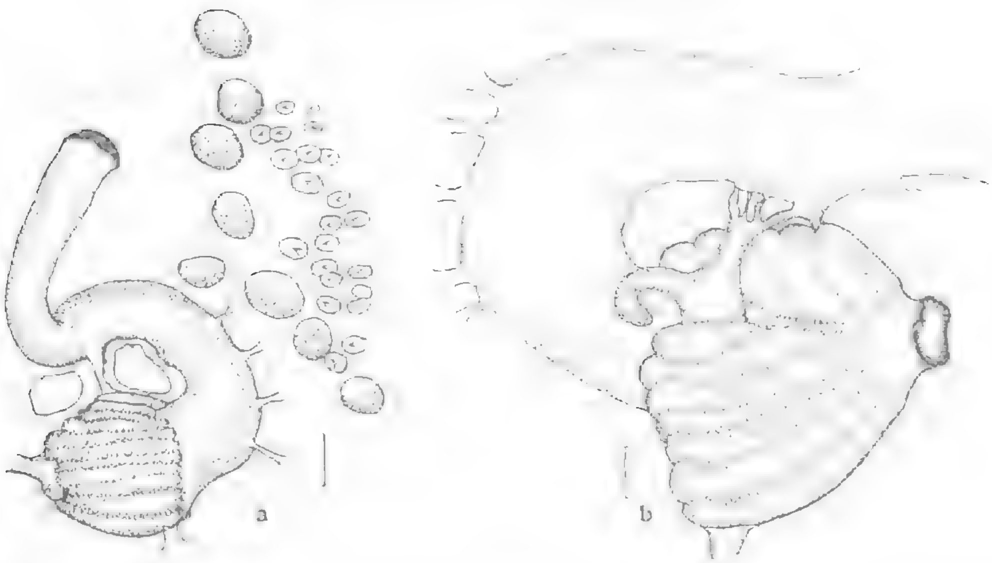


FIG. 117: *Amphicarpa diptycha* (WAM 1231.83) — a, left side of body wall showing gut, large eggs and small testes; b, parietal view of stomach. (Scales: a, 1.0 mm; b, 0.5 mm).

REMARKS: The species can be distinguished by its iridescent siphonal scales, purplish, muscular body wall, and close-set apertures enclosed by the characteristic ridge around the upper border of each zooid. The dark siphonal linings with iridescent scales and the siphonal vela distinguish the species from *A.meridiana* n.sp. *Amphicarpa duploplicata* has darkly pigmented siphonal linings as in the present species, lacks siphonal armature and gastric caecum and has long oviducts, and a very much longer body with more rows of stigmata. The larvae resemble those of *A. duploplicata*, but lack the black pigmentation that is present in the ectodermal ampullae of the latter species.

Amphicarpa nodula n.sp. is smaller than the present species and is further distinguished by having 3 branchial folds each side, hermaphrodite gonads only on the right side of the branchial sac and neither stomach caecum nor siphonal armature.

Amphicarpa inhacae: Vasseur, 1967a, from Ile Maurice in the Indian Ocean, bears a close resemblance to the present species, although the presence of siphonal spines is not reported.

Amphicarpa duploplicata (Sluiter, 1913)
(Fig. 118)

Stolonica duploplicata Sluiter, 1913, p.67.
Stolonica styeliformis Van Name, 1918, p.107. Tokioka, 1967a, p.165. Millar, 1975, p.278.

DISTRIBUTION

NEW RECORDS: Western Australia (Port Hedland, WAM 1234.83 1236.83; Cape Preston, WAM 868.83; Montebello Is, WAM 1235.83; Dampier Archipelago, WAM 1237.83).

PREVIOUSLY RECORDED: Aru I. (syntypes *S. duploplicata* ZMA V.TU986 Sluiter 1913). Philippines (Sulu Archipelago — Van Name 1918, Tokioka 1967a, Millar 1975).

The species has been taken from 10 to 64 m.

DESCRIPTION

EXTERNAL APPEARANCE: Upright, elongate zooids up to 3 cm high and 1 cm in diameter are attached to basal stolons by short, thick posterior stalks. They are crowded together and adhere to one another by short, fine test processes along about 4 sharp longitudinal ridges of the external test. The zooids sometimes form a compact, hemispherical mass, or they are found around stalks of weed. The test is often naked, but may have a light covering of sand that is easily rubbed off. The branchial aperture is terminal, and the atrial aperture subterminal. The test lining the short siphons is always black in preservative. The borders of the apertures are not lobed. The test is tough and leathery, whitish-beige in preservative.

INTERNAL STRUCTURE: The body wall is muscular, with inner longitudinal bands and an external layer of circular mucles. There are muscular vela at the base of the atrial and branchial siphons. About 20 tentacles of two size

FIG. 118: *Amphicarpa duploplicata* (WAM 868.83) — a, single zooid; b, internal body wall. (Scales: a, 2.5 mm; b, 2.0 mm).

orders alternate with rudimentary ones. The dorsal tubercle has a longitudinal slit. The dorsal lamina is long, the oesophagus opening from the posterior end of the branchial sac.

The branchial sac, which is attached to the body wall with very tough ligaments, has 2 folds on each side of the body. There are about 28 rows of stigmata, with 2 to 4 stigmata per mesh. The branchial formula for a typical specimen is: DL4(18)6(15)8E11(13)9(15)5DL.

The gut forms a short loop across the posterior end of the body and the rectum extends anteriorly at right angles to it. The stomach is rounded, with about 25 parallel longitudinal folds. There is a strong gastro-intestinal connective, but no gastric caecum. A small endocarp is present in the gut loop. A row of short ligaments beneath the gut attach it to the body wall, while a row around the stomach attaches it to the body wall and branchial sac.

The very numerous, small male follicles, each with a separate small duct, are crowded around the dorsal and ventral borders of both sides of the body and scattered over the middle of the body wall. One-egg ovaries are present, each associated with a small male follicle in a single, rather irregular row on each side of the endostyle, interrupting the crowded male follicles. The dorsally directed oviducts are wide and rather long.

Irregularly shaped endocarps are scattered over the internal body wall between the male follicles.

Larvae are present in the peribranchial cavity on both sides of the body. The larval trunk is 1.2 mm long and the tail about 3 mm. Primitive adhesive organs are arranged in a triangle at the anterior end of the trunk. There are 18 darkly pigmented, rounded ectodermal ampullae around the anterior end of the trunk.

REMARKS: The species appears to be abundant on the north-western continental shelf of Australia and off the Jolo Light in the Philippines. The Philippine and Australian populations do not have any apparent differences in morphology. The species is larger than others of this genus. The black siphonal lining is distinctive. The large number of rows of stigmata, the absence of a gastric caecum, the tough gastro-intestinal connective and the long oviducts are characteristic. *A. diptycha* is further distinguished by its siphonal spines, fewer rows of stigmata and internal longitudinal vessels, shorter zooid, longer gastric caecum and shorter oviducts.

Amphicarpa sigma (Tokioka, 1952) has similar dark pigment in the larval ampullae and its larva is much the same size as that of the present species. It also has 2 branchial folds on each side, an endocarp enclosed by the gut loop, long oviducts and lacks a gastric caecum. However, its zooids are only about one-third of the length of *A. duploplicata* and it has only 8 stomach folds and a long, vertical gut loop.

Amphicarpa meridiana n.sp.

(Fig. 119; Pl.IVk)

Amphicarpa diptycha: Kott, 1952, p.254; 1976a, p.74. Millar, 1960b, p.99; 1963, p.734.

Stolonica australis: Kott, 1972a, p.28; 1972b, p.183.

DISTRIBUTION

TYPE LOCALITY: New South Wales (Port Stephens, Fly Point, 10m, coll. P. Frederickson, October 1977, holotype QM GH2231; paratypes QM G10172).

NEW RECORDS: South Australia (St Vincent Gulf, QM G9316; Kangaroo I., QM G11995 GH2233; Yorke Peninsula, QM GH2322). Tasmania (Bruny I., NMV F51599). Victoria (Bass Strait, NMV H415 H448 H758 H405; QM G11873 GH2232; Seaspray, QM GH12714; Deal I., QM GH2239). New South Wales (Nambucca Heads, QM G10011; Solitary I., QM G9604; Port Kembla, QM G9605).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1972a; Great Australian Bight — Kott 1972b). Tasmania (d'Entrecasteaux Channel — Kott 1952). Victoria (Anglesea — Kott 1952; Cape Grant, Portland, Western Port — Kott 1976a; Port Phillip Bay — BM 1960.10.13.219 Millar 1960b). New South Wales (Port Jackson — BM 1886.6.3.56–7 Millar 1963).

The species has been taken from jetty piles and other fixtures, and from weed and other ascidians, from shallow depths down to 82 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright, up to 8 mm long. Posteriorly they may narrow to a short stalk fixed to basal stolons or they are sessile and cylindrical. The stalk is sometimes wide and flattened. They are often crowded together and adhere to one another along their sides to form a compact colony. The sessile apertures are on opposite sides of the rounded anterior end of the body. The test is thin, and usually translucent over the zooids, but always covered with a layer of sand except on a very small area around each aperture. The test of the basal stolons is tougher and often white and opaque. It is also covered with sand. The rim of the apertures is gathered when they are contracted, but it does not appear to be lobed.

INTERNAL STRUCTURE: The body wall is thin and translucent, with only thin layers of muscles and circular sphincter muscles around the apertures. The body wall does not adhere very closely to the test. Three test vessels (one ventral and one from each side of the mid dorsal line) and a terminal stolonic vessel project from the posterior end of the body. The tentacles are crowded and numerous, with larger and smaller sizes (about 25 of each) alternating with rudimentary ones. The dorsal tubercle is a large swollen cushion with a longitudinal slit in the V-shaped peritubercular area. The dorsal lamina is very long, the oesophageal opening being at the posterior end of the branchial sac.

There are 2 well defined and rather straight folds on each side of the body. The internal longitudinal vessels vary in number, but there are never more, and usually less, than 12 on a fold. Branchial formulae of individuals from different colonies are: DL2(10)4(8)5E5; DL0(5)1(5)2E; DL0(12) 4(8)5E; E5(5)4(7)0DL. An expanse of flat branchial sac lies on each side of the endostyle, but the most dorsal folds are very close to the dorsal lamina. The stigmata are in 15 to 19 rows, 4 to 6 stigmata per mesh.

The gut forms a short loop across the posterior end of the body, and the rectum continues anteriorly to open at the base of the atrial siphon in a two-lipped anus. The stomach is cylindrical and expands slightly distally. There are about 18 stomach folds. Those on the mesial surface are parallel to one another and extend the whole length of the stomach, but those on the parietal wall extend obliquely from each side of the suture line to the distal end of the stomach. A caecum extends into the gut loop from the distal end of the suture-line. It is of variable length and is sometimes curved. It may be very short and inconspicuous, however. A flat-topped endocarp is enclosed in the gut loop on each side of the gastro-intestinal connective. The intestinal part of the gut loop is short, and the rectum is long, curving up to the atrial aperture. The gut is fixed to the body wall by numerous tough ligaments from the outer border of the loop.

Male gonads consist of a single, small comma-shaped follicle. Ovaries are small, containing 2 or 3 ova at varying stages of development. There are hermaphrodite organs in a row along each side of the endostyle and across the top of the gut loop, and crowded patches of separate male follicles posterior, ventral and dorsal to the hermaphrodite organs. Larvae are sometimes present in the peribranchial cavity (QM G9310). The larval trunk is 1.2 mm long, the tail broad and only slightly longer (1.5 mm). The larval epidermis has about

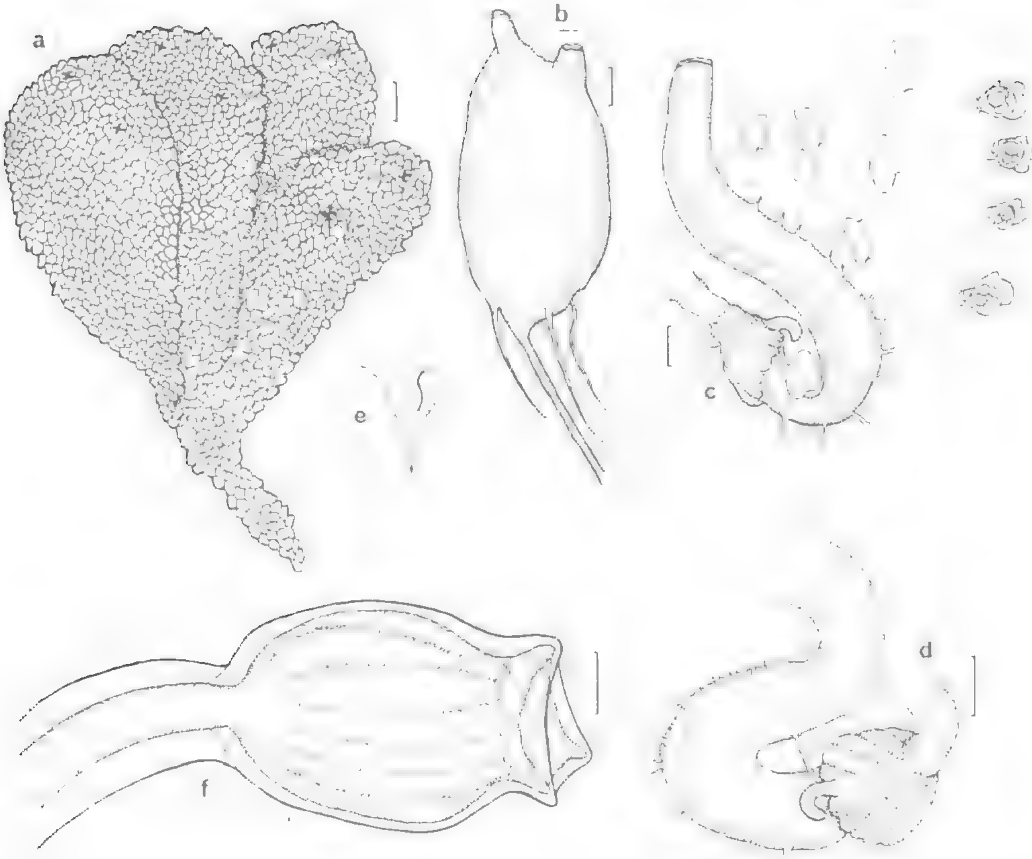


FIG. 119: *Amphicarpa meridiana* n.sp. — **a**, part of a colony (QM GH2231); **b**, body removed from test (QM G10011); **c**, inner body wall, left side (QM G10011); **d**, stomach and gut loop (BM 1960.10.13.219); **e**, dorsal tubercle with large, round neural ganglion; **f**, larva (QM G9310). (Scales: **a**, **b**, 1.0 mm; **c** – **e**, 0.5 mm; **f**, 0.2 mm).

12 parallel longitudinal furrows along the length of the trunk.

There are numerous small endocarps on the body wall.

REMARKS: The species has been confused with *A. diptycha*, as the shape of the colony, the gonads and the gut closely resemble those of the latter species. However, in the present species the zooids are smaller and more sandy, the dorsal lamina is longer, there are fewer internal longitudinal branchial vessels and there is no siphonal armature. The larval trunk is much the same length in both species, but the tail is longer and thinner and the parallel ectodermal furrows conspicuous in *A. diptycha*.

Amphicarpa nodula n.sp.
(Fig. 120)

DISTRIBUTION

TYPE LOCALITY: Queensland (Abbot Point, sandy mud, 20 m, coll. C. Roberts and L. Hammond, Ockleman Sledge, 19.3.81, holotype QM GH702)

FURTHER RECORDS: Queensland (Abbot Bay, paratypes QM GH1309 GH2308).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies consist of small, spherical, sand-encased ascidians about 5 mm in diameter on short, narrow stalks connected by stolons. The apertures are on the upper surface, about one third of the body length apart, and sessile. The test is strong and rather thick and, strengthened by the sand, is quite hard and rigid.

INTERNAL STRUCTURE: The body wall is muscular and purple in colour. It extends down into the narrow stalk. The dorsal tubercle has a simple longitudinal slit. The dorsal lamina is long and wide. The oesophagus opens at the posterior end of the branchial sac.

There are 3 rounded folds on each side of the body. Internal longitudinal vessels are very irregular and sometimes run obliquely across the stigmata. They are arranged according to the following formula: E1(3)3(7)3(10)1DL1(8)4(6)2(3)E. There are 15 rows of stigmata.

The gut loop is rather long, curving around in the posterior end of the body. The voluminous rectum extends forwards to the atrial aperture to form a deep secondary loop. The stomach is short, occupying less than a quarter of the ascending limb of the gut loop. It is also relatively narrow, with 15 longitudinal folds that extend the whole length of the stomach. There is only a very short gastric caecum that scarcely projects beyond the pyloric end of the stomach. The intestinal part of the loop is long, and of variable width. It encloses a large endocarp, which is usually compressed between the limbs of the loop. There is a gastro-intestinal connective. There is also a long endocarp in the secondary gut loop. The anal border is smooth and bilabiate.

Hermaphrodite gonads lie in a row on the right side of the endostyle, but they appear to be absent from the left side. They consist of small, flask-shaped, 2- or 3-egg ovaries and a single, small male follicle. Patches of male follicles occur anterior and posterior to the hermaphrodite organs on the right and in a wide band around the ventral border to the left of the endostyle.

Large endocarps are present on the body wall dorsal to the gonads. They are usually a dark colour.

REMARKS: The species resembles *Amphicarpa duploplicata* in having virtually no gastric caecum. However, it is readily distinguished by its small size, sandy test, very small stomach, long gut loop, the presence of 3 rather than 2 branchial folds on each side of the body and the absence of female glands on the left side of body.

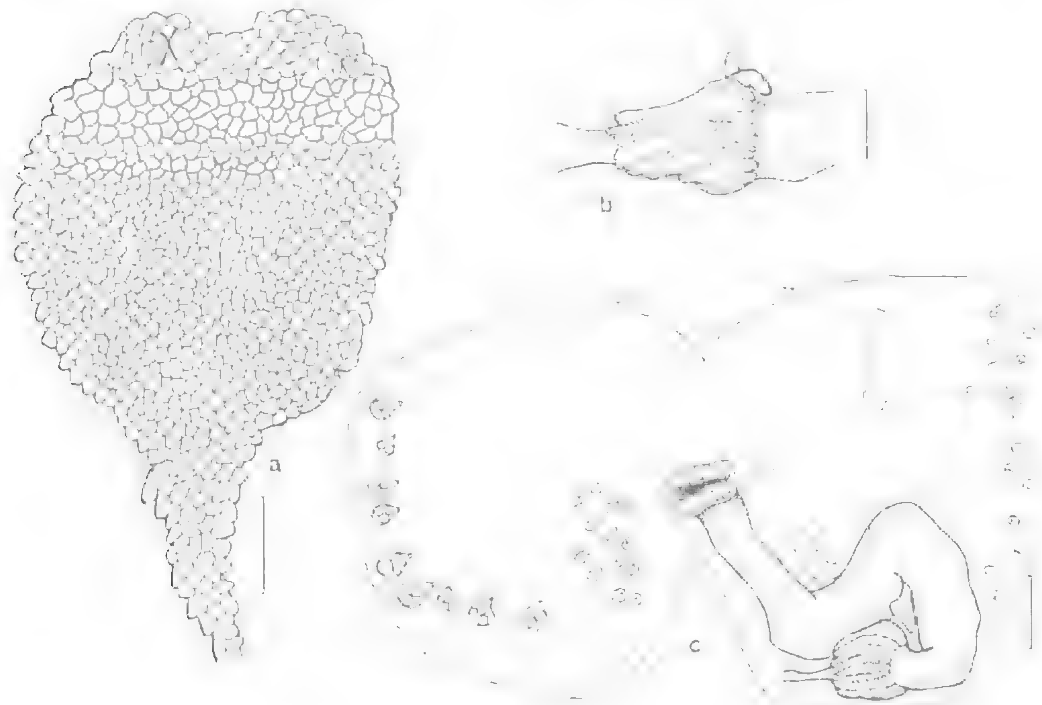


FIG. 120: *Amphicarpa nodula* n.sp. (QM GH309) — a, single zooid; b, stomach with caecum and part of gastro-intestinal connective; c, inner body wall, showing small testis on both sides of the body and ovaries on the right side. (Scales: a, c, 1.0 mm; b, 0.5 mm).

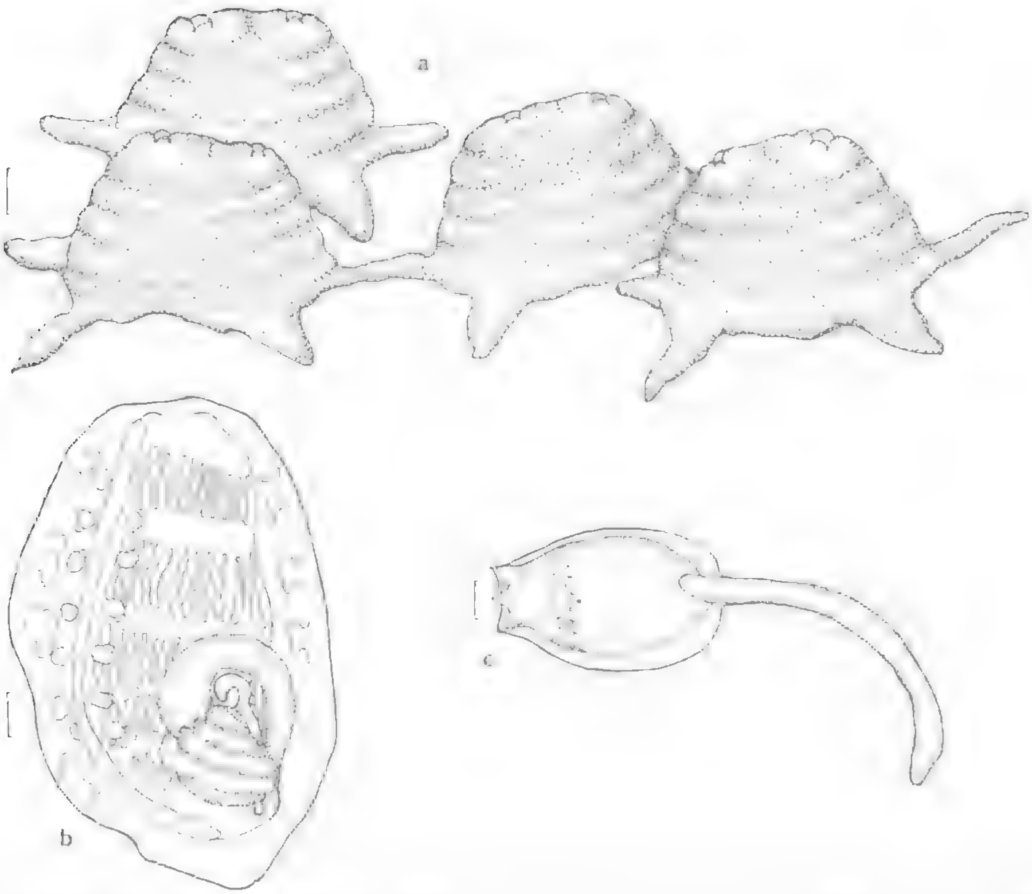


FIG. 121: *Polyzoa violacea* — a, colony (QM GH1842); b, zooid from ventral surface (QM G10038); c, larva (WAM 1229.83). (Scales: a, 0.5 mm; b, 0.25 mm; c, 0.1 mm).

Genus **Polyzoa** Lesson, 1831

Type species: *Polyzoa opuntia* Lesson, 1831

Polyzoinae without branchial folds and with hermaphrodite gonads. The ovaries have a small number of eggs. One or 2 testis follicles are associated with each ovary.

Dictyostyela Oka, 1906, is defined as having 2 male follicles, and *Polyzoa* as having a single male follicle associated with each ovary. However, observations on *P. violacea* suggest that this is a variable character, and that only a single genus is represented. *Monobotryllus* Oka, 1915 is a synonym of *Polyzoa*.

The genus is not diverse but is known from the sub-Antarctic, southern California, Japan and the Indo-West Pacific. It has not been recorded from the Atlantic Ocean.

Gynandrocarpa nigricans Sluiter, 1904, has embedded zooids and 4 internal longitudinal vessels, a single male follicle in each of 3 or 4 hermaphrodite sacs on each side of the body. It may also be species of *Polyzoa*.

Polyzoa violacea (Oka, 1915)
(Fig. 121)

Monobotryllus violaceus Oka, 1915b, p.20.
Dictyostyela depressa Oka, 1926, p.348.
Polyzoa depressa: Kott, 1981, p.198.
Polyzoa sagamiana Tokioka, 1953a, p.245. Kott, 1964, p.131.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 1229.83). Queensland (Point Vernon, QM GH1842; Heron I., QM GH805 GH2082 GH2728-9 GH2731; Northwest I., QM GH2730; Deltaic Reef, QM GH251).

PREVIOUSLY RECORDED: Queensland (Heron I. — Kott 1964). Japan (Oka 1926, Tokioka 1953a). Fiji (Kott 1981). Indian Ocean (Oka 1915b).

Specimens from Heron I. are often found growing on *Cnemidocarpa areolata* and *Herdmania momus*. The species has been taken on the surface of rubble, shells etc. from intertidal waters down to 64 m.

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of hemispherical or oval zooids up to 3 mm long, firmly fixed to the substrate by their flat bases and connected to each other by basal stolons or a basal membrane. The apertures are both on the upper surface, the atrial aperture in the centre and the branchial aperture toward one end of the upper surface. The apertures are smooth when extended, and are sessile. The test is thin and transparent, but tough, with the red body wall showing through it. It is often wrinkled. Living colonies appear as groups of pink or red scales.

INTERNAL STRUCTURE: The body wall is delicate. There are short muscle-bands radiating from each siphon and an external layer of fine, circular muscles. There are about 12 relatively short and stubby branchial tentacles. The dorsal lamina is long, the oesophageal opening being at the posterior end of the body.

There are 8 to 10 internal longitudinal vessels in the branchial sac, no folds, 5 to 10 rows of 20 to 30 stigmata, and 3 to 4 stigmata per mesh, each crossed by a parastigmatic vessel.

The gut forms a compact loop in the posterior third of the body, and the rectum curves up to the atrial aperture. The stomach is short and broad, with 12 longitudinal stomach folds that are long toward the outer curve of the gut and very short toward the inner curve. A large gastric caecum curves into the pole of the gut loop. The anal border is smooth.

There are about 4 large eggs in the ovaries associated with 1 or 2 male follicles beneath the ovary. The male follicles are sometimes slightly lobed. Up to 6 gonads lie in a row to the right of the endostyle and up to 4 on the left. Larvae are sometimes present in the atrial cavity. They are almost spherical, the larval trunk about 0.6 mm long, with a single sense organ, 3 conical adhesive organs arranged in a triangle anteriorly, about 16 ectodermal ampullae around the trunk, and a tail about 1 mm long

REMARKS: This species is distinguished by its short, broad stomach with long, curved caecum. The number of internal longitudinal branchial vessels, number of rows of stigmata and numbers of stigmata per row are all variable. The number of testis follicles beneath each ovary also varies from one to a pair.

Genus **Metandrocarpa** Michaelsen, 1904

Type species: *Goodsiria dura* Ritter, 1896

Small polyzoinid zooids in which male and female gonads are separate. Gonads are present on both sides of the body, the female on the left or on both sides, and the club-shaped male gonads on both sides. The branchial wall is usually flat.

The zooids have fewer (less than 15) rows of stigmata and a shorter stomach than have most other genera of the Polyzoinae. The number of internal longitudinal branchial vessels varies greatly from 4 to 30. In the single species with 30 internal longitudinal vessels, there are 2 or 3 branchial folds on each side (*Metandrocarpa agitata* n.sp.).

The definition of the genus is modified from that of Michaelsen, 1922 to include species in which there are more than the usual number of internal longitudinal branchial vessels, and in which the branchial sac is folded. The modification of the generic definition to include species with a folded branchial sac is based on the close relationship, evidenced by the identical form and arrangement of their gonads, between *M. thilenii* Michaelsen, 1922 and *M. miniscula* n.sp. (without folds) and *M. agitata* n.sp. (with folds).

Brewin (1948) has discussed at some length the position of the ovaries in relation to the mid-ventral line in *M. thilenii* and has argued that their presence on the left side of the body is sufficiently exceptional to justify the erection of the genus *Okamia*, distinct from *Metandrocarpa*. In fact, the gonads are crowded along the mid-line, and it appears from Michaelsen's (1922) description that their provenance is from both sides of the body. The position of the ovaries in *M. miniscula* n.sp. confirms this view. Accordingly, *Okamia* is regarded here as a synonym of *Metandrocarpa*.

In the antipodean western Pacific species *M. thilenii* Michaelsen, *M. agitata* n.sp. and *M. miniscula* n.sp., the gonads are almost identical. However, the postero-ventral position of the ovaries contrasts with their anterior position in the other known species of the genus, *M. taylori* Huntsman, 1912 and *M. dura* (Ritter, 1896), found along the western coast of North America (see Van Name 1945). This difference may be found to constitute a generic distinction, but for the present the western Pacific species are retained in *Metandrocarpa*.

Vegetative reproduction in the species *M. taylori* has been studied by Newberry (1965).

TABLE XI — SUMMARY OF CHARACTERS OF SPECIES OF *METANDROCARPA* RECORDED FROM AUSTRALIA

Species	[1]Range	Zooids: test; shape	Branchial folds	[2]Branchial sac	Rows of stigmata	Stomach folds	Stomach caecum	♂ L:R	♀	Additional features
M. agitata n.sp.	Townsville - Dongara	rough naked; upright	2/side	7(11)	17	15	narrow	8:8	5, median	—
M. miniscula n.sp.	Innisfail	smooth, sandy; spherical	none	4/side	8	8	none	1:4	1/side	—
M. indica	Dongara - SA	smooth, sandy; laterally flat	"	4/side	10	10	long	?	?	long atrial siphon

[1]All species indigenous. Range given anti-clockwise around the continent. [2]Internal longitudinal vessels: between folds (on folds)

Australian records are few and widely separated. It is possible that the small zooids are overlooked by collectors and that the genus is more common than the present records indicate.

KEY TO THE SPECIES OF *METANDROCARPA* REPORTED FROM AUSTRALIA

1. Branchial folds present........*M. agitata* n.sp.
   Branchial folds not present 2
2. Gastric caecum and spur present ... *M. indica*
   Gastric caecum and spur not present
   .... *M. miniscula* n.sp.

Metandrocarpa agitata n.sp.
(Fig. 122)

DISTRIBUTION

TYPE LOCALITY: Western Australia (92 km W of Dongara, 29°07.5S, 113°57.4′E, 110 m, rubble with sponges, coll. L. Marsh on M.V. Sprightly, triangular dredge, 17.2.76, holotype WAM 970.83, paratypes WAM 41.84).

FURTHER RECORD: Queensland (Cleveland Bay, QM GH3051).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are small and upright, up to 7 mm high and more or less cylindrical. The body is fixed posteriorly and there is no stalk. The apertures are either depressed slightly into the surface on opposite sides of the rounded upper surface or there is a terminal branchial aperture and an atrial aperture up to halfway down the dorsal surface when the body is very contracted. There are no distinct lobes around the apertures, and the test appears to be gathered around them when they are contracted. The test is very tough and leathery and of moderate thickness. It has slight, irregular swellings and creases on the surface, which may be partly the result of contraction. The test is cream-coloured in preservative.

INTERNAL STRUCTURE: The body wall is very thin and adheres closely to the test. Delicate muscle bands are arranged in an external layer of circular fibres over an internal layer of longitudinal fibres. There are about 20 rather short and sturdy branchial tentacles. The small, circular opening of the neural gland is in a small, V-shaped peritubercular area and is directed anteriorly. The dorsal lamina is a narrow, plain-edged membrane.

There are 2 branchial folds on each side of the body, with sometimes an additional fold on the right. They are low and wide, formed by the crowding together of a number of internal longitudinal vessels. They flatten out posteriorly.

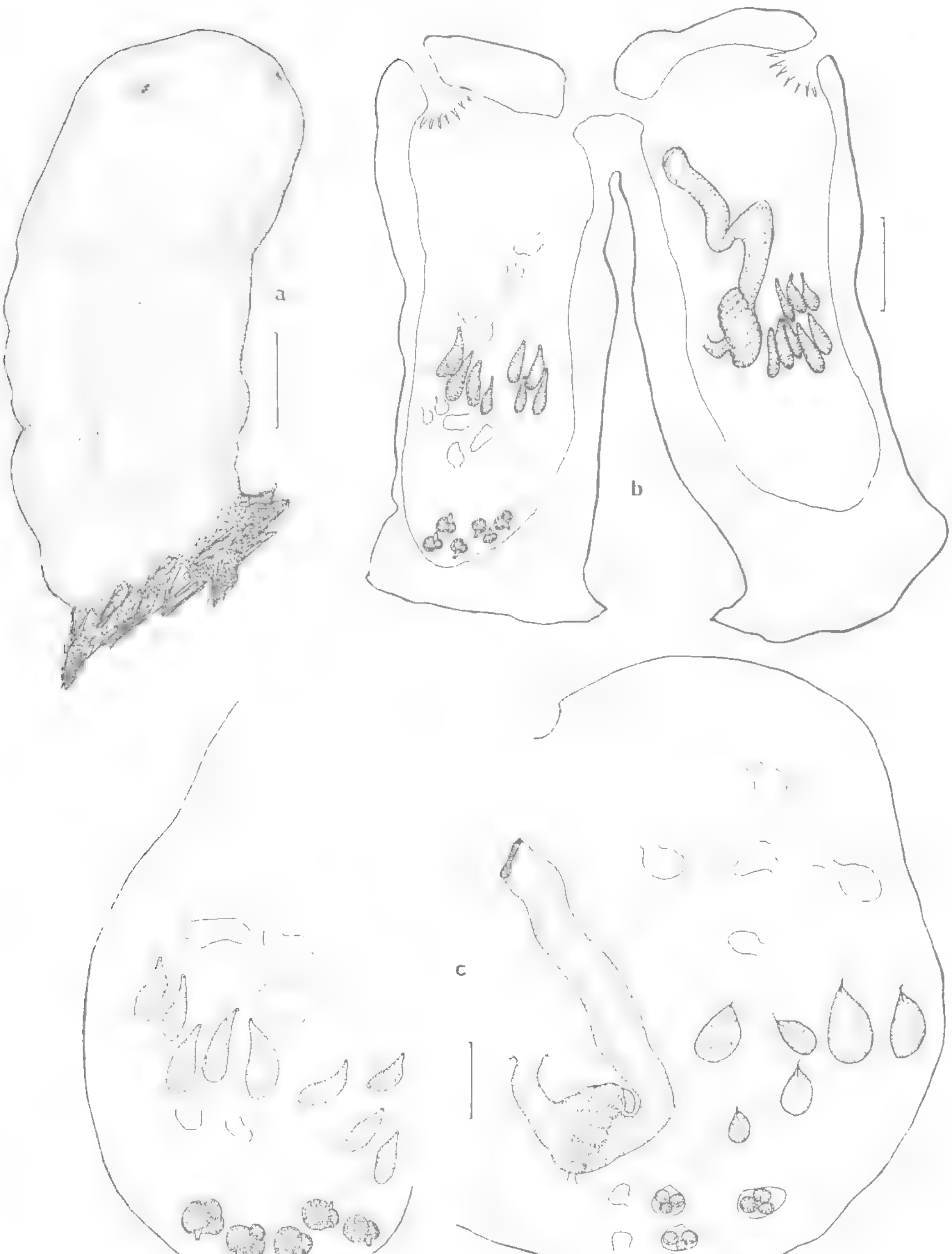


FIG. 122: *Metandrocarpa agitata* n.sp. (WAM 960.83) — **a**, single zooid; **b**, **c**, body wall on right and left sides of the body respectively. (Scales: **a**, **b**, 1.0 mm; **c**, 0.5 mm).

internal longitudinal vessels in the holotype are arranged according to the following formula: E7(7)6(7)1DL1(7)4(11)6E. There are 17 rows of stigmata, with 2 or 3 stigmata in each mesh, crossed by parastigmatic vessels and set slightly obliquely to the internal longitudinal vessels.

The gut forms a very short loop with a rather variable course that may result from different degrees of body contraction. The oesphagus is moderately long, and the stomach short and pyriform, widest at the distal end. It is covered by a rather thick layer of body wall. Consequently the 15 longitudinal gastric folds are rather inconspicuous externally. There is a narrow curved caecum in the loop of the gut. The rectum is rather long and the anal border is smooth. The gut is attached to the body wall by a number of fine ligaments: several lie in a row halfway across the lateral side of the stomach, one is at the pole of the gut loop and about 6 lie along the length of the rectum. The changes in the shape of the gut loop as a result of muscle contraction of the body are probably accommodated by these ligaments.

There is an arc of about 8 large, club-shaped single testis follicles about two-thirds of the way down each side of the body, their short ducts (from the distal end of each gonad) directed anteriorly and toward the atrial aperture. A few of these male glands are slightly posterior or anterior to the main arc. Up to 7 small, spherical ovaries, each with 2 or 3 eggs, are crowded in a curve around the mid-ventral line at the posterior end of the body. Very short oviducts are present, oriented to the right or left. Large, more or less irregular, endocarps are present between the gonads, and a few are scattered over the body wall anterior to the gonads.

REMARKS: The characters of the present species are intermediate between *Metandrocarpa thilenii* Michaelsen, 1922 from New Zealand (see also Brewin, 1948) and *Metandrocarpa miniscula* n.sp. from Queensland. The former has a similar number of gonads and the latter has fewer gonads. Of these two, *M. thilenii* most closely resembles the present species both in internal and external structure, but is distinguishable by its flat branchial sac.

Metandrocarpa indica Kott, 1972
(Fig. 123)

Metandrocarpa indica, Kott, 1972b, p.182.

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, WAM 874.83).

PREVIOUSLY RECORDED: South Australia (Investigator Strait — Kott 1972b).

In South Australia, the species is recorded from 23 m on a sand and shell bottom in strong surge. The record from Western Australia is from 44 m.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies consist of crowded, sessile, more or less circular, laterally flattened zooids up to 5 mm in diameter fixed to common basal stalks that often expand into a wider membrane. The test is thin, and brittle with embedded sand. Apertures are close together on the upper surface. The branchial aperture is sessile, but the atrial aperture is on a conspicuous, narrow, conical siphon directed away from the branchial aperture.

INTERNAL STRUCTURE: The body wall is thin and closely adheres to the test. It has a close mesh of fine circular and longitudinal muscle fibres, which is continuous over the body. The dorsal tubercle has a simple longitudinal slit. There are 12 very delicate branchial tentacles.

There are 4 internal longitudinal branchial vessels on each side of the unfolded pharynx. The stigmata, 6 to 8 per mesh, are in 9 or 10 rows. Fine parastigmatic vessels cross each mesh.

The gut forms a simple open loop across the posterior end of the body. The rectum extends anteriorly to the atrial opening and forms a wide angle with the gut loop. The stomach is short and wide, the inner side expanding into a slight spur projecting into the gut loop. The stomach suture line diverges from the longitudinal axis of the stomach and extends up the outside of the spur. A long caecum continuous with the suture line curves around in the pole of the gut loop. There are 6 broad, longitudinal stomach folds lying parallel to the suture line and extending the full length of the stomach. On the mesial surface are 4 additional anterior folds that become progressively shorter as they extend out along the spur, their proximal ends terminating against the suture line. The intestine is relatively narrow. The anal border is smooth and bilabiate. There are a few broad ligaments from the outer curve of the caecum to the intestine.

Gonads have not been detected in the any of the available material.

REMARKS: The peculiar, slightly spurred stomach of the present species resembles those of other species of the genus (Van Name 1945). It is also similar to the stomach of *Stolonica vesicularis*. The conspicuous, pointed atrial siphon directing the excurrent water away from the sessile branchial aperture is unique.

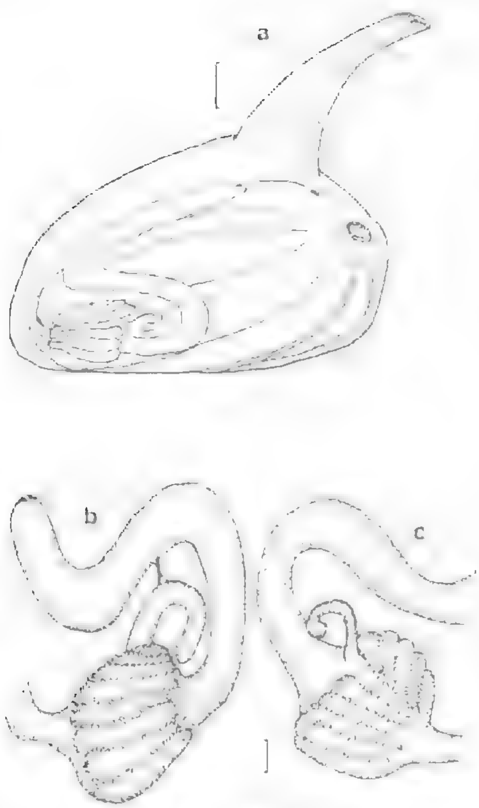


FIG. 123: *Metandrocarpa indica* (WAM 874.83) — **a**, zooid removed from sandy test showing protruding atrial siphon; **b**, **c**, mesial and parietal side of gut loop respectively. (Scales: **a**, 0.5 mm; **b**, **c**, 1.0 mm).

Metandrocarpa miniscula n.sp.
(Fig. 124)

DISTRIBUTION

TYPE LOCALITY: Queensland (Mission Beach, intertidal epibiont on *Ascidia* sp., attached to underside of rubble, coll. P. Kott, August 1961, syntypes QM GH1500).

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of very small, almost spherical, zooids up to 3 mm in diameter with branching basal stolons that have wide, flat membranous expansions along each side. The zooid is encased in a dense coat of sand and the apertures are very inconspicuous and sessile.

INTERNAL STRUCTURE: When removed from the test, the body is seen to be slightly elongate, with a terminal branchial aperture on a short siphon turned slightly toward the side, away from the atrial siphon, which projects straight forward from about one-third of the distance along the dorsal surface. Fine longitudinal muscles radiate from the siphons and circular fibres are particularly conspicuous across the anterior part of the ventral border. The branchial tentacles are short, and the neural gland has a simple opening.

There are 4 internal longitudinal vessels on each side of the branchial sac and 4 or 5 elliptical stigmata in each mesh. There are 8 rows of stigmata.

The gut forms a slightly curved loop across the posterior half of the body. The short, rounded stomach has about 8 wide stomach folds. There is no caecum, but a wide gastro-intestinal connective is present.

There is a single, small 2- or -3 egg ovary about halfway up the body on each side of the endostyle. Single, large, oval male follicles are also present on each side of the body dorsal to the ovary, 1 anterior to the gut loop on the left and 3 or 4 radiating inside the ventral curve of the body on the right. A relatively large larva, with a trunk about 0.4 mm long, was present in the peribranchial cavity. It has a single sense organ, a circle of rounded ectodermal ampullae and triradially arranged adhesive organs.

REMARKS: The present species is distinguished from *Metandrocarpa indica* by its sessile apertures, and the absence of gastric spur and caecum. The relative position of the male and female gonads resembles that in the New Zealand species, *M. thilenii* Michaelsen, 1922 (see Brewin, 1948), and *M. agitata* n.sp. from Western Australia. In both these species the gonads are more numerous than in *M. miniscula* and their zooids are not sandy.

Genus **Symplegma** Herdman, 1886

Type species: *Symplegma viride* Herdman, 1886

The genus contains species with 4 internal longitudinal vessels, without branchial folds and with a single hermaphrodite gonad on each side of the body.

The condition of the branchial sac resembles that of *Metandrocarpa* and *Alloeocarpa* and, as in those genera, species are either embedded or upright and connected by stolons. However, the gonads, each with a central ovary and 2 male follicles (anterior and posterior to the ovary, respectively) are distinctive and are known only in the genus *Symplegma*.

Two species (*S. oceania* and *S. reptans*) and a possible third (*S. arenosa*) are known from Australia. The last, a seldom-encountered upright species, is probably indigenous. However, mature

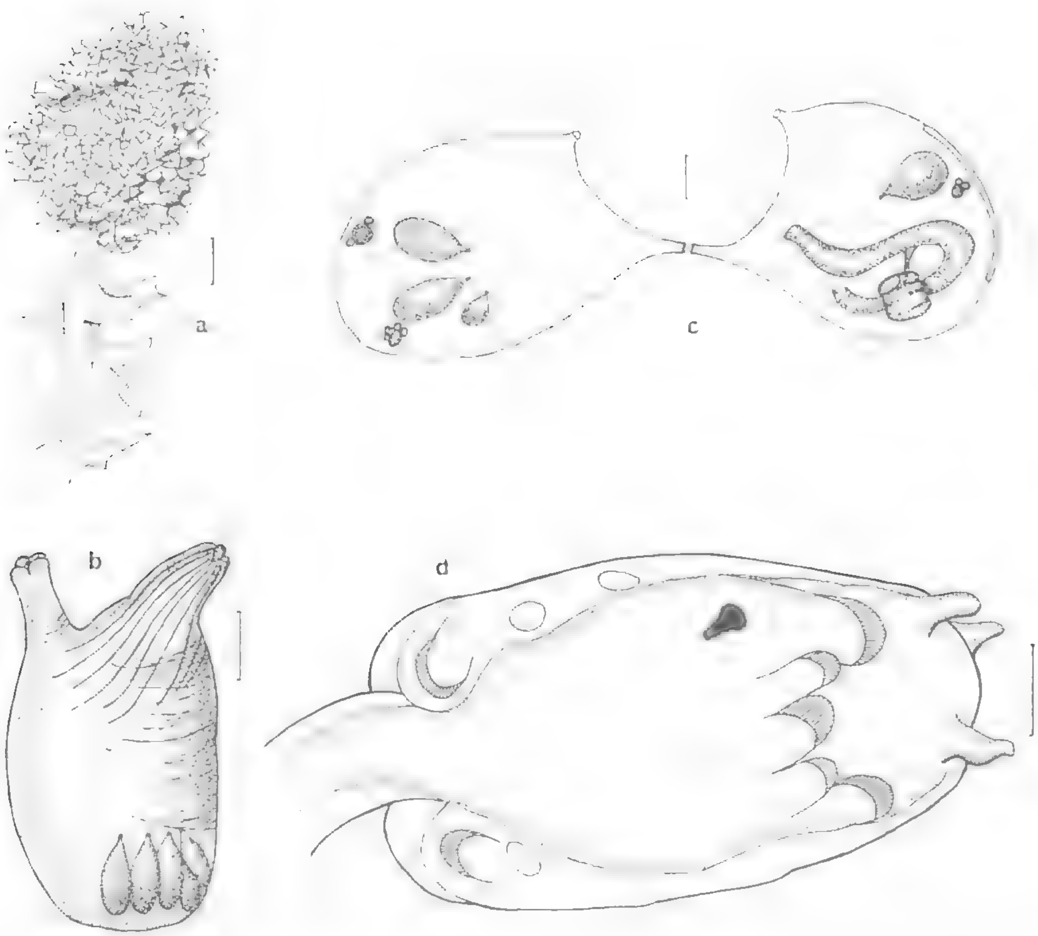


FIG. 124: *Metandrocarpa miniscula* n.sp. (QM GH1500) — **a**, external appearance; **b**, zooid removed from test; **c**, inner body wall; **d**, larval trunk. (Scales: **a**, 0.5 mm; **b**, **c**, 0.25 mm; **d**, 0.05 mm).

specimens with gonads have not yet been taken and the species is included only provisionally in this genus. The first two species have a wide range in the western Pacific. *Symplegma oceania* is a commonly reported encrusting species which forms extensive sheets over a variety of weed and rubble substrates in shallow water, often where sediments and brackish water create habitats that are less than optimal for other ascidian species.

The other species of *Symplegma* known from the western Pacific is *S. connectens* Tokioka, 1949b, from Japan. It closely resembles *S. reptans*.

Botryllocarpa Hartmeyer, 1909 is separated from *Symplegma* only by the presence of 3 internal longitudinal vessels rather than 4. It is a monotypic genus, represented by *B. viridis* (Pizon, 1908) recorded once only, from Indonesia.

KEY TO THE SPECIES OF *SYMPLEGMA* RECORDED FROM AUSTRALIA

1. Upright zooids joined by stolons .. *S. arenosa*
   Zooids prostrate and embedded 2
2. Not more than 8 stomach folds; caecum short, straight .... *S. reptans*
   More than 8 stomach folds; caecum long, curved .... *S. oceania*

Symplegma arenosa Kott, 1972
(Fig. 125)

Symplegma arenosa Kott, 1972b, p.182.

DISTRIBUTION

NEW RECORDS: South Australia (Waldegrave I., specimen lost).

PREVIOUSLY RECORDED: South Australia (Waldegrave I. — Kott 1972b).

TABLE XII — SUMMARY OF CHARACTERS OF THE GENUS *SYMPLEGMA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Colony	Sand in test	Zooid arrangement	Stigmata: no. rows	Stomach folds	Stomach caecum
? *S. arenosa*	—	Waldegrave I.	upright zooids with basal stolons	present	random	15	14	straight
S. reptans	WP	Capricorn Gp	thin investing sheets with prostrate embedded zooids	absent	circles	8–14	8	curved
S. oceania	IWP	Dampier Arch. - Lizard I.	"	"	random	11	10–16	straight

[1]IWP, Indo-West Pacific. [2]Range given anti-clockwise around the continent.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are formed of upright, sandy individuals, which are sessile and attached to basal stolons that form a tangled basal plate. The sessile apertures are close together on the upper surface in a sand-free circular area surrounded by a rounded ridge of sandy test. When the apertures are contracted, the whole upper surface is depressed, and the sandy test on each side comes together along the mid-line, forming a cover over the apertures.

INTERNAL STRUCTURE: The body musculature is strong anteriorly. Longitudinal bands radiate from each siphon and short transverse bands cross the mid-line dorsal and ventral to the apertures. These bands are probably associated with the closure of the test over the withdrawn apertures. The muscles fade out about one third of the distance down the body.

There are 4 internal longitudinal vessels on each side of the flat branchial sac, 6 to 8 stigmata per mesh and 15 rows of stigmata.

The gut forms a very short loop across the posterior end of the body, and the rectum is long, extending forwards to the atrial opening. The stomach is short and barrel-shaped, with about 14 longitudinal folds. There is a short, straight gastric caecum and a divided ligament between the caecum and the intestine.

Gonads are not present in any of the available specimens.

REMARKS: Kott (1972b) believed that this was a species of the genus *Symplegma* (rather than *Metandrocarpa* or *Polyzoa*) on the basis of the form of the divided gastro-intestinal ligament, which resembles the ligament in *Symplegma oceania*. The numbers of rows of stigmata and stomach folds are rather high for *Metandrocarpa*.

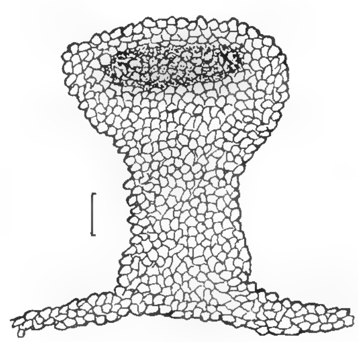


FIG. 125: *Symplegma arenosa* (after Kott 1972b) — external appearance. (Scale: 1.0 mm).

However, the possibility that this species does not belong in the genus *Symplegma* should not be overlooked.

Symplegma oceania Tokioka, 1961
(Fig. 126; Pl.Va)

Symplegma oceania Tokioka, 1961, p.114. Kott, 1981, p.199. Kott and Goodbody, 1982, p.531.

Symplegma viride: Michaelsen, 1904a, p.50; 1918, p.39; 1919, p.101. Hartmeyer and Michaelsen, 1928, p.358. Van Name, 1945, p.232 (part, not Atlantic Ocean records). Kott, 1952, p.253; 1964, p.129; 1975, p.11; 1976a, p.74. Millar, 1966, p.368. Plante and Vasseur, 1966, p.149. Vasseur, 1967a, p.111. Tokioka, 1967a, p.162. Kawamura and Nakauchi, 1976, p.4.

Symplegma aff. *viride*: Tokioka and Nishikawa, 1975, p.334.

Diandrocarpa brakenhielmi Michaelsen, 1904a, p.50. Herdman, 1906, p.33.

Gynandrocarpa quadricornulis Sluiter, 1904, p.127.

?*Gynandrocarpa similis* Sluiter, 1904, p.97.

DISTRIBUTION

NEW RECORDS: Western Australia (Cape Preston, WAM 1239.83; Port Hedland, WAM 1240.83; Rowley Shoals, WAM 1243–4.83; Houtman's Abrolhos, WAM 1241-2.83; Cockburn Sound, WAM 1238.83, QM G9659). South Australia (Great Australian Bight, QM GH945 GH2411; St. Vincent Gulf, QM G9589; Kangaroo I., QM G11991). Queensland (Moreton Bay, QM GH339, QM GH364; Pt. Vernon, QM GH9417 G9413 (with larvae); Heron I., QM GH2224-5 GH2724-5; Wistari Reef, QM GH2602; Townsville; Lizard I., QM G9773; Martha Ridgeway Reef, QM GH549).

PREVIOUSLY RECORDED: Victoria (Port Phillip Bay — Millar 1966; Western Port — Kott 1976a). Queensland (Bargara Gladstone, Yeppoon, Mackay — Kott 1964). Indonesia (*Gynandrocarpa quadricornulis* holotype ZMA V.TU562.4 Sluiter 1904; ? *G. similis* type ZMA V.TU562.5 Sluiter 1904). Noumea (Tokioka 1961). Palau Is (Tokioka 1967a). Fiji (Kott 1981). Thailand (Tokioka 1967). Hong Kong (Kott and Goodbody 1982). China (Tokioka 1967a). Sri Lanka (Herdman 1906). Indian Ocean (Vasseur 1967a, Plante and Vasseur 1966).

DESCRIPTION

EXTERNAL APPEARANCE: In life, the colonies are thin and bright or pastel coloured, pomegranate purple or sulphur yellow (Ridgeway 1886), orange-red, pale lemon, or greenish lemon, sometimes with clear red lines outlining the apertures and in the prepharyngeal band. The colonies are usually extensive, covering weed, shell or other substrates. The test is transparent and the completely embedded zooids are fairly crowded. Spherical terminal ampullae are evident in the test between the zooids, but are more conspicuous around the margins of the colony where they are elongate and parallel to one another.

Colonies from Kangaroo I. (QM G11991) are hemispherical rather than flat and sheet-like and the zooids tend to stand upright in the test (rather than lying on their ventral surface). In life, these specimens were green with white rims around the apertures. No morphological differences from other specimens were detected.

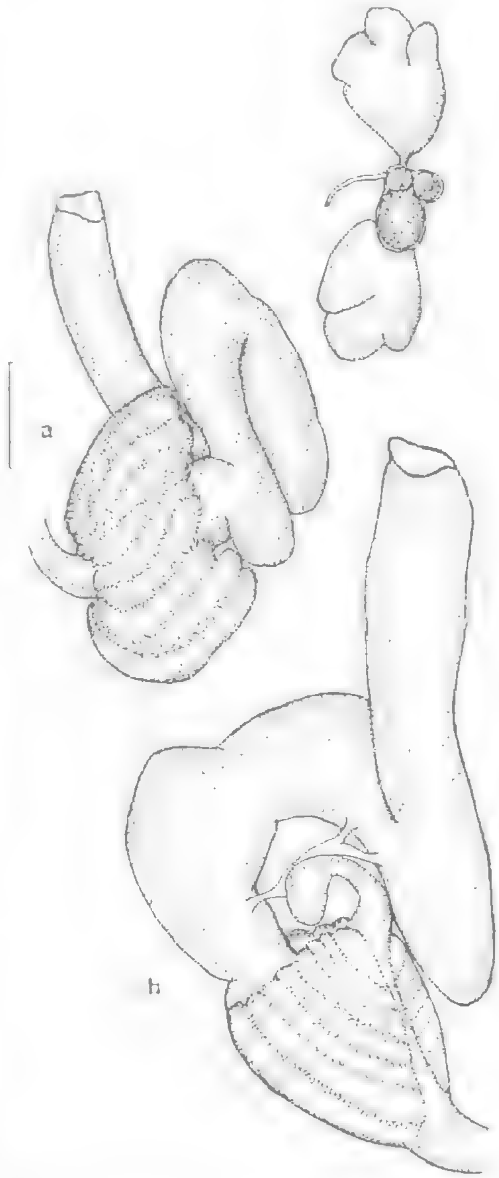


FIG. 126: *Symplegma oceania* — a, ventral view of gut loop with left gonad; b, dorsal view of gut loop. (Scale: 0.25 mm).

INTERNAL STRUCTURE: Zooids are dorso-ventrally flattened and lie obliquely on their postero-ventral surface, with both sessile apertures on the dorsal surface, the branchial aperture near the anterior end and the atrial aperture about halfway along. The body musculature consists of an outer layer of fine circular bands and an inner layer of longitudinal bands. There are variable numbers of branchial tentacles (up to 40: Tokioka 1967a), but they are often less numerous. There is an elongate slit on the dorsal tubercle.

The flat branchial sac has 4 internal longitudinal vessels and 8 to 14 rows of stigmata, with up to 30 stigmata in a row. The second row of stigmata on the left does not reach the dorsal line. There is an area of unperforated pharyngeal wall at the anterior end of the pharynx that is traversed by internal longitudinal vessels.

The gut forms a short loop at the posterior end of the right side of the body, and the rectum extends anteriorly and around the side of the body onto the dorsal surface. The stomach is short and very wide. It occupies about half of the length of the proximal limb of the loop. It has 10 to 16 conspicuous parallel folds. A long gastric caecum curves around in the pole of the gut loop from the distal end of the stomach. There are 1 or 2 gastro-intestinal connectives from the outer curve of the caecum (one from near its distal tip, the other from about halfway along it) to the pole of the gut loop and the distal end of the intestine respectively. One or both of these connectives are often branched. They are embedded in a membrane from the body wall.

The gonads consist of a small rounded ovary, with 2 or 3 eggs, in the centre of each side of the body wall. There are two pyriform male follicles sometimes deeply divided around their proximal ends, one anterior and one posterior to the ovary. Their ducts join at the base of the short oviduct to form a fairly long, narrow vas deferens that projects free into the atrial cavity.

Larvae are present in specimens collected from Hervey Bay in November (QM G9413). They have a larval trunk of 0.6 mm, 3 triradially arranged adhesive organs, a single sense organ near the middle of the body, about 8 ectodermal ampullae, and parallel ridges along each side of the trunk.

REMARKS: There are two related species (*S. reptans* and *S. connectens*) in the western Pacific, from which *S. oceania* is distinguished by its long, curved gastric caecum and 2 gastro-intestinal connectives (Tokioka 1967a, Kott 1981, Kott and Goodbody 1982). Adult colonies of *S. viride* from the Atlantic also closely resemble those of the present species. However, protostigmata (which are present in *S. viride*) do not form in the developing branchial sac of *S. oceania*, but are suppressed in favour of the direct development of true stigmata. There are also differences in the formation of the test vessels in these two species (Kawamura and Nakauchi 1976).

The type specimen of *G. similis* Sluiter, 1904 resembles this species in most characters. However, although a cluster of 2 or 3 eggs is present on each side, no male follicles were seen, and the synonymy is not confirmed.

The colony and its habit superficially resemble *Chorizocarpa sydneyensis*; preserved specimens can be readily confused.

Symplegma reptans (Oka, 1927)

(Fig. 127; Pl.Vb)

Synstyela reptans Oka, 1927b, p.496.

Symplegma reptans: Tokioka, 1949b, p.49; 1951b, p.173; 1953a, p.243; 1954b, p.85; 1959a, p.227. Kott and Goodbody, 1982, p.529.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM GH2633-6; Wistari Reef, QM GH2603 GH2632 GH2985).

PREVIOUSLY RECORDED: Hong Kong (Kott and Goodbody 1982). Japan (coast of Honsyu, Sikoku and Kyusyu — Oka 1927b, Tokioka 1949b 1951b 1953a 1954b 1959a).

DESCRIPTION

EXTERNAL APPEARANCE: The colony, which is very thin, is stretched over the surface of the substrate. When removed from the substrate, it contracts. The living colony is dramatic: it is pink, with large, triangular white patches (looking like petals of daisies) arranged in circles, indicating the circular arrangement of the zooids, the atrial apertures opening in the centre. These white triangles (seen in the living specimen) are the prebranchial areas around the branchial apertures. In freshly preserved material, there is a mosaic of more or less opaque, granular patches in this region, but they do not always persist and zooids usually become pale pink, cloudy and translucent. In the preserved colonies removed from the substrate, the circular arrangement of the zooids is obscured. There is a network of blood vessels in the body wall. The test is whitish and translucent, and is very thin indeed. Terminal ampullae of test vessels are present in the narrow test partitions between the zooids, but they are relatively sparse and are not a conspicuous feature of the test.

INTERNAL STRUCTURE: Zooids lie on their ventral surface in the test and are dorso-ventrally flattened. They are about 3 mm long. Both

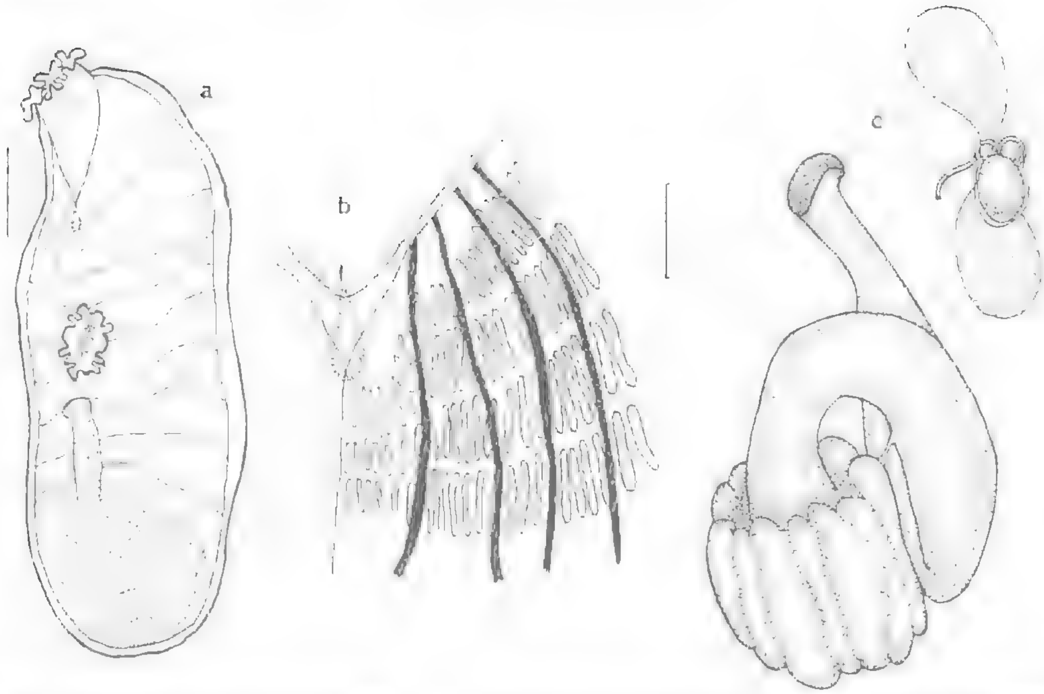


FIG. 127: *Symplegma reptans* (QM GH2603) — a, zooid from dorsal surface; b, branchial sac showing incomplete second row of stigmata; c, ventral view of gut loop and gonad. (Scales: a, 0.5 mm; b, c, 0.25 mm).

apertures are on the upper surface, the branchial aperture a little way from the anterior end of the body. The atrial aperture is from one half to two-thirds of the body length from the anterior end of the body. Both apertures are on very small, short siphons. The borders are not lobed, but sometimes are slightly frilled with contraction of the apertures. In freshly preserved material there are minute red spots evenly spaced around the border of each aperture, about 60 around the atrial aperture but fewer around the branchial aperture. Patches of red pigment are randomly distributed on the body wall. There are about 20 branchial tentacles. The prebranchial area is quite extensive. The peritubercular area is V-shaped, and the neural gland opens by a simple longitudinal slit.

There are 11 rows of stigmata. The second row of stigmata on each side never reaches the mid-dorsal line, the first row curving dorsal to it at about the level of the dorsal internal longitudinal vessel. There are up to 28 stigmata in each row; 4 internal longitudinal vessels extend the whole length of the branchial sac. The long, regular stigmata are arranged according to the following formula: E6,4,6,5,7DL. They are reduced in length near the dorsal lamina. The half-row of stigmata at the anterior end of the branchial sac appears to extend its length ventrally, forcing the branchial aperture around onto the dorsal surface.

The gut forms a tight loop confined to the posterior one-third of the body. The stomach is more or less barrel-shaped and has 8 distinct longitudinal folds, more numerous on the lateral side of the stomach than on the mesial side. A short, straight gastric caecum extends up into the tight pole of the loop. It is connected to the descending intestinal limb of the loop by a single, straight ligament. The descending limb of the gut loop extends more or less parallel to, and to the left of, the stomach. It then turns dorsally and anteriorly into the rectum, which extends along the dorsal surface to terminate in a smooth-rimmed anus near the atrial aperture.

There are undivided, pyriform male follicles anterior and posterior to the single ovary on each side of the body. The male follicles converge to the short vas deferens that projects from beneath the ovary. The larvae have no ampullae in the anterior part of the trunk (Tokioka 1951b).

REMARKS: The species is characterised by its relatively short gut loop; wide stomach folds; short, straight gastric caecum; and completely prostrate orientation of the zooids. The living specimens are very readily distinguished from *Symplegma oceania*. However, preserved colonies are superficially very similar. Although *S. oceania* has a similar half row of stigmata at the anterior end of the branchial sac, it has a larger stomach, with a long, curved caecum and two branched gastro-intestinal connectives.

Symplegma connectens Tokioka, 1949b from Japan (Tokioka 1953b) is distinguished from the present species only by its more numerous stomach folds. Like *S. reptans*, it lacks larval ectodermal ampullae at the anterior end of the trunk.

Genus **Chorizocarpa** Michaelsen, 1904

Type species: *Chorizocormus sydneyensis* Herdman, 1891

The genus has zooids embedded in firm gelatinous test, a flat branchial sac, 3 internal longitudinal branchial vessels, and a single unisexual gonad on each side of the body, the male on the left and the female on the right. It has very conspicuous branching test vessels and large, crowded, spherical, terminal ampullae. The gonads appear to be very ephemeral, and are seldom present in preserved specimens.

The genus is distinguished from the related genus, *Symplegma* Herdman, 1886 by its more randomly oriented zooids, 3 rather than 4 internal longitudinal branchial vessels and from *Botryllocarpa* Hartmeyer, 1911 by its unisexual rather than hermaphrodite gonads. The colony form of the type species is very similar to that of *Symplegma oceania* and related forms. *Chorizocarpa* is separated from the Botryllinae by its gonads and usually by the absence of colonial systems. However, *Botryllus primigenus* Oka, 1928, recorded from Japan, China and the Palau Is (see Tokioka 1967a), differs from other botryllids by its independently opening zooids. Its gonads must be relied on to distinguish it from *Chorizocarpa, Symplegma* and *Botryllocarpa*.

Although *C. sydneyensis* is recorded relatively frequently at locations from Port Jackson to Indonesia, the other 2 known species have been collected only from Port Jackson and from Torres Strait respectively. As single colonies of all three species are extensive and conspicuous, it is surprising that they have not been collected more often. The fact that 2 of the 3 known species were taken in close association in Port Jackson in the late 19th century, but have not been collected there since is also surprising. There is no evidence that they still occur in that heavily industrialised harbour.

TABLE XIII: Summary of Characters of Species of *Chorizocarpa* recorded from Australia

Species	Range	Colony	Stomach	♂ follicles
C. guttata	Port Jackson	zooids project; lobed	long, sub-spherical	numerous
C. michaelseni	Thursday I.	zooids project; not lobed	short, sub-spherical	single
C. sydneyenis	Port Jackson - Lizard Is., W Pacific	zooids completely embedded; not lobed	long, trumpet-shaped	2

KEY TO THE SPECIES OF *CHORIZOCARPA* RECORDED FROM AUSTRALIA

1. Stomach occupies no more than half of the ascending limb of the gut loop .... *C. michaelseni*
   Stomach occupies more than half of the ascending limb of the gut loop 2
2. Stomach long and narrow ......*C. sydneyensis*
   Stomach not long and narrow...... *C. guttata*

Chorizocarpa guttata Michaelsen, 1904
(Fig. 128)

Chorizocarpa guttata Michaelsen, 1904a, p.104.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: New South Wales (Port Jackson — AM Y2012 Y2013 Michaelsen 1904a).

A depth of 20 m is recorded for one of the specimens from Port Jackson.

DESCRIPTION

EXTERNAL APPEARANCE: The colony consists of a continuous layer of firm basal test, crowded with branching test vessels and spherical terminal ampullae, with projecting zooids. The test is constricted to form rounded lobes containing one or two zooids. Terminal ampullae are seldom present in the thin layer of test that covers the zooids. The zooids lie on their ventral surface with both their apertures projecting slightly from their upper or dorsal surface. In some places, where the zooids appear to be regressing, they are completely embedded in tough and shiny test without terminal ampullae. The collector's note for specimen AM Y2013 states that it is a "fluorescent composite ascidian".

INTERNAL STRUCTURE: The body wall is delicate, with fine longitudinal muscles extending only halfway across the body and circular muscles confined to the siphons. The body is only about 4 mm long and does not adhere closely to the thin test that covers it. There are 20 simple tentacles of varying length. The very small dorsal tubercle has a simple opening.

The branchial sac is robust, and the internal longitudinal vessels thick and conspicuous. There are 6 rows of long, oval stigmata arranged between the longitudinal vessels: DL2,3,4,6E.

FIG. 128: *Chorizocarpa guttata* (AM Y2012) — a, colony showing terminal ampullae packed in basal test; b, gut and gonad on left side of the body; c parietal view of gut. (Scales: a, 1.0 mm; b, c, 0.5 mm).

The gut is voluminous and occupies the posterior half of the body. It forms a tight primary loop and a deep, open, secondary loop. The stomach is large and almost spherical, occupying almost the whole of the ascending limb of the loop. There are 10 wide, parallel longitudinal gastric folds. There is a very short, straight caecum at the distal end of the suture line, with a short gastro-intestinal connective extending from near its base across to the intestine. The anal border is bifid.

The male gonad is conspicuous, consisting of a large circle of long, pyriform, lobed follicles, which taper to the centre of the circle, where they join a short vas deferens projecting into the atrial cavity. The testis occupies the whole antero-ventral part of the left body wall anterior to the gut. No ovary was detected, although Michaelsen (1904a) reported a sac-like ovary on the right side of the body.

REMARKS: Specimens of this species are mixed with the types of *Chorizocormus subfuscus* (AM U272 < *Chorizocarpa sydneyensis*). The two species are distinguished by their colonies: the small projecting lobes of the present species, containing one or a small group of zooids, appearing as small nodules along the fronds of weed on which it is growing. The relatively few rows of stigmata, the short stomach and gastric caecum are also distinctive.

Chorizocarpa michaelseni (Sluiter, 1900)

Synstyela incrustans: Sluiter, 1895, p.183.
Synstyela monocarpa Sluiter, 1898a, p.55 (part).
Synstyela michaelseni Sluiter, 1900b, p.110.
Gynandrocarpa michaelseni: Michaelsen, 1900, p.24.
Chorizocarpa michaelseni: Michaelsen, 1904a, p.108.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Queensland (Thursday I. — Sluiter 1895).

DESCRIPTION (after Michaelsen 1904a)

EXTERNAL APPEARANCE: The colony forms a translucent encrusting layer from 1 to 3 mm thick. Zooids are 2.8 mm long and 2 mm wide. Apertures are sessile. Large (0.25 mm) terminal ampullae of test vessels are present in the test.

INTERNAL STRUCTURE: There are 16 branchial tentacles: 4 long, 4 moderately long and 8 short. The dorsal tubercle is an oval papilla with a longitudinal slit. The branchial sac has the usual 3 internal longitudinal vessels on each side. There are no parastigmatic vessels, and 4 to 6 stigmata are present in each mesh. The dorsal lamina is long.

The gut is present in the posterior half of the left side of the body. It forms a rather straight loop. The stomach is very short, occupying only about half of the ascending limb of the loop. There are 8 broad, parallel folds. There is a conspicuous, bulbous gastric caecum. A gastro-intestinal connective extends from the base of the caecum to the intestine. The anal border is smooth and the rectum short.

The gonads consist of a single, pyriform male follicle on the left anterior to the gut and a sac-like ovary in a corresponding position on the right. Both ovary and testis project from the body wall.

REMARKS: The species is distinguished from others in the genus by its projecting gonads, very short stomach and conspicuous gastric caecum.

Chorizocarpa sydneyensis (Herdman, 1891)
(Fig. 129)

Chorizocormus sydneyensis Herdman, 1891, p.636; 1899, p.95.
Chorizocarpa sydneyensis: Michaelsen, 1904a, p.93. Sluiter, 1904, p.100. Hastings, 1931, p.77.
Chorizocormus subfuscus Herdman, 1891, p.636; 1899, p.96.
Chorizocormus leucophaeus Herdman, 1891, p.636; 1899, p.97.
Gynandrocarpa systematica Sluiter, 1904, p.98.
Symplegma systematica: Nishikawa, 1984, p.130.
Gynandrocarpa purpurea Sluiter, 1904, p.96.

DISTRIBUTION

NEW RECORDS: Queensland (Wistari Reef, QM GH2638; Heron I., QM GH2639 GH2687; Lizard I., QM GH2637).

PREVIOUSLY RECORDED: New South Wales (Port Jackson — AM U257 U261 U272 U169 Y1983 Herdman 1891 1899). Queensland (Low Isles — BM 1930.12.17.18 Hastings 1931). Indonesia (*Gynandrocarpa systematica* lectotype ZMA V.TU562.4, paratypes V.TU1265 Sluiter 1904; *G. purpurea* types ZMA V.TU551.3 Sluiter 1904). Truk I. (Nishikawa 1984).

DESCRIPTION

EXTERNAL APPEARANCE: The colony forms a smooth, gelatinous layer about 3 mm thick, encrusting the stalks and fronds of weed. The test is fairly firm, with the zooids completely embedded in it. The zooids lie on their ventral surface, with their dorsal surface just beneath the upper surface of the colony. The sessile apertures, which are both on the dorsal surface of the zooid, open separately to the exterior. Blood vessels branch through the test from a main vessel that extends the length of the basal test of the colony.

The branches terminate in pear-shaped to spherical ampullae about 0.2 mm in diameter. These terminal ampullae are sometimes very crowded at the surface. They are present also in the test over the zooids, but are never as crowded there as between the zooids. Living colonies superficially appear to be slate coloured with paired rows of oblique, cream marks. However, closer examination shows them to have a clear test with greenish yellow corpuscles crowded in the terminal ampullae of test vessels. The upper surface of each zooid, seen clearly through the test, has a mosaic of white patches (caused by crowded white corpuscles in the body wall) at the posterior end; similar white and blue corpuscles in symmetrically arranged triangular areas between the apertures; and an auricular purple (Ridgeway 1886) patch each side of the atrial aperture. Zooids are arranged obliquely in paired symmetrical rows, the terminal branchial apertures toward the outside, the mid-dorsal atrial apertures and posterior ends of the zooids toward the centre of each pair of rows. In preservative, the zooids are brown, the test is colourless and the arrangement of the zooids in long, double-rows is not apparent. In preservative, zooids appear to be arranged at random in the test and occur in clumps, with an area of unoccupied test between these clumps. The zooids are up to 4 mm long and are not dorso-ventrally flattened. They are often actively budding, the bud lying alongside the parent zooid.

INTERNAL STRUCTURE: The body wall is delicate and adheres closely to the test. Fine longitudinal muscles radiate from the siphons over the upper (dorsal) half of the body. Circular muscles are present only around the apertures. The branchial tentacles are relatively short and, although their numbers vary, there are never very many: there are from 4 to 8 longer tentacles and a similar number of shorter ones. In some specimens, the longer tentacles form a cone or funnel that projects back into the siphon, while short tentacles project into the centre of the lumen across the top of the funnel formed by the longer tentacles. Some rudimentary tentacles fill in gaps around the circumference of the tentacular ring. The neural gland has a simple opening. The dorsal lamina is long, the oesophagus opening at the posterior end of the branchial sac.

The 10 rows of stigmata are distributed between the 3 internal longitudinal vessels in the following way: E6,6,5,10DL. There are no parastigmatic vessels.

The gut forms a narrow loop extending about halfway up the ventral half of the body. The rectum forms a wide, secondary loop, curving anteriorly onto the dorsal surface to open at the base of the atrial opening in a 2-lipped anus. The oesophagus is long and curved. It expands abruptly into the very long, trumpet-shaped stomach that occupies almost the whole of the ascending limb of the gut loop. There are 10 long, parallel gastric folds which, at the proximal end, continue into rather long pouches that flare out from the stomach and overlap the oesophagus. These pouches progressively increase in length from the parietal to the mesial side of the gut, where they often separate from one another and curve away from the oesophagus. The distal end of the stomach gradually narrows to the intestine. There are 4 short, wide ligaments along the ventral border of the stomach that bind it to the body wall. A further 2 ligaments from the outer curve bind the pole of the gut to the body wall. Two gastro-intestinal connectives are present, one at the proximal end of the stomach and one at the distal end. These branch into tubules, which surround the gut. The tubules from the distal connective, which surround the intestine about halfway down the descending limb of the gut loop, are more numerous and more conspicuous than those from the proximal end of the stomach, which cross to the distal end of the intestine. The rectum is swollen. There is no gastric caecum. Michaelsen (1904a), who examined Herdman's specimens, commented that he had difficulty reconciling Herdman's description of the gonads with his own observations. Michaelsen found gonads only in the specimen lot AM U272 (*C. subfuscus* Herdman). They consisted of a sac-like ovary on the right side of the endostyle about halfway up the body and a pair of undivided male follicles in a similar position on the left, just anterior to the gut loop, the vasa efferentia joining to a short vas deferens that projected into the atrial cavity on a small papilla. Unfortunately no gonads can now be detected in this specimen and none were found in the newly recorded material, which all appear to be in an active vegetative phase.

REMARKS: The species is readily distinguished by the extensive and smooth-surfaced, firm, sheet-like colonies, completely embedded zooids, and long, trumpet shaped stomach.

Gonads are not present in any of the material examined. Their presence is apparently ephemeral.

In Port Jackson the species was taken with *C. guttata*, which it resembles, being distinguished from the latter species by the shape of its stomach and its longer and more deeply embedded zooids.

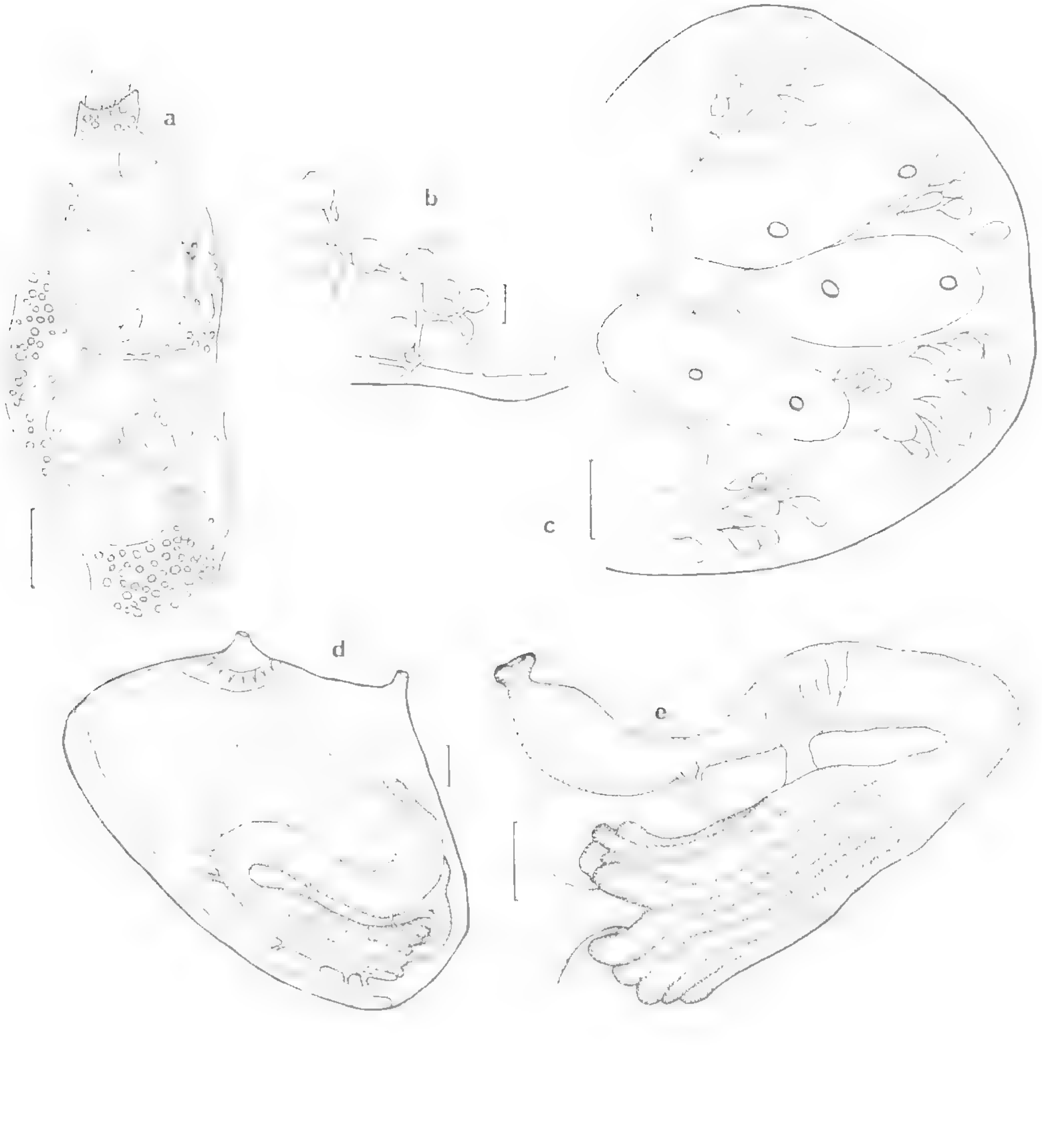


FIG. 129: *Chorizocarpa sydneyensis* — **a**, colony (AM U257); **b**, terminal ampullae and test vessels near the base of the colony (AM U257); **c**, growing margin of colony showing club-shaped terminal ampullae (QM GH2687); **d**, zooid removed from test (AM U257); **e**, gut loop (AM U257). (Scales: **a**, 2.0 mm; **b**, **d**, **e**, 0.25 mm; **c**, 0.5 mm).

Subfamily BOTRYLLINAE Adams and Adams, 1858

Vegetatively reproducing species of the Styelidae in which the small zooids are completely embedded in common test and arranged in systems. The branchial aperture is smooth; the atrial aperture usually has a lip from the anterior border. The branchial sac is without folds, and there are 3 internal longitudinal vessels on each side of the body. The gonads consists of 1 to 4 ovaries and a single testis on each side of the body. Fertilisation is internal. The embryos develop to tailed larvae attached to the body wall and protruding from it either from the outside of the body wall (*Botrylloides*) or into the atrial cavity (*Botryllus*). There is an extensive system of test vessels, terminating in spherical to elongate ampullae near the surface of the test between the zooid systems and around the borders of the colony.

The integration of the colonies in this subfamily is greater than is known for any other phlebobranch or stolidobranch ascidian. It is the only subfamily outside the Aplousobranchia in which the zooids form systems. Development of vegetative zooids in each new generation is integrated and occurs by pallial budding and by vascular budding in the test vessels. Thus a colony can regenerate even in the absence of zooids (Oka and Watanabe 1957; Sabbadin *et al.* 1975). Cloning of colonies can occur, although genotypes are self-recognising and usually are not self-fertilising (Sabbadin 1971).

The larvae of the subfamily are large with a large yolk mass and well developed larval organs, including a light and gravity sensitive organ (photolith) and ectodermal ampullae, as in the viviparous larvae of most colonial families (Berrill 1935a, 1950).

The subfamily is most closely related to the polyzoinid genera *Symplegma* and *Chorizocarpa*, both of which have zooids completely embedded in the common test, branchial sacs without folds and with a limited number of internal longitudinal vessels, single gonads on each side of the body, and an extensive system of test vessels with crowded terminal ampullae. The Botryllinae are distinguished mainly by their systems of zooids, which never occur in the Polyzoinae. Only in a single species (*Botryllus primigenus* Oka, 1928) does each zooid retain a separate atrial opening to the exterior, but that species is separated from *Symplegma* by its 3, rather than 4, internal longitudinal vessels; and from *Chorizocarpa* by the presence of both male and female gonads on each side of the body.

Species of the subfamily are extremely variable in pigmentation and colour pattern. Sabbadin and Graziani (1967) recognise 48 colour morphs in *Botryllus schlosseri*, a species that has been used extensively for experimental work on its genetics and vegetative processes (see Sabbadin 1979). Variations are in pattern as well as in the types and combinations of pigments:

> The blood in *Botryllus schlosseri* is the source of a variety of pigment cells, which, diffusing into the connective tissue or crowding into certain preferential areas on the surface of the zooids, give rise to many different pigmentation patterns. It is almost impossible to find two colonies equally pigmented even if closely related. Moreover increase in the numbers of pigment cells with age, and minor differences in their arrangement according to the functional stage, determine changes of pigmentation within its life cycle. No wonder that in the last century numerous species and sub-species of *Botryllus* were established on the grounds of impressive pigmentation diffferences. (Sabbadin and Graziani 1967, p. 596).

Both the form and systems of the colonies are also variable. Their external appearance is affected by the maturity, size and crowding of systems, and the particular blastogenic generation of zooids that is present at any time (Sabbadin 1979). *Botrylloides* spp. are equally variable.

All species, with the exception of *B. stewartensis*, form investing sheets in which the zooids are arranged in circular or double-row branching systems. The extent to which the systems are crowded together appears to be variable. Terminal ampullae are crowded in the test between the systems. Three-dimensional growth often appears to be initiated from these zooid-free expanses of test between the systems to form lobed rather than sheet-like colonies (see, especially, *Botryllus schlosseri*, *Botrylloides leachi* and *B. magnicoecum*).

There is also a possibility that the size of the zooids, the numbers of rows of stigmata and the number per row increase with maturity, probably with successive vegetative generations.

In this subfamily, intraspecific variability, together with the lack of inter-species diversity, has led to confusion in the taxonomy. Species distinctions based on the shape of terminal ampullae of test vessels or on the colour, shape or size of the colony and its systems are probably invalid in most cases, if the shape of the atrial aperture, stomach and gastric caecum are the same. The level of generic diversity is also low, there being only two related genera (*Botryllus* and *Botrylloides*), each with a relatively small number of species.

Botryllinae are common fouling organisms in estuaries and in shallow waters. The opportunistic behaviour of their populations and the wide geographic range that most species enjoy may be the result of flexibility conferred by their highly integrated colonies (Kott 1982).

The sub-family is represented in the Arctic (see Berrill 1950, Van Name 1945) and south to the temperate waters of southern Australia, New Zealand and South Africa (Millar 1962a). Neither of the genera is represented in the Antarctic or sub-antarctic, and they have not been recorded from the southern part of the American continent. Records from Stewart I., New Zealand (Brewin 1960, Millar 1982a) are the most southerly for species of Botryllinae.

KEY TO THE GENERA OF BOTRYLLINAE

Developing embryos protrude into atrial cavity .... *Botryllus*

Developing embryos protrude outside the body wall .... *Botrylloides*

Genus **Botryllus** Gaertner, 1774

Type species: *Alcyonium schlosseri* Pallas, 1766

The genus is characterised by the endogenous development of ova, which remain attached to the body wall and protrude into the atrial cavity as they develop. The ovaries are always anterior to the testis. There are up to 4 ova on each side in some species.

Australian species of *Botryllus* have a more restricted atrial aperture than do *Botrylloides* spp., and it is often produced forward on a siphon with a small lip from the anterior border of the opening. The stomach is short and barrel-shaped, with about 8 deep folds. The most common species in Australian waters is *Botryllus schlosseri*, which has a wide cosmopolitan distribution. *Botryllus stewartensis* occurs around the south-eastern corner of the Australian continent, and off Stewart I. and to the east of South I., New Zealand.

KEY TO THE SPECIES OF *BOTRYLLUS* RECORDED FROM AUSTRALIA

1. Stigmata in 4 or 5 rows .... *B. tuberatus*
   Stigmata in more than 5 rows 2
2. Test with embedded sand....................... 3
   No sand embedded in the test ... *B. schlosseri*
3. Zooids in terminal-free ends of cylindrical stalks .... *B. stewartensis*
   Colony a cushion-like mass without upright cylindrical stalks containing zooid systems .... *B. purpureus*

TABLE XIV — SUMMARY OF CHARACTERS OF SPECIES OF *BOTRYLLUS* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Colony	Test	Systems	Rows of Stigmata	Gastric caecum
B. tuberatus	WP	Mid Qld; mid WA	thin, investing	soft	circular	4	L-shaped
B. schlosseri	NE Atlantic - Mediterranean	NW Aust. - NE Aust.	investing to stalked lobes	firm, fleshy	circular to elongate	8–12	"
B. purpureus	Japan	SW Aust.	investing	sandy	circular	7	short curve
B. stewartensis	New Zealand	S Aust. - NSW	cylindrical stalks	"	"	8–12	"

[1] WP, western Pacific. [2] Range given anti-clockwise around continent.

In addition to the species recorded from Australia, the following species are known from the western Pacific:

Botryllus primigenus Oka, 1928 from Japan and the Palau Is (Tokioka 1967a) has zooids with 4 rows of stigmata but, unlike *B. tuberatus*, with separate atrial openings to the exterior.

Botryllus magnicoecus; Nishikawa, 1984, from Truk I., has circular systems and some sand on the surface of the test. The species is not conspecific with *Botrylloides magnicoecum* Hartmeyer, 1912. It appears to have features in common with *Botryllus purpureus*.

Botryllus purpureus (Oka, 1932)

Psammobotrus purpureus Oka, 1932d, p. 102.
Botryllus schlosseri: Kott, 1952, p. 259 (part, specimens from Hamelin Bay and Green Pools, SW Australia).

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Western Australia (SW Australia — Kott 1952).

DESCRIPTION

EXTERNAL APPEARANCE: The test is full of embedded sand, and the zooids and terminal ampullae of test vessels are relatively inconspicuous. The zooids are arranged in circular systems. They are orange in preservative.

INTERNAL STRUCTURE: The zooids are not more than 2 mm long. The branchial apertures are terminal and smooth-bordered. The atrial apertures are small, produced forward on a more or less tubular projection of the body wall that forms a pseudo-siphon. There are 8 branchial tentacles; the 4 that are arranged radially are longer than the others.

There are 7 rows of stigmata, with about 16 per row. The gut forms a simple loop across the posterior end of the left side of the body, and the rectum extends forward to the atrial aperture. The stomach is small, with 8 conspicuous folds and a moderately long, curved caecum.

Gonads were not detected in the Australian specimens. In juveniles of the Japanese material, there were 2 or 3 spherical eggs and a pyriform testis follicle (Oka 1932d).

REMARKS: The species is not often recorded, probably because the sandy colony is so inconspicuous. Kott (1952) regarded the species as conspecific with *B. schlosseri*. Sand is never included in the test of the latter species, however, and despite the fact that the zooids are very much the same, the sandy form appears to be a distinct species.

The records, indicating a range from Japan to south-western Australia, suggest that the species will be found to occur throughout the tropical western Pacific.

Botryllus schlosseri (Pallas, 1766)
(Fig. 130; Pl.Vc)

Alcyonium schlosseri Pallas, 1766, p.355.
Botryllus schlosseri: Savigny, 1816, p.200. Binney, 1870, p.3. Dall, 1870, p.255. Bancroft, 1903, p.149. Hartmeyer, 1909, p.1379; 1923, f. typica p.344. Van Name, 1910, p.350; 1921, p.398; 1930, p.477; 1945, p.220. Sumner, Osborne and Cole, 1913, p.731. Pratt, 1916, p.669; 1935, p.746. Michaelsen, 1921a, p.108; 1922, p.481. Arnback, 1923, p.12. Harant, 1927a, f. typica p.245; 1927b, f. typica p.9; 1930, p.22; 1931, f. typica p.342. Hartmeyer and Michaelsen, 1928, f. typica and f. aureus p.330. Salfi, 1932, p. 338. Harant and Vernières, 1933, f. typica p. 37. Huus, 1936, p. 12. Plough and Jones, 1937, p.101. Grave, 1937, p.563. Richards, 1938, p.254. Brewin, 1946, p.112; 1950b, p.344; 1958, p.439; 1960, p.119. Pérès, 1949, p.203; 1951, p.1070. Berrill, 1950, p.216. Tokioka, 1951a, p. 9; 1953a, p. 239. Kott, 1952, p.259 (part, not sandy colonies); 1972a, p.31. Sabbadin, 1971, p.379; 1979, p.433. Sabbadin and Graziani, 1967, p.559. Millar, 1982a, p.61. Kott and Goodbody, 1982, p.532.
Botryllus stellatus Gaertner, 1774, p.37. Couthouy, 1838, p.11. Gould, 1841, p.320.
Botryllus gouldii Verrill, 1871, p.211.
Botryllus rubens Alder and Hancock, 1912, p.62.
Botryllus virescens Alder and Hancock, 1912, p.64.
?*Sarcobotrylloides racemosus*: Hartmeyer, 1912, p.274.

DISTRIBUTION

NEW RECORDS: Western Australia (Rowley Shoals, WAM 945-6.83; Shark Bay, WAM 963.83; Cockburn Sound, WAM 929.83; Swan River Estuary, WAM 938.83). South Australia (E Great Australian Bight, QM GH2315; St Vincent Gulf, QM GH2289 GH2314; Yorke Peninsula, QM GH2414). Tasmania (Bruny I., QM G9595). Victoria (Port Phillip Bay, QM G10054). Queensland (Moreton Bay, QM GH2796; Wistari Reef, QM GH 2702; Heron I., QM GH1825 GH2700-1 GH2703-7; Lizard I., QM GH153).

PREVIOUSLY RECORDED: Western Australia (Shark Bay, Cockburn Sound, Albany — Hartmeyer and Michaelsen 1928, Kott 1952). South Australia (St Vincent Gulf — Kott 1972a). Victoria (? Port Phillip Bay — Millar 1966). Hong Kong (Kott and Goodbody 1982). Japan (Tokioka 1951a 1953a). New Zealand (North and South Is and Stewart I. — Brewin 1946 1950b 1958 1960, Millar 1982a). Atlantic coast of North America (see Van Name 1945). Europe (Faroe Is. and southern Norway, Great Britain, western France to Mediterranean, Adriatic and Black Seas — see Hartmeyer 1923).

The species is mainly recorded from temperate waters, its records from the Mediterranean and sub-tropical locations on the eastern and western coast of Australia (where it is not common) being the only ones from warmer waters.

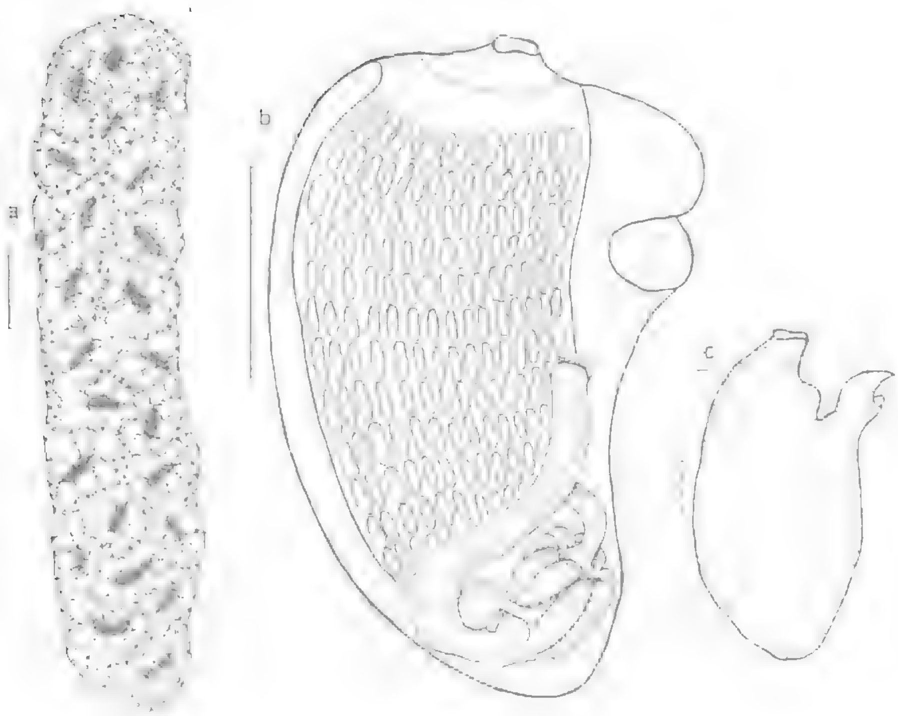


FIG. 130: *Botryllus schlosseri* — a, colony (QM GH2289); b, zooid showing body organs, from outside (QM GH2702); c, contracted zooid. (Scales: a, 5.0 mm; b, c, 0.5 mm).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies vary from investing sheets to stalked or sessile, fleshy lobes up to 5 cm long and 2 cm broad. The zooids are arranged in circular to elongate, and often very crowded, systems, sometimes arranged in longitudinal rows along the length of the fleshy lobes. Some of the common cloacal apertures are elongate, but they are more often large, circular openings. There are crowded terminal ampullae in the test between the systems and around the borders of the colony. These spherical to pear-shaped ampullae become elongate in the borders of the colony. In preservative, the test is transparent and soft between the systems; and the zooids are usually dark, brownish or bluish-black. In life, however, there is a bewildering variety of colours and colour combinations. Living colonies have been described as buff yellow with indian purple test; purplish brown with dense yellow around common cloacal apertures and along canals; lavender with opaque white in atrial lips and around branchial apertures with darker purple pigment cells in test and in zooids; orange zooids, colourless test; and orange and gray.

INTERNAL STRUCTURE: The zooids are about 3 mm long. The atrial aperture is small, the body wall being produced to form a broad siphon. There is a small atrial lip on the upper border of the opening. There are 16 branchial tentacles, 4 larger and 4 middle-sized with smaller ones alternating. The dorsal lamina is a wide, conspicuous membrane. There are from 8 to 12 rows of stigmata, the greatest number being present in robust zooids from large, lobed colonies from South Australia (QM GH2289). Similarly, stigmata in each row range from 16 to 25, the larger number being in the larger zooids with more rows of stigmata.

The stomach is always short and more or less spherical or barrel-shaped, with 10 glandular folds extending along its length. A moderately long, L-shaped caecum rising from the pyloric end of the suture line, and at right angles to it, bends ventrally about halfway along its length. The caecum has a conspicuous, bulb-like, terminal expansion. A gastro-intestinal connective from about halfway along the caecum divides into branches that form a glandular collar around the distal part of the intestine.

The testes, one on each side of the body, consist of a rosette of 5 to 9 follicles. Two or 3 large ova are present in the body wall on each side anterior to the testis, although ova and testis do not mature at the same time. Eggs develop endogenously, projecting into the atrial cavity.

REMARKS: The possibility that the large, fleshy, lobed colones from Cockburn Sound, St Vincent Gulf and Tasmania are a distinct species from the sheet-like investing colonies should not be overlooked. However, both sheet-like and lobed colonies have the same apparently characteristic atrial aperture with an anterior lip, more or less spherical stomach with a bulbous terminal expansion on the caecum and a testis consisting of a rosette of lobes.

Sarcobotrylloides racemosum: Hartmeyer, 1912b from South Africa has fleshy, stalked heads similar to those of the southern Australian colonies referred to above. The zooids, and especially the stomach and gastric caecum, are also similar. *Botrylloides racemosum* (Quoy and Gaimard, 1834) from New Zealand may be conspecific with the South African colonies, and possibly with *Botryllus schlosseri*; or with *Botrylloides perspicuum*.

The stomach and the gastric caecum of *B. schlosseri* are similar to those of *Botrylloides violaceum*, but even in the absence of gonads, the species can be distinguished by the smaller atrial aperture of the former species.

Botryllus stewartensis Brewin, 1958
(Fig. 131)

Botryllus stewartensis Brewin, 1958, p.444. Millar, 1966, p.368; 1982a, p.61.
Parabotryllus nemorus Kott, 1975, p.11.

DISTRIBUTION

NEW RECORDS: South Australia (upper Spencer Gulf, QM G12798; St Vincent Gulf, QM GH2720). Victoria (off Ninety Mile Beach, QM G12723-4). New South Wales (Port Kembla, QM GH2003; Port Stephens, QM GH2054).

PREVIOUSLY RECORDED: South Australia (Spencer Gulf — *P. nemorus* paratypes QM G7507 Kott 1975). Victoria (Port Phillip Bay — Millar 1966). New Zealand (Stewart I., Foveaux Strait — Brewin 1958, Millar 1982a; E of South I. — Millar 1982a).

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are long (up to 1.5 cm) narrow (about 0.5 cm in diameter), sandy, branching stalks. In preservative they are soft and collapsed. One circular system of crowded zooids is usually present in the slightly expanded head at the terminal-free ends of the stalks. However, there are occasionally up to 3 systems in a head. Such heads are almost as wide as they are long (up to 1 cm). The upper, free end of each head is more or less flattened, with a central depression surrounding the common cloacal aperture. The external test is sandy, although sand is absent internally and the test is soft, consisting of thin layers between the zooids. Adjacent stalks sometimes adhere to one another so that the surface of the colony, consisting of crowded heads, has a cauliflower-like appearance. The stalks narrow basally where they are attached to common basal stalks.

INTERNAL STRUCTURE: Zooids are up to 3 mm long. They have a terminal branchial aperture. The atrial aperture is on the anterior end of the dorsal surface. The opening projects forward and there is a single, small, pointed tongue on the anterior rim of the opening. The atrial aperture is sometimes produced forwards on a tubular siphon.

There are 8 to 12 rows of 15 or 16 stigmata. Three delicate internal longitudinal vessels extend the whole length of the branchial sac. The most ventral internal longitudinal vessel is close to the endostyle and often difficult to demonstrate.

The gut loop is large and projects behind the branchial sac from the left side. The oesophagus is of moderate length and extends posteriorly to open into the barrel-shaped stomach. The stomach has 10 distinct folds and a conspicuous caecum that curves around in the pole of the short intestinal loop. The ascending limb of the intestinal loop curves anteriorly and dorsally, and there is no distinct demarcation between the intestine and the long rectum, which extends almost the whole length of the thorax to the atrial opening.

On each side of the posterior end of the branchial sac is a wide, flat, fan-shaped testis follicle, subdivided into lobes around its postero-ventral border. There is a very short vas deferens from the pointed antero-dorsal aspect of the testis. Up to 4 embryos are developing in the peribranchial cavity anterior to the testis. The larva has a single, botryllid photolith and a circle of about 8 ectodermal ampullae around the anterior part of the trunk. The larval trunk is 0.5

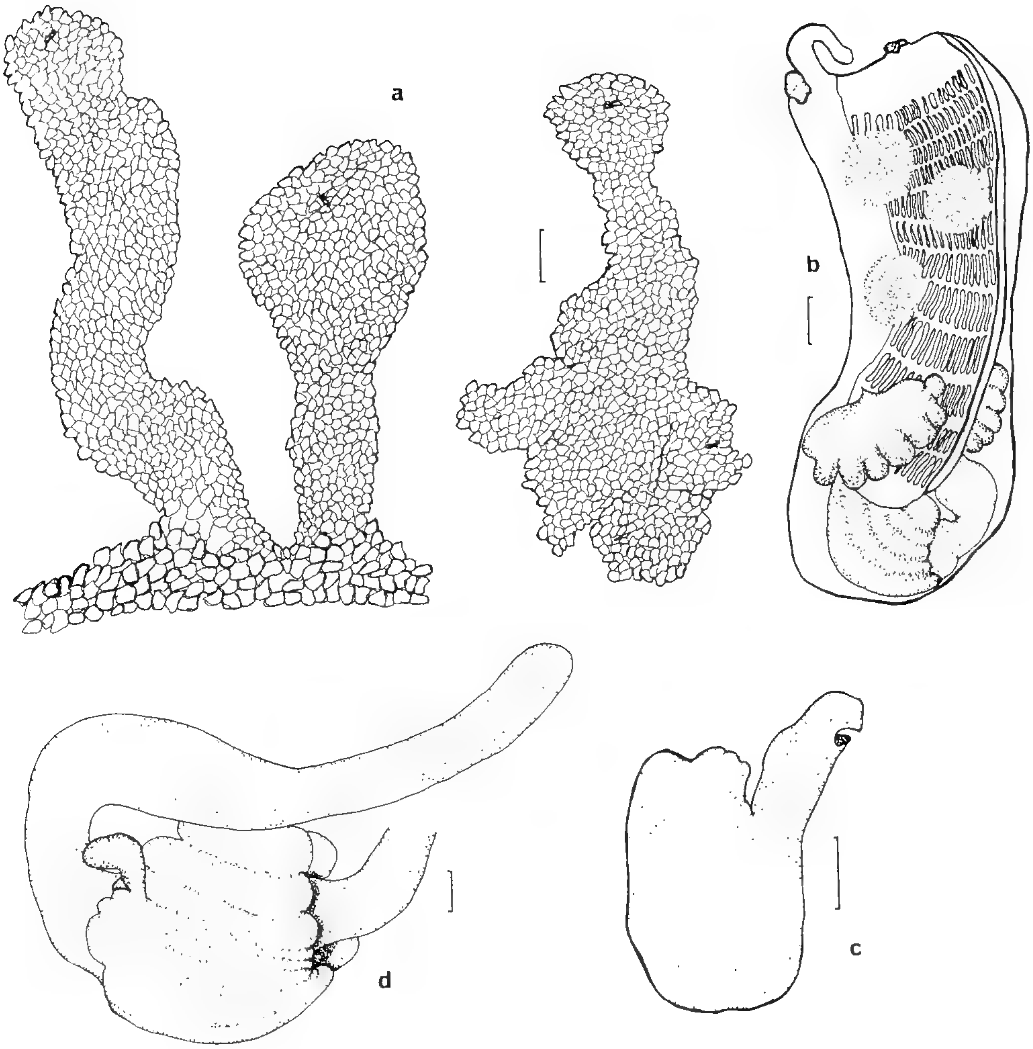


FIG. 131. *Botryllus stewartensis* — **a**, colonies (QM G12723); **b**, **c**, zooids removed from test (QM GH2054, G12724); **d**, stomach (QM GH2054). (Scales: **a**, 2.0 mm; **b**, **c**, 0.25 mm; **d**, 0.1 mm).

mm long; the tail is wound three quarters of the way around it. Buds form from the body wall and cluster in the test around the posterior end of the zooid.

Blood vessels from the posterior part of the left side of the zooid terminate in oval to elliptical ampullae at the surface of the test.

REMARKS: Kott (1975) overlooked the third internal longitudinal branching vessel in describing a new genus for this unusual species. The stalks of the New Zealand specimens are from 0.5 to 3.5 cm long and up to 1.5 cm in diameter. Their characters agree in all respects with the Australian material.

The single, wide, flat, fan-shaped testis follicle is characteristic, as are the sandy, cylindrical stalks with zooid systems confined to the terminal free ends. With the exception of the testis, the zooids are similar to those of other species of the genus *Botryllus*.

Botryllus tuberatus Ritter and Forsyth, 1917
(Fig. 132)

Botryllus tuberatus Ritter and Forsyth, 1917, p.461. Van Name, 1945, p.225. Tokioka, 1967a, p.151. Millar, 1975, p.280.

Botryllus communis Oka, 1927c, p.607. Tokioka, 1951a, p.8; 1951b, p.172; 1953a, p.237.

?*Botryllus gracilis* Michaelsen, 1927, p.203. Hartmeyer and Michaelsen, 1928, p.338.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 918.63). Queensland (Hervey Bay, QM GH2711 GH2713; Heron I., QM GH2709–10; Wistari Reef, QM GH2712; Lizard I., QM GH2708).

PREVIOUSLY RECORDED: Indonesia (Millar 1975). Palau Is (Tokioka 1967a). Gilbert Is. (Tokioka 1967a). Japan (Oka 1927c, Tokioka 1951a,b 1953a). Southern California (Ritter and Forsyth 1917).

The species is not often recorded. The record from Southern California (Santa Barbara) relates to the type material only. It has not been taken more than once from the type location, nor has it been taken from other locations in Southern California (Van Name 1945). It is recorded more frequently from the southern Pacific. The Australian records are from intertidal, reef-flat habitats on the undersurfaces of rubble.

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are very thin and investing. In the preserved colonies, the dark zooids are clearly seen in the translucent test. They are arranged in circular systems, with rarely more than 12 zooids in a system. The systems are evenly spaced and are not crowded. The conspicuous test vessels form a 3-dimensional network. The large spherical terminal ampullae in the surface also contain dark pigment. Sometimes, elongate terminal ampullae are crowded together in the border of the colony. There is a large common cloacal aperture in the centre of each system. Living colonies have dahlia red or heliotrope (Ridgeway 1886) zooids in a colourless test.

INTERNAL STRUCTURE: The zooids are very small and rounded, from 0.6 mm to just under 1.0 mm in length, and often almost as long as wide. Sometimes they are deep black and opaque in preservative, sometimes slightly translucent. The branchial aperture, which is terminal and sessile, occasionally has a ring of darker pigment around its border. In younger zooids, the atrial aperture is on the end of a long, tapering siphon. With maturity, the aperture becomes wider and the siphon shorter, and most mature zooids have a moderately wide aperture (exposing part of the anterior half of the branchial sac) and a narrow, pointed lip from the anterior border of the aperture. There are only 4 stout branchial tentacles.

There are usually 4 rows of oval stigmata on each side, with 3 stigmata in each mesh (10 to 12 per row), although colonies from Lizard I. have an extra row of irregular stigmata at the posterior end of the right side of the body. In these colonies, the second or third row does not reach the dorsal mid-line.

The gut forms an almost horizontal loop, sometimes partly behind the branchial sac. The rectum curves at right angles to it. The stomach is short and almost spherical, with 10 distinct longitudinal folds extending its whole length. The moderately long caecum, which rises from about halfway along the stomach, curves into the gut loop.

Testes have not been observed for this species. A large egg is present on each side of the body in some of the specimens (from Hervey Bay, QM GH2711).

REMARKS: This is a very inconspicuous species. Its unusual atrial siphon, few rows of branchial stigmata, relatively long gastric caecum, circular systems, and even the dark pigmentation in the body wall, are also reported for the type material from the eastern Pacific. Nevertheless its geographic range is most unusual. It is rare for a western Pacific species – even one with a pan-tropical range between the Atlantic and Indo-West Pacific – to be recorded from the eastern Pacific.

Botryllus gracilis Michaelsen, 1928 (Hartmeyer and Michaelsen 1928) has zooids with long atrial siphons and long, curved gastric caecae arranged in circular systems. It closely resembles the present

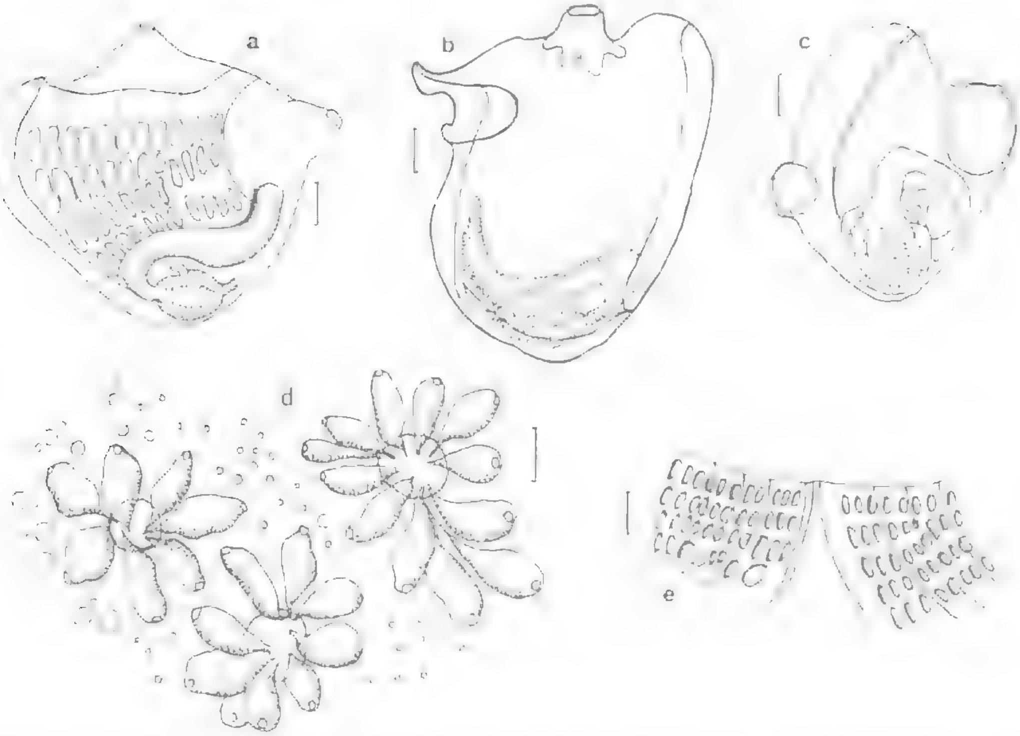


FIG. 132. *Botryllus tuberatus* — a, b, zooids (QM GH2708, GH2709); c, ventral view of zooid showing developing eggs; d, colony (QM GH2709); e, branchial sac (QM GH2708). (Scales: a – c, e, 0.1 mm; d, 0.5 mm).

species, differing only in having more (7) rows of stigmata.

Genus **Botrylloides** Milne-Edwards, 1841

Type species: *Botrylloides rotifera* Milne-Edwards, 1841 (< *B. leachii* Savigny, 1816)

The genus is characterised principally by the exogenous development of eggs, which project from the body wall as they incubate. The single ova on each side of the body develops from the body wall close to, and slightly dorsal and anterior to, the testis. The atrial opening is wide, exposing a large part of the branchial sac to the cloacal cavity, and its upper border projects out into a broad lip. This large atrial opening contrasts with the more limited apertures of *Botryllus* spp., although in other respects, the zooids are similar, even in their arrangement in circular to elongate or double-row systems.

There is also some degree of apparently intraspecific variation in both the arrangement of zooids and the colour and form of the colonies, and the species in both genera usually have the same wide geographic range.

KEY TO THE SECIES OF *BOTRYLLOIDES* RECORDED FROM AUSTRALIA

1. Gastric caecum, long, curved; stomach barrel-shaped..3
   Gastric caecum not long and curved; stomach trumpet-shaped 2
2. Systems surrounding protruding areas of well-vascularised test................*B. perspicuum*
   Systems, usually crowded, do not surround protruding areas of well-vascularised test .... *B. leachi*
3. Numerous randomly distributed, circular common cloacal apertures; test firm ....*B. violaceum*
   Few and very large, usually terminal, cloacal apertures; test very soft ... *B. magnicoecum*

Botrylloides leachi (Savigny, 1816)
(Fig. 133; Pl.Vd-h)

Botryllus leachii Savigny, 1816, p.199. Michaelsen, 1921a, p.101; 1922, p.479. Hartmeyer, 1923, p.361. Brewin, 1946, p.111; 1948, p.115; 1950b, p.344; 1951, p.104; 1952b, p.187; 1956, p.122; 1958, p.440; 1960, p.119

TABLE XV — SUMMARY OF CHARACTERS OF SPECIES OF *BOTRYLLOIDES* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australian waters	[2]Range in Australian waters	Colony	Test	Systems	Rows of stigmata	Stomach	Gastric caecum	Additional features
B. leachi	Red Sea, NE Atlantic - Mediterranean	NW Aust. - NE Aust.	investing to irregular	soft	long curving double rows	10–12	trumpet-shaped	very short	elongate cloacal apertures expose canals
B. perspicuum	WP, Hong Kong, Red Sea	NW Aust. - mid Qld	investing to stalked lobes	firm	circular to long parallel double rows	14–18	"	"	large areas zooid free test protrude between systems
B. violaceum	WP, Japan	mid Qld	investing to sessile lobes	"	long parallel double-rows	14	barrel-shaped	L-shaped	systems close together; cloacal apertures random
B. magnicoecum	China, West Indian Ocean, S. Africa, west Africa, NZ	NW Aust. - Low Isles	investing to stalked lobes	soft	"	12	"	C-shaped	system close; clocal apertures large, terminal

[1]WP, western Pacific. [2]Range given anti-clockwise around continent.

Botrylloides leachii: Milne-Edwards, 1841, p.304. Alder and Hancock, 1912, p.77. Hartmeyer and Michaelsen, 1928, p.341. Millar, 1952, p.24; 1962a, p.177; 1982a, p.62. Kott, 1952, p.258; 1966, p.297; (not: 1972a, p.24; 1972b, p.185; 1972d, p.253; 1976a, p.74, < *Botrylloides perspicuum*).
Metrocarpa leachi: Arnback, 1923, p.5.
Botrylloides rotifera Milne-Edwards, 1841, p.301.
Botrylloides rubrum Milne-Edwards, 1841, p.303. Alder and Hancock, 1912, p.79.
Botrylloides albicans Milne-Edwards, 1841, p.304.
Botrylloides radiata Alder and Hancock, 1848, p.206.
Botrylloides ramulosa Alder and Hancock, 1848, p.207.
Botrylloides sparsa Alder, 1863, p.172.
Botrylloides pusilla Alder, 1863, p.173.
Botrylloides prostratum Giard, 1872, p.632.
Botrylloides clavelina Giard, 1872, p.632.
Botrylloides insigne Giard, 1872, p.633.
Botrylloides boloniense Giard, 1875, p.77.
Botrylloides fulgurale Herdman, 1886, p.52.
Botrylloides purpureum: Herdman, 1886, p.41.
Botrylloides tyreum Herdman, 1886, nom. nov. pp.344, 391. Gottschaldt, 1898, p.642. Sluiter, 1904, p.101. Van Name, 1918, p.111. Millar, 1975, p.280. Kott, 1981, p.200. (Not: Tokioka, 1967a, p.156, < *B. violaceum*).
Botrylloides cyanescens Giard, 1888, p.513.
Botrylloides parvulus Huitfield-Kaas, 1896, p.24.
Sarcobotrylloides espevaerense Huitfield-Kaas, 1896, p.25.
Botrylloides nigrum: Sluiter, 1898a, p.49. Hartmeyer, 1912b, p.270 (part, colony with small gastric caecum). Kott, 1952, p.257; 1972c, p.238; 1972d, p.252.
Botrylloides leptum Herdman, 1899, p.101.
Sarcobotrylloides jacksonianum Herdman, 1899, p.102.
Sarcobotrylloides pannosum Herdman, 1899, p.105.
Sarcobotrylloides pannosum: Sluiter, 1904, p.102.
Botrylloides perspicuum: Sluiter, 1904, p.101.
Botrylloides vinosa Alder and Hancock, 1912, p.81.
Botrylloides niger: Michaelsen, 1918, p.45; 1919, p.705 (part, not colonies with oval systems placed end to end).
Botrylloides translucidum Hartmeyer, 1912b, p.272.
Botryllus sp. Bovien, 1922, p.44.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 145.75 225.75; Rowley Shoals, WAM 938.83; Pt. Gregory, QM G9393; Houtmans Abrolhos, WAM 389.91; Cockburn Sound, QM G9399 G9663, WAM 25.75 137.75 171.75 922.83). South Australia (Topgallant I., QM GH1284). Victoria (Bass Strait, NMV H390, QM G12737 GH2691; Portsea Pier, QM GH11929–32). New South Wales (Bateman's Bay, QM G10087; Port Hacking, QM GH33 G9392; Lord Howe I. QM GH43–4; Solitary I., QM G9497; Norfolk I., QM GH2697). Queensland (Moreton Bay, QM G4972 G5139–40 G5954 GH338 GH2241; Pt Vernon, QM G9396 G9596; Wistari Reef, QM GH2646 GH2664–5 GH2667 GH2671; Northwest I., QM GH2645; Heron I., QM G10099 GH2643–4 GH2647 GH2656–2663 GH2666 GH2668–70 GH2672–75; Townsville, QM GH295–6; Green I., QM GH435; Lizard I., QM GH2648–53; Cape Flattery, QM GH795).

PREVIOUSLY RECORDED: Western Australia (Geraldton, Cockburn Sound, Bunbury, Albany — Hartmeyer and Michaelsen 1928). New South Wales (Port Jackson — Herdman 1899, Kott 1952; Port Hacking — Kott 1972d) Queensland (Moreton Bay — Kott 1972c). Indonesia (Sluiter 1904). New Zealand (North, South and Stewart Is — Bovien 1922, Michaelsen 1922, Brewin 1946–1960, Millar 1982a). West Indian Ocean (Michaelsen 1918). Red Sea (Michaelsen 1919). South Africa (Hartmeyer 1912b, Sluiter 1898a, Millar 1962a)

The species also occurs around the British Isles, in the North Sea, the western Mediterranean, the Adriatic and the Black Seas (see Berrill 1950). It appears to have a range from the north-eastern Atlantic Ocean to the Mediterranean, and from the Red Sea to the tropical Indo-West Pacific and down into temperate waters across the southern coast of Australia.

DESCRIPTION

EXTERNAL APPEARANCE: Colonies are thin and investing to irregular, with rather flat lobes projecting from the surface. When lobes are present, the zooids open on the upper surface of the basal test and on both sides of the lobes. The surface of the thin and usually delicate test is even and smooth. Zooids are crowded in long, curving and branching double-row systems, as well as some circular or oval systems. The systems are often very crowded, and only in small colonies are there conspicuous areas of zooid-free test between them. The spherical to pear-shaped terminal ampullae of the test vessels are rather randomly distributed in the surface test in the narrow spaces between the systems. The terminal ampullae crowded around the border of the colony where it is growing out over the substrate are often long (from 0.2 to 0.3 mm) and parallel to one another. Common cloacal apertures are circular or elongate slits that leave the cloacal canal open to the surface along a considerable part of its length.

The colours of the colonies are very variable. Certain colour-morphs can be recognised, but there seems to be no limit to the possible colours and colour combinations. As in *Botryllus schlosseri* (see Sabbadin and Graziani 1967) variations also occur in the paired bands of pigment between the siphons (intersiphonal bars), which affects the pattern of pigmentation visible on the surface, since the anterior end of the zooid and the atrial lip are level with the upper surface. Colonies from Heron I. and Wistari Reef have the following range of colours: lavender and white; purplish pink and pink with white; dark brown with fine yellow zig-zag pattern along the double-

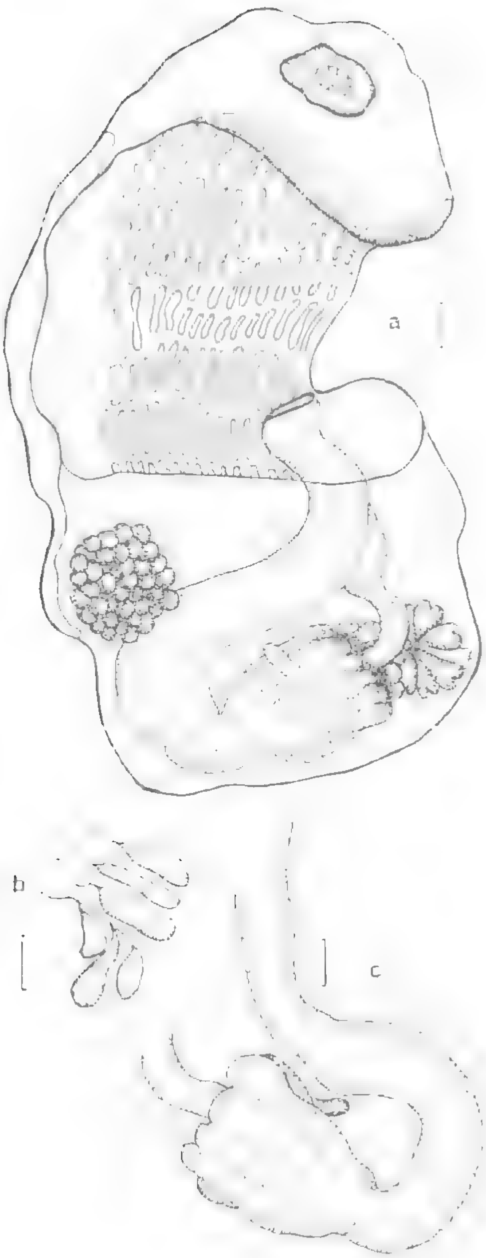


FIG. 133: *Botrylloides leachi* — a, zooid removed from test (QM G4972); b, terminal ampullae (QM GH33); c, gut loop (QM G9596). (Scales: a, c, 0.1 mm; b, 0.5 mm).

row systems; black, with white on the atrial lips; orange, with brown and white in the atrial lips; black, orange and vermilion zooids; purple zooids with white. In preservative, the test is colourless, with dark purple or brown pigment in the body wall and sometimes in the terminal ampullae of the test vessels.

INTERNAL STRUCTURE: The zooids are up to 2 mm long. The atrial aperture is very wide, exposing a large part of the branchial sac. There are 4 larger branchial tentacles and 4 smaller ones, alternating with rudimentary tentacles. The 10 or 11 rows of stigmata have about 16 stigmata per row.

The gut forms an almost horizontal loop across the posterior end of the zooid, partly posterior to and partly to the left of the branchial sac. The oesophagus curves posteriorly and ventrally, openinginto a trumpet-shaped stomach. At their cardiac end, the 9 gastric folds are deep and flare out away from the oesophagus. Toward the pyloric end of the stomach, the gastric folds become shallow and gradually flatten as the stomach narrows. About halfway along, a short caecum curves anteriorly across the lateral aspect of the stomach and at an angle to its long axis, and then projects very slightly into the gut loop about halfway along the anterior border of the stomach. The stomach occupies more than half of the length of the ascending limb of the gut loop. The narrow duodenal section opens into a wider intestine in the pole of the loop. The rectum curves anteriorly from a position alongside the oesophagus and terminates in a smooth-rimmed anus that projects up into the wide atrial opening.

The fan-shaped testis follicles, are crowded together to form a hemispherical mass. They are lobed around their outer border, giving the testis a mulberry-like appearance. On the right, the testis is almost level with the oesophagus; on the left, it is just anterior to the gut loop. The ova and testis are not mature at the same time. The ova are dorsal, and slightly posterior, to the testis. They project from the body wall as they mature.

REMARKS: Characteristics of *B. leachi* are its very soft test, thin colony; smooth surface; long, crowded and curved double-row systems (usually very close together) with unevenly distributed spherical terminal ampullae in the narrow spaces between the systems. Specimens with the same trumpet-shaped stomach, small caecum and extensive atrial aperture as the present species, but with circular systems separated by expanses of zooid-free raised test, were assigned by Kott (1972a, 1972b, 1972d, 1976) to *B. leachi* and resemble some described by Michaelsen 1919 as *B. niger*. These appear to be a different species (*Botrylloides perspicuum*).

Botrylloides racemosum: Hartmeyer 1912 from South Africa has a short stomach with a curved caecum (Hartmeyer 1912b) and small circular to elongate systems. It resembles the clavate colonies of *Botryllus schlosseri* from South Australia, rather than *B. leachi*, with which it had been synonymised (Hartmeyer and Michaelsen 1928).

Although Herdman (1886) has not described the small stomach caecum in his specimens of *Botrylloides tyreum* from the Philippines, Van Name's (1918) material from the same location is identical with the present species, which suggests that *B. tyreum* is not a distinct species. A specimen from the Palau Is assigned to *B. tyreum* by Tokioka (1967a), may be a specimen of *B. violaceum*, as its zooids have a long stomach caecum, arising at right angles to the long axis of the stomach.

Botrylloides nigrum Herdman, 1886 from the eastern Atlantic is distinguished from *B. leachi* by its closely packed systems, black pigmentation, shorter stomach and slightly longer gastric caecum.

Botrylloides magnicoecum Hartmeyer, 1912
(Fig. 134; Pl VIa-d)

Botrylloides nigrum: Hartmeyer, 1912b, var. magnicoecum p.271; 1913, var. magnicoecum p.135

Botryllus magnicoecus Michaelsen, 1915, p.419; 1921b, p.6; 1922, p.480; 1923, p.50. Hartmeyer and Michaelsen, 1928, p.331. Hastings, 1931, p.79. Brewin, 1951, p.109; 1952b, p.187; 1957, p.577; 1958, p.440. Millar, 1955a, p.195; 1962a, p.175. (Not Tokioka, 1967a, p.153).

Botrylloides magnicoecum: Kott, 1952, p.258; 1972a, p.30; 1972b, p.185; 1972d, p.252. Millar, 1966, p.368; 1982a, p.62.

Sarcobotrylloides anceps Herdman, 1891, p.609; 1899, p.103.

Botryllus anceps: Hartmeyer and Michaelsen, 1928, p.335. Millar, 1963, p.736.

DISTRIBUTION

NEW RECORDS: Western Australia (Pt Gregory, QM G9405; Shark Bay, WAM 962.83). South Australia (Yorke Peninsula, QM GH2298 GH2395; Nuyts Archipelago, QM GH2301; Onkaparinga, QM G9593; St Vincent Gulf, QM GH2376). Tasmania (Pt Davey, QM GH2026). Victoria (Bass Strait, QM G11875 GH1466; Western Port, QM G10121-2 G12717; Port Phillip Bay, QM G10123 GH36). New South Wales (Jervis Bay, QM GH10094; Port Hacking, QM G9403; Wreck Bay, QM G9404). Queensland (Hervey Bay, QM G9401; Gladstone, QM G11882 GH2156).

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Hartmeyer and Michaelsen 1928). South Australia (Kott 1952; St Vincent Gulf — Kott 1972a; Great Australian Bight — Kott 1972b). Tasmania (Kott 1952). Victoria (Port Phillip Bay — Millar 1963 1966). New South Wales (Port Jackson — Herdman 1899, Millar 1963; Port Hacking — Kott 1972d). Queensland (Low Isles — Hastings 1931). New Zealand (Michaelsen 1922, Brewin 1951 1952b 1957 1958, Millar 1982a). West Indian Ocean (Michaelsen 1921b). South Africa (Hartmeyer 1912b, Millar 1955a 1962a). West Africa (Michaelsen 1915, Hartmeyer 1913). ? China (Michaelsen 1923).

There are anomalies in the recorded distribution of this species. Records from South Africa and across the southern coast of Australia and from South Island of New Zealand suggest it is a temperate species, extending up to Shark Bay on the western Australian coast, and to Port Jackson on the eastern coast of Australia. The species has not been recorded from Moreton Bay. However, records from both Hervey Bay and Low Isles indicate that Port Jackson is not the northern limit of its range on the eastern coast of Australia. Michaelsen's (1923) record from Hong Kong is also anomalous.

DESCRIPTION

EXTERNAL APPEARANCE: This is one of the most spectacular ascidians known from the Australian coast. Its colonies are flat and investing to conical and often stalked, and the colours of the living specimens are dark purple and yellow; purple, white and yellow; bright yellow; or greyish with pale zooids. However, in preservative zooids are always a dark purple colour.

The zooids are arranged in crowded, long, straight double-row systems which radiate from a few large common cloacal apertures. As the colonies develop, the common cloacal apertures are raised on the top of large conical elevations, with parallel double-rows of zooids extending down the sides of the cones. Occasionally cones are subdivided and 2 or 3 secondary elevations project from the sides. The common cloacal apertures are unusually large, exposing the terminal part of the canals that extend between the rows of zooids. The borders of the cloacal apertures are formed of the atrial lips of the zooids around the top of the colony. The colonies are often sessile, but frequently have a basal, fleshy, zooid-free stalk containing a network of blood vessels with pear-shaped terminal ampullae. Long, crowded terminal ampullae are often present in the borders of investing sheets. There is very little zooid-free test between the systems. The test is very soft, and preserved colonies are collapsed.

INTERNAL STRUCTURE: Zooids are up to 1.7 mm long. The border of the branchial aperture has very fine serrations. The 8 branchial tentacles are about equal in size. The atrial opening is very wide and open, exposing a large part of the branchial sac

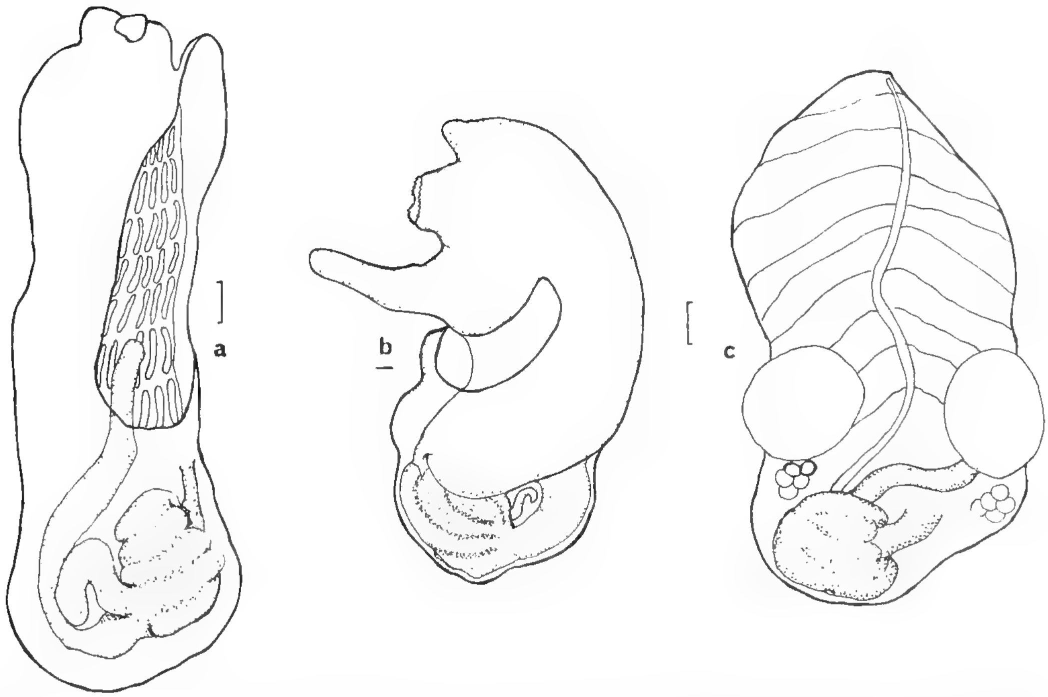


FIG. 134: *Botrylloides magnicoecus* - **a**, **b**, side view of zooids (QM G10123, G9401); **c**, ventral view of zooids with developing eggs projecting from the body (QM G9401). (Scales: 0.1 mm).

directly to the cloacal canal. There is a long, sometimes pointed, tongue-like extension of the body wall from the upper rim of the opening.

The 12 rows of stigmata have 12 to 14 stigmata in each row. In preserved specimens, there are patches of dark pigment on the body wall over the ventral end of each row of stigmata.

The stomach is short and wide, and occupies only about one-third of the ascending limb of the gut loop. The loop is partly behind the branchial sac and partly to the left of it. There are 8 deep stomach folds extending the whole length of the stomach, with the longest folds on its outer curve. A long caecum curves around at the side of the gut loop, in the opposite direction to the curve of the loop (i.e., anticlockwise). The intestine curves anteriorly into the rectum, which opens by a smooth rimmed anus in the wide atrial opening.

The gonads are present on each side of the body near the posterior end. Those on the left are anterior to the gut loop. The testes are circular clusters of about 8 male follicles. A single ovary on each side is present just anterior and dorsal to the testis.

REMARKS: The conical stalked lobes (which appear to develop from the flat colonies) have been described only from Australia. Although these stalked lobes are more often collected than the sheet-like colonies, Michaelsen and Hartmeyer (1928) do not record stalked colonies either as *B. magnicoecum* or *B. anceps*. They distinguish these two species by the shape of their terminal ampullae, the former having spherical to short oval ampullae sharply cut-off from the terminal vessel and the latter having pear-shaped ampullae that gradually expand from the vessel. None of the specimens examined in connection with the present study has spherical ampullae, although some ampullae in the border of expanding colonies are elongate. Ampullae do not appear, therefore, to be a reliable distinguishing characters in this case. In other respects, the Australian specimens, conform with both Hartmeyer's (1912b) and other specimens assigned to this species: they have the characteristic long, close, double-row systems, few cloacal apertures and long gastric caecum. Brewin (1951) describes colonies with common cloacal apertures 2 to 5 cm apart.

Botryllus rufus (Oka 1927c) was synonymised with the present species by Tokioka (1967a). However, the very much shorter gastric caecum of *B. rufus* and its circular systems and long male follicles distinguish it from the present species.

Botrylloides perspicuum Herdman, 1886
(Fig. 135; Pl VIe-h)

Botrylloides perspicuum Herdman, 1886, p.45. Sluiter, 1904, p.101. Kott and Goodbody, 1982, p.533.

Botrylloides niger: Michaelsen, 1919, p.105 (part, specimens with closed oval systems and high ridges of test between).

Botrylloides leachii: Kott, 1972a, p.29; 1972b, p.185; 1972d, p.253; 1976a, p.74.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago WAM 171.75; Houtman's Abrolhos, WAM 389.75 391.75 949.83; Shark Bay, WAM 964–5.83; Cockburn Sound, WAM 913.83, 930–1.83 935.83 949.83; Busselton). South Australia (Ward I., QM GH950; Top Gallant I., QM GH929 GH949; Pearson I., QM GH1281; Kingston, QM G10117; Roxby I., QM GH2372 GH2378 GH2380 GH2383). Tasmania (Roches Beach; Bruny I., QM G9598; Tinderbox, QM G9998 G10157). Victoria (Portland Harbour, QM GH37; Portsea, QM G10136–7 G12719; Pope's Eye, QM G12718; Lakes Entrance, QM G11874; Bass Strait, QM G11874 G12737; Western Port, QM G12720). New South Wales (Lord Howe I., QM GH42–3; Port Hacking, QM G9392 G9395). Queensland (Hervey Bay, QM G9401 GH2462).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1972a; Great Australian Bight — Kott 1972b). Victoria (Western Port — Kott 1976a). Indonesia (Sluiter 1904). Philippines (Herdman 1886). Hong Kong (Kott and Goodbody 1982). Red Sea (Michaelsen 1919).

The species has not been recorded north of Hervey Bay on the eastern Australian coast. However, it is recorded well to the north on the western coast. Its records from locations to the north of Australia are limited to the type location off the Philippines and from Hong Kong (Kott and Goodbody 1982) and the Red Sea (Michaelsen 1919).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are always robust, but very variable. Some are large, flat, stalked or sessile lobes up to about 4 cm long, while others are thick, investing colonies, sometimes growing around weed or other debris. Occasionally, the lobes are constricted along their length, and sometimes a stalked lobe grows out from a sessile cushion.

The test is always firm, translucent and smooth. However, in preserved specimens, the surface is always depressed over the zooid systems, with raised areas of zooid-free test between them. Zooid are sometimes in circular systems, arranged in rows along the length of the colony. These systems become elongate as more zooids are added and eventually join to form long double-row systems extending parallel to one another, with long ridges of zooid-free test between them. However, common cloacal apertures are rounded, sometimes conspicuously protruding at intervals between the double-rows. The longitudinal test ridges between the systems are sometimes divided along their length to form circular, protruding areas where the double rows of zooids divide and cross to join an adjacent row. The test is filled with the evenly spaced, large, spherical terminal ampullae of the test vessels. These ampullae are often elongate and crowded in the borders of the colonies.

As with other species in the subfamily, the colours of the living colony are very variable indeed. The following colour combinations are recorded: grey test and yellow-green zooids; yellow zooids with white atrial lips; pale olive-green matrix with yellow zooids; orange zooids. In preservative, the test is always colourless, but there is dark purplish black to blue pigment in the body wall and sometimes in the terminal ampullae.

INTERNAL STRUCTURE: The zooids are relatively large. There are 4 large and 4 moderately sized branchial tentacles with rudimentary ones between. The atrial aperture is very large and wide, exposing a large part of the branchial sac. The branchial sac has 14 to 18 rows, each of up to 20 stigmata.

The gut loop is horizontal, partly posterior to the branchial sac, with the rectum extending anteriorly at right angles to it. The anal opening projects above the posterior rim of the atrial opening and is exposed to the cloacal canal. The stomach is long and trumpet-shaped, wide at the cardiac end where the deep gastric folds flare out around the oesophagus. The folds are less deep toward the pyloric end of the stomach, which narrows to the intestine and often appears to be smooth. A short caecum rises from the suture line about halfway along its length, curves anteriorly across the stomach and projects very slightly into the gut loop.

There is a rounded to hemispherical testis each side of the posterior end of the body. Testes consist of male follicles radiating inwards and divided into rounded lobes on the convex surface of the hemisphere. A large embryo projects from the body wall, usually only on the right side of the body dorsal and anterior to the testis.

REMARKS: The zooids of this species closely resemble those of *B. leachi*. However, the test is always very firm, with the inter-zooidal areas raised in long ridges or circular swellings while in *B. leachi* the test is soft and without raised interzooidal areas. Herdman (1886) described these raised areas of test in the type material. Further, the zooids of the present species are larger than those of *B. leachi* and have 14 to 18 rows of

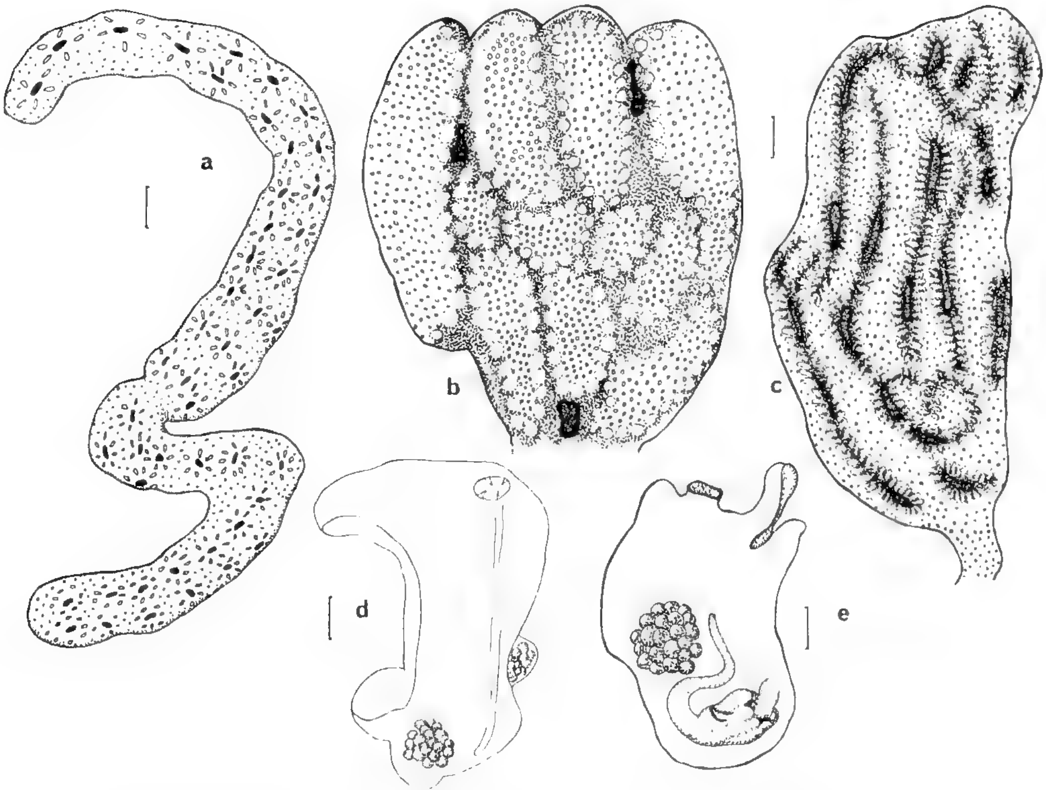


FIG. 135: *Botrylloides perspicuum* — **a** - **c**, colonies (QM G12719, GH2383, GH2380); **d**, ventral view of zooid (QM G10136); **e**, parietal view of zooid (QM G10136). (Scales: **a** - **c**, 5.0 mm; **d**, **e**, 0.25 mm).

stigmata, in contrast to the 10 to 12 in the latter species.

Botrylloides violaceum Oka, 1927
(Fig. 136)

Botrylloides violaceum Oka, 1927c, p.608. Tokioka, 1949a, p.7; 1951a, p.10; 1951b, p.173; 1953a, p.241; 1967a, p.158, ? s.sp. *marginatus* p.160.
?*Botrylloides tyreum*: Tokioka 1967a, p.157.

DESCRIPTION

NEW RECORDS: Queensland (Sarina, QM GH2686).

PREVIOUSLY RECORDED: Japan (Oka 1927c, Tokioka 1949a 1951a,b 1953a). Palau Is (Tokioka 1967a).

DESCRIPTION

EXTERNAL APPEARANCE: The colonies are firm, ridged and vary from sessile cushions to upright plates. The zooids are in more or less straight double-row systems parallel to one another. Not all the systems in the colony run in the same direction since there are groups of parallel rows at angles to one another. In the present colonies, the double-row systems are conspicuously depressed between the high, narrow ridges of test that separate them. The colour in preservative is greenish beige. There are large pear-shaped to spherical terminal ampullae crowded in the test. Circular common cloacal apertures are randomly distributed along the cloacal canals.

INTERNAL STRUCTURE: The 4 larger branchial tentacles alternate with 4 of moderate length, with rudimentary tentacles between. The atrial aperture is very wide indeed, exposing a large part of the branchial sac. The upper border of the opening is extended into a fairly short but wide, rounded lip. The 14 rows of stigmata have no more than 14 stigmata per row.

The gut forms a horizontal loop partly behind the branchial sac and the rectum extends anteriorly to open about halfway up the branchial sac. The wide atrial opening exposes a large part of the rectum. The stomach is short and wide, occupying about half of the ascending limb of the loop. There are 8 deep gastric folds extending the whole length of the stomach. The gastric caecum joins the suture line on the lateral aspect of the stomach, near its pyloric end. The caecum is L-shaped. It

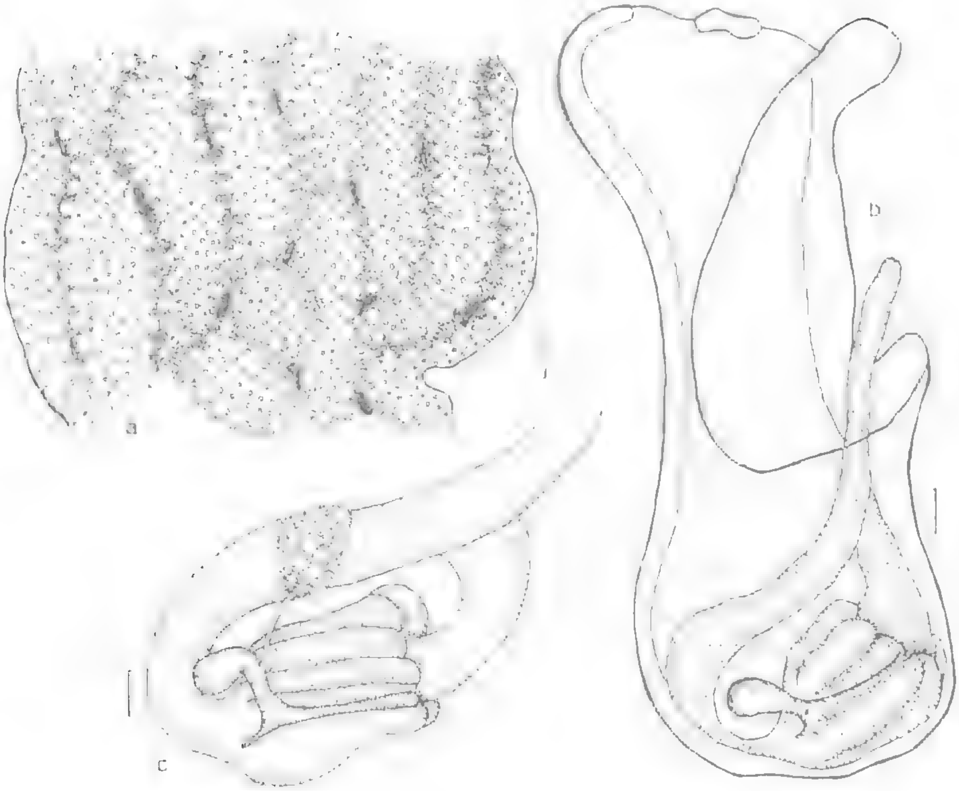


FIG. 136: *Botrylloides violaceus* (QM GH2686) — a, part of colony. b, lateral view of zooid; c, gut loop. (Scales: a, 2.0 mm; b, c, 0.1 mm)

arises at right angles to the longitudinal axis of the stomach and extends anteriorly before curving into the gut loop, where its terminal tip forms a bulb-like expansion. There is a collar of conspicuous glandular material where the gastro-intestinal duct (from about halfway along the caecum) branches over the intestine.

No gonads are developed in the newly recorded specimens, although Tokioka (1949a) reports characteristically *Botrylloides* gonads in his specimens (Tokioka 1949a, Pl. 3, Fig. 4).

REMARKS: Tokioka (1967a) suggests that *B. violaceum* may be synonymous with *B. leachi*. However, the rather long gastric caecum of the present species distinguishes it from all others except *Botryllus schlosseri*. The latter species is distinguished by its atrial siphon and restricted atrial opening and by its generic characters.

Botrylloides tyreum: Tokioka 1967a appears to be an immature colony of the present species rather than of *B. leachi*, which has an inconspicuous gastric caecum.

The colony from Queensland with its close, parallel, double row systems and firm, ridged test appears to be identical with specimens from Japan (Tokioka 1951a).

Family PYURIDAE Hartmeyer, 1908

Stolidobranch ascidians with branched branchial tentacles and more than 4 (usually 6 to 10) branchial folds on each side of the body. The dorsal lamina is either a smooth-edged membrane or is represented by a series of pointed languets. The pyloric part of the gut has a distinct liver that protrudes from the gut wall. There is usually only one gonad on each side of the body, although it is often lobed or divided into separate sacs, each joined to common gonoducts. Vegetative reproduction has not been reported in this family.

The siphonal armature is well developed and more diverse than it is in the Styelidae, varying from round-edged, curved scales, to pointed hooks or long pointed needles, sometimes with secondary scales. Only in a very few species has the siphonal armature not been detected. These crowded, overlapping, cuticular structures often cause iridescence in the siphonal lining and around the outside of the apertures. The test is usually very tough and leathery in this family and often the superfical cuticle is thickened into circular or polygonal scales (see *Pyura, irregularis* group).

The body musculature consists of internal longitudinal bands that usually radiate from each siphon to cross those from the other siphon on the sides of the body, creating more or less rectangular meshes. There are external circular muscles around each siphon and around the base of each siphon, sometimes spreading out from the latter over a wide radius. Occasionally there are also circular muscles posterior to the siphonal muscles. These surround the body and receive branches from the radiating longitudinal bands. Stigmata are usually longitudinally oriented, but may be curved and irregular (*Bathypera*) or coiled to form infundibula approaching the molgulid condition (*Heterostigma, Bolteniopsis, Cratostigmata, Hartmeyeria* and *Ctenyura*). This coiling of stigmata usually occurs only in the top of the branchial folds and is not always conspicuous.

Although the stomach wall is glandular and folded in most families of the Ascidiacea, the elaboration of glandular epithelium into pouches that project out from the pyloric part of the gut to form a distinct digestive gland or liver occurs only in the Pyuridae and Molgulidae. Its greatest development is in the genera *Pyura* and *Ctenyura* where it forms an arborescent structure that branches off the gut and projects into the atrial cavity.

Species are, so far as is known, oviparous. Those larvae that are known have small, undeveloped organs and the adhesive papillae are in the primitive triradial arrangement. There is an ocellus and an otolith. In the laboratory, larvae settle and metamorphose within a few hours of hatching. There are no devices to retain eggs in the peribranchial cavity. Since both male and female ducts open near the base of the atrial siphon, fertilisation is very probably external. During the prehatching period of up to 12 hours for some species (Anderson *et al.* 1975), the embryos are subject to dispersal.

The family is diverse, the genera *Pyura* and *Microcosmus* especially being well represented in Australian waters. Although there are species in both genera with a wide geographic range in the Indo-West Pacific, a majority of the species are indigenous and temperate in their range.

Abyssal genera not yet recorded from Australian waters are *Bolteniopsis* Harant, 1927c (polytypic) from the northern Atlantic; *Bathypera* Michaelsen, 1904b (polytypic) from the eastern Pacific and Antarctic; *Pyurella* Monniot and Monniot, 1973 (monotypic) from the northern Atlantic; *Bathypyura* Monniot, 1971 (polytypic) from the northern and tropical Atlantic; *Culeolus* Herdman, 1881a (polytypic) from all oceans; and *Paraculeolus* Vinogradova, 1970 (monotypic) from the north-western Pacific.

Interstitial polytypic genera not yet recorded from Australia are *Heterostigma* Arnback, 1924 from Europe (see Monniot and Monniot 1961) and *Cratostigmata* Monniot and Monniot, 1961 from the northern Atlantic and Mediterranean. The monotypic genus *Eupera* Michaelsen, 1904b is known only from western Africa. The cosmopolitan polytypic genus *Boltenia* Savigny, 1816 is represented by *B. transversaria* (Sluiter, 1904) in Indonesian waters, but is not yet recorded from Australia.

Key to the Genera of Pyuridae
(* not recorded from Australia)

1. Tentacles not branched 2
   Tentacles branched 5
2. Gonads 3 per side; stigmata straight .... *Eupera* *
   Gonads never more than 1 per side; stigmata coiled 3
3. Branchial sac folded 4
   Branchial sac not folded .... *Heterostigma* *
4. Protostigmata in posterior part of branchial sac .... *Bolteniopsis* *
   No protostigmata in posterior part of branchial sac .... *Cratostigmata* *
5. Stigmata present 6
   Stigmata absent 15
6. Stigmata irregular .... *Bathypera* *
   Stigmata not irregular 7
7. Dorsal lamina smooth 8
   Dorsal lamina with languets 10
8. A gonad on each side of the body 9
   A gonad on the right side of the body only .... *Pyurella* *
9. Stigmata coil in the edge of the branchial folds .... *Hartmeyeria*
   Stigmata do not coil in the edge of the branchial folds .... *Microcosmus*
10. Stigmata transverse .... *Boltenia* *
    Stigmata not transverse 11
11. Gonad completely enclosed in primary gut loop on left 12

Gonad outside or partially outside primary gut loop on left 14
12. Arborescent liver diverticulum protrudes freely into atrial cavity; no barbed calcareous spicules 13
No arborescent liver diverticulum protruding freely into atrial cavity; with barbed calcareous spicules ....*Herdmania*
13. Stigmata form infundibula..............*Ctenyura*
Stigmata do not form infundibula ......*Pyura*
14. More than one gonad per side....*Halocynthia*
Not more than one gonad per side .*Ctenicella*
15. Branchial folds present..........*Paraculeolus* *
Branchial folds absent............................16
16. Protostigmata present ....*Bathypyura* *
Protostigmata not present..........*Culeolus* *

Genus **Pyura** Molina, 1782

Type species: *Pyura chilensis* Molina, 1782

The genus is characterised by the presence of dorsal languets rather than a continuous fold or lamina along the mid-dorsal line of the pharynx. The liver diverticula consist of a main stem that branches off the gut and primary, secondary and tertiary branches ending in crowded, small, rounded terminal lobules. The main liver diverticula project free of the gut into the peribranchial cavity. A single, elongate gonad on each side of the body usually divides into separate, polycarp-like sacs along each side of a central common oviduct and vas deferens. The left gonad is entirely enclosed in the gut loop.

The branchial folds in this genus are wide, and are separated by a strip of flat branchial sac on which there are usually a relatively large number of internal longitudinal vessels.

The polycarp-like gonad sacs develop as pouches from a tubular ovary, with the male follicles closely applied along their outer borders. In most species, the ovarian pouches and their associated male follicles are constricted from the primary tube, which persists as the central oviduct accompanying the vas deferens, both receiving individual ducts from each sac before opening together near the atrial aperture. In their primitive arrangement, the sacs on opposite sides of the central ducts alternate with one another, but that arrangement is often obscured. In several species (*Pyura sacciformis*, *P. arenosa*, and *P. obesa*), sessile pouches, rather than constricted sacs, alternate along each side of the central ducts. A continuous mass of crowded ova fills the pouches and the central duct such that the ovary appears as a continuous, rather sinuous tube. Sometimes gonad sacs on the posterior side of the gonoducts are not developed and there is only a single row, on the anterior side.

Variations in siphonal armature, number of branchial folds, length of the dorsal lamina and related curvature of the gut loop, distance apart of siphons and related position of the neural complex and dorsal tubercle, shape and type of fixation of gonad sacs to the body wall and the development of the liver diverticula and endocarps are the principal morphological characters by which the species are characterised. A few species also have calcareous inclusions in the test (*Pyura spinosa*, *P. littoralis*, *P. gibbosa* and *P. australis*). The horny branching fibres sometimes observed in the body wall and pharynx of *P. sacciformis* and *P. stolonifera* only occur occasionally, and do not constitute a reliable specific character. The siphonal armature appears to represent a reliable plesiomorphic character by which most of the species occurring in Australia may be grouped:

1. *Pachydermatina* group: The species in this group are commonly known as Sea Tulips. They usually have a naked, leathery test, although *P. ostreophila* and *P. spinifera* have an investment of a *Halisarca* sponge. The siphonal spines are conical but asymmetrical, the outer side is longer than the inner side, and is flat and scale-like posteriorly. Sand is never included in the test. With the exception of *P. ostreophila* and *P. spinifera*, the species have calcareous spicules embedded in the test. There is usually a long, narrow stalk from the anterior end of the body. The apertures, both on the side of the head, are directed away from one another. The stalk does not, however, originate from the anterior end of the body in *P. littoralis* and *P. spinosa* (which have posterior stalks and both apertures on the upper surface) and *P. ostreophila* (which has small, narrow stolons randomly developed from various parts of the body). The branchial aperture is never terminal in the *pachydermatina* group of species, the majority of which appear to be adapted to habitats where water currents change direction, since the head on its long stalk moves with the current, its branchial aperture always presented toward the oncoming current.

   There are always 6 branchial folds. The dorsal lamina is long, the branchial folds not very deeply curved, and the gut forms a narrow, J-shaped loop. The paired liver diverticula from opposite sides of the gut are of more of less equal size (in contrast to other species, which usually have a single main diverticulum and proximal (sometimes paired) accessory outgrowths). The gonads are fixed firmly to the body wall.

Australian members of the group are *Pyura gibbosa gibbosa, P. gibbosa draschii, P. spinifera, P. australis* and probably *P. littoralis, P. spinosa* and *P. ostreophila*. The last 3 species have largely diverged from the usual morphology. The New Zealand species, *P. pachydermatina* (Herdman), *P. lutea* (Sluiter), *P. spinossissima* (Michaelsen), are closely related to the typical Australian members of the group (see Millar 1982a). Antarctic species *P. legumen* (Lesson) and *P. georgiana* (Michaelsen), which extend up the Scotia Ridge into Patagonian waters, are also related (Kott 1969a). There appears not to be a related species in South African waters. The group is apparently confined to temperate and southern polar seas.

2. *Irregularis* group: Species are usually sessile with a very hard, irregular test, often impregnated with sand, or with scale-like cuticular thickenings. The siphonal armature consists of minute (0.01 to 0.02 mm), curved scales with a rounded margin. The atrial aperture, which is usually well removed from the branchial aperture, is sometimes directed posteriorly. The dorsal ganglion is often very long and the peritubercular area very deep. The oesophagus opens at the posterior end of the branchial sac and the folds are not deeply curved. The gut forms a simple, often wide, loop. With the exception of *P. elongata*, the species of this group have more than 6 folds in the branchial sac. The gonads are invariably lightly fixed to the thin body wall by very fine ligaments and are readily dislodged.

   Australian members of the group are *Pyura viarecta* n.sp., *P. confragosa* n.sp., *P. abradata* n.sp., *P. fissa.*, *P. navicula* n.sp., *P. scortea* n.sp., *P. irregularis, P. crassacapitata* n.sp. *P. molguloides, P. pantex* and *P. elongata*. Only *P. pantex* and *P. elongata* have a wide Indo-West Pacific range.

   Although the majority are indigenous Australian species in either temperate or tropical waters, the affinities of this group of species appear to be with southern rather than tropical fauna. The Antarctic species, *P. squamata* Hartmeyer, *P. discoveryi* (Herdman) and *P. tunica* Kott, are probable relatives of *P. elongata, P. irregularis* and *P. molguloides*, respectively (see Kott 1969a). New Zealand species *P. trita* (Sluiter), *P. carnea* (Brewin) and *P. cancellata* (Brewin) also appear to be related to *P. molguloides* (see Millar 1982a).

3. *Obesa* group: The surface of the test is often impregnated with sand and may be hard, but it is not especially irregular. The apertures are often close together on the upper surface. The siphonal armature consists of long, iridescent, needle-like spines, sometimes expanded along their length (*P. isobella, P. curvigona*) and usually narrowing toward the base. The dorsal border of the body is short, the apertures close together. Often the dorsal lamina is also very short, and the branchial folds deeply curved. The gut loop is often expanded at the pole and deeply curved. There are always 6 branchial folds on each side. The gonads are firmly attached to the body wall, and often embedded deeply in it.

   Australian species in this group are *P. tasmanensis* n.sp., *P. isobella* n.sp., *P. curvigona, P. arenosa* and *P. obesa*. *Pyura baliensis* Millar, 1975 (with siphonal armature identical to that of *P. tasmanensis*) is a related species from Indonesia. *Pyura zansibarica* Michaelsen, which is closely related to *P. isobella* n.sp., is known from the West Indian Ocean. Many of these species have previously been confused with *Pyura vittata* (Stimpson) (see Kott 1976a) owing to their long, iridescent siphonal spines, and they may be related phylogenetically. Although 3 of the indigenous Australian species appear to be primarily temperate (*P. tasmanensis* n.sp., *P. isobella* n.sp., *P. obesa*) they appear to have close affinities with tropical species; while *P. curvigona* and *P. arenosa* extend into the tropical waters of the western Pacific. This is the only one of the 3 groups of *Pyura* spp. that possibly have a closer relationship with tropical than with subantarctic fauna.

The ungrouped species (*P. sacciformis* and *P. stolonifera*) have curved pointed spines in the siphonal lining and occasionally branched, horny spicules in the test. The last two species are unusual in having very wide geographic ranges (in

TABLE XVI SUMMARY OF CHARACTERS OF SPECIES OF *PYURA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Attachment	Surface	Apertures	Siphonal	Perituber-cular area	Branchial folds	[3]Internal lon-gitudinal vessels
P. scortea n.sp.	—	Cockburn Sd	sessile	naked	apart	round scales	shallow	6	(22)8
P. elongata	IWP	Dampier Arch. -Mossman	"	"	"	"	deep	"	(30)6
P. pantex	Red Sea	Shark Bay	"	"	"	"	?	7	(16)5
P. crassacapitata n.sp.	—	Cockburn Sd – Moreton Bay	"	"	"	"	deep	"	(16)4
P. molguloides	—	SA-NSW	"	sandy	"	"	"	8–9	(20)4
P. navicula n.sp.	—	Moreton Bay	stalked	"	"	"	"	"	"
P. abradata n.sp.	—	SA – Bass St	sessile	naked	"	"	narrow, deep	9	(16) 1–2
P. viarecta n.sp.	—	Heron I.	"	sandy	"	"	deep	"	(20)3
P. confragosa n.sp.	—	Moreton Bay – Lizard I.	"	naked	"	"	wide	"	(25)8
P. irregularis	—	Tas. – NSW	"	"	"	"	narrow, deep	7–8	(24)7
P. fissa	—	Bass St	"	"	"	"	deep	7	(16)4
P. arenosa	WP	Bowen – Abrolhos	"	sandy	close	flattened spines	shallow	6	(25)10
P. tasmanensis n.sp.	—	Tas.	"	"	"	long needles	"	"	(25)6
P. obesa	—	Dampier Arch. Cape Melville	stalked or sessile	"	"	"	"	"	(42)12
P. isobella n.sp	—	Cockburn Sd – NSW	sessile	"	"	"	"	"	(25)6
P. curvigona	WP	Heron I. – Shark Bay	"	naked	apart	"	"	"	(12)6
P. sacciformis	WP	Albany – Cape Kimberley	"	"	"	conical spines	"	6–7	(20)3
P. stolonifera	pan-te	Shark Bay – Noosa	"	variable	"	"	"	6–7	(18)3
P. littoralis	—	Tas.	"	naked	"	"	none	6	(13)1
P. spinosa	—	Cockburn Sd – NSW	stalked or sessile	"	apart	"	shallow	"	(12)1–2
P. australis	—	Dongara – NSW	stalked	"	"	"	"	"	(18)4
P. gibbosa gibbosa	—	Tas – Moreton Bay	"	"	"	"	"	"	(15)1–2
P. gibbosa draschii	—	Cockburn Sd – Pt Phillip Bay	"	"	"	"	"	"	"
P. ostreophila	—	Albany – Bass St	stolons	sponge investment	"	"	"	"	(11)3
P. spinifera	—	Carnavon – NSW	stalked	"	"	"	"	6–7	(30)4–6

[1]Pan-te, pan temperate; WP, western Pacific; IWP, Indo-West Pacific. [2]Range given anti-clockwise around the continent. [3](on folds) between folds. [4]Number of rows; shape; number/row.

TABLE XVI — SUMMARY OF CHARACTERS OF SPECIES OF *PYURA* RECORDED FROM AUSTRALIA (cont.)

Species	Gut loop	Endocarps on gut	*Polycarp sacs	Gonad attachment	No. liver diverticula	Additional features
P. scortea n.sp.	closed	absent	2; cuboid;10	ligaments	4	—
P. elongata	open	"	2; rounded; 7–8	"	1+	surface test with thickened scales
P. pantex	"	"	2;7	?	"	"
P. crassacapitata n.sp.	"	"	2; irregular;12+	ligaments	"	ridge of thick test between apertures
P. molguloides	"	"	2; rounded;12+	"	"	straight branchial folds
P. navicula n.sp.	"	"	2; lobed;5	"	"	sandy papillae on hard test
P. abradata n.sp.	"	"	2; lobed;9	"	"	hard wrinkled test
P. viarecta n.sp.	"	"	2; rounded	"	"	sand enmeshed long hairs around surface
P. confragosa n.sp.	"	present	2; rounded proliferated	"	"	hard wrinkled test often with thickened scales
P. irregularis	"	"	2; rounded;8–10	"	"	dorsal tubercle in posterior end of deep peritubercular area
P. fissa	"	"	2; irregular; proliferated	"	1	surface test with thickened scales
P. arenosa	closed	absent	2; continuous;8–10	membrane	"	flexible test
P. tasmanensis n.sp.	"	present	2; rounded;12+	embedded	"	hard wrinkled test
P. obesa	"	"	2; continuous;10+	"	"	siphonal spines of 2 sizes; short dorsal lamina; deeply curved gut loop
P. isobella n.sp.	"	"	2; lobed;12	membrane	"	siphonal spines inflated basally
P. curvigona	"	"	2; rounded;10+	"	"	siphonal spines with scales
P. sacciformis	"	"	2; continuous;10+	"	4 prs	siphonal spines large striated
P. stolonifera	"	"	1 or 2 cuboid;	embedded	2	very short dorsal lamina
P. littoralis	"	"	2; irregular	membrane	4 prs	spherical spicules in test; multiple ♀ openings
P. spinosa	"	"	2; rounded	"	6 prs	"
P. australis	"	"	1; elongate	"	5 prs	stallate spicules in test
P. gibbosa gibbosa	"	"	1; elongate;8	"	3 prs	"
P. gibbosa draschii	"	"	"	"	5–6 prs	"
P. ostreophila	"	"	2; rounded	"	4 prs	aggregates embedded in sponge
P. spinifera	"	"	1; elongate	embedded	3 prs	usually covered by sponge

tropical and temperate waters respectively). With *Pyura curvigona, P. elongata* and *P. pantex* they are the only species recorded from Australia that are not indigenous.

As in other ascidian genera species of *Pyura* have a tendency to become isolated in Australian temperate waters. The genus differs from *Polycarpa,* Polyzoinae and *Microcosmus,* however, in that the affinities of the Australian species appear to be primarily with the subantarctic, rather than the tropical fauna (see Biogeography).

Key to the Species of *Pyura* Recored from Australia

1. Stalk originates from anterior end of head .. 2
   Stalk, when present, does not originate from anterior end of head 5
2. With horny mesh cylinder in stalk .... *P. spinifera*
   No horny mesh cylinder in stalk 3
3. Anal border usually with long, flattened lobes; spicules from layer under cuticle of stalk do not spread into centre of stalk .. *P. australis*
   Anal border without long, flattened lobes; spicules from layer under cuticle of stalk do spread into centre of stalk 4
4. Anal border with long, branched, feathery fringe .... *P. gibbosa draschii*
   Anal border without long, branched, feathery fringe .... *P. gibbosa gibbosa*
5. Test crowded with hard, spherical, calcareous spicules 6
   Test not crowded with hard, spherical, calcareous spicules 7
6. Ovarian sacs with separate ducts . *P. littoralis*
   Ovarian sacs joined by single common duct .... *P. spinosa*
7. Individuals form aggregates embedded in sponge .... *P. ostreophila*
   Individuals do not form aggregates embedded in sponge 8
8. Siphonal armature consists of strongly curved hooks with a wide basal flange .... *P. sacciformis*
   Siphonal armature does not consist of strongly curved hooks with a wide basal flange 9
9. Siphonal armature consists of sharply pointed spines; 6 branchial folds on each side 10
   Siphonal armature, when present, consists of rounded scales; 6 or more branchial folds on each side 15
10. Gut loop with endocarps 11
    Gut loop without endocarps .... *P. arenosa*
11. Siphonal spines with opalescent, flattened scale halfway along their length; apertures separated .... *P. curvigona*
    Siphonal spines without opalescent, flattened scale halfway along their length; apertures close 12
12. Siphonal spines with expanded, opalescent basal half .... *P. isobella* n.sp.
    Siphonal spines without opalescent expanded basal half 13
13. Siphonal spines of two sizes, large scattered amongst small .... *P. obesa*
    Siphonal spines not of two sizes 14
14. Dorsal lamina short .... *P. stolonifera*
    Dorsal lamina long .... *P. tasmanensis* n.sp.
15. Branchial folds 6 per side 16
    Branchial folds more than 6 per side 17
16. Surface test with scale-like thickenings .... *P. elongata*
    Surface test without scale-like thickenings .... *P. scortea* n.sp.
17. Endocarps present on gut 18
    Endocarps not present on gut 20
18. Dorsal tubercle in base of deep peritubercular area .... *P. irregularis*
    Dorsal tubercle not in base of deep peritubercular area 19
19. Apertures on long siphons .... *P. fissa*
    Apertures not on long siphons .... *P. confragosa* n.sp.
20. Test with thick, sandy, outer casing .... *P. molguloides*
    Test without thick, sandy, outer casing .. 21
21. 9 branchial folds per side ... *P. abradata* n.sp.
    7 branchial folds per side 22
22. Hard papillae crowded on surface test .... *P. navicula* n.sp
    No hard papillae crowded on surface test .. 23
23. Scale-like thickenings in surface test .... *P. pantex*
    No scale-like thickenings in surface test 24
24. Thick ridge of test between apertures; curved branchial folds ...... *P. crassacapitata* n.sp.
    No thick ridge of test between apertures; straight branchial folds ... *P. viarecta* n.sp.

The following species recorded from the Indo-West Pacific have not been recorded from Australian waters:

Pyura aripuensis Herdman, 1906, from Sri Lanka (BM 1907.8.30.12), has long, pointed spines in the siphonal lining, but otherwise resembles *P. confragosa* n.sp. in many of its characters. Both apertures are on the upper surface of a long, curved body, the branchial siphon at the anterior end being longer than the atrial siphon, which is about two-thirds of the distance along the upper surface. The gut has endocarps along the descending limb, and the gonads consist of very numerous polycarp sacs.

Pyura breviramosa (Sluiter, 1904) from Indonesia may be related to *P. obesa*, as the gut forms a deep double loop. It has fewer internal longitudinal branchial vessels than *P. obesa*.

Pyura lanka (Herdman, 1906) from Sri Lanka is similar to *P. arenosa* in its overlapping siphonal spines, 6 branchial folds, continous gonads, long gut loop, inconspicuous external apertures, long branchial siphon, and sand embedded test. Herdman noted its similarity to *P. jacatrensis* Sluiter, 1904 (< *P. arenosa*). However, *P. lanka* has a ridge of thickened test along the upper part of the body, through which the siphons extend, as in *P. crassacapitata* n.sp.

Pyura polycarpa (Sluiter, 1904), also from Indonesia, has a wide gut loop, a large number of polycarp sacs well removed from the common ducts, and a large number of internal branchial vessels in the interspace. Although many of the characters suggest a relationship with *P. confragosa* n.sp., Sluiter's species has only 6 branchial folds on each side of the body.

Pyura abradata n.sp.
(Fig. 137)

Pyura irregularis: Kott, 1952, p.271 (part, specimens from St Vincent Gulf); 1972a, p.38; 1972b, p.187.

DISTRIBUTION

TYPE LOCALITY: South Australia (Kangaroo I., American River Inlet, coll. H. Duyverman, 1976, holotype QM G10001).

NEW RECORDS: South Australia (St Vincent Gulf, paratypes QM G9301 G9312 G9327 G9331). Victoria (Bass Strait, NMV H400 H445 H460 H464-5 H912 H924).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1952 1972a; Investigator Strait — Kott 1972b).

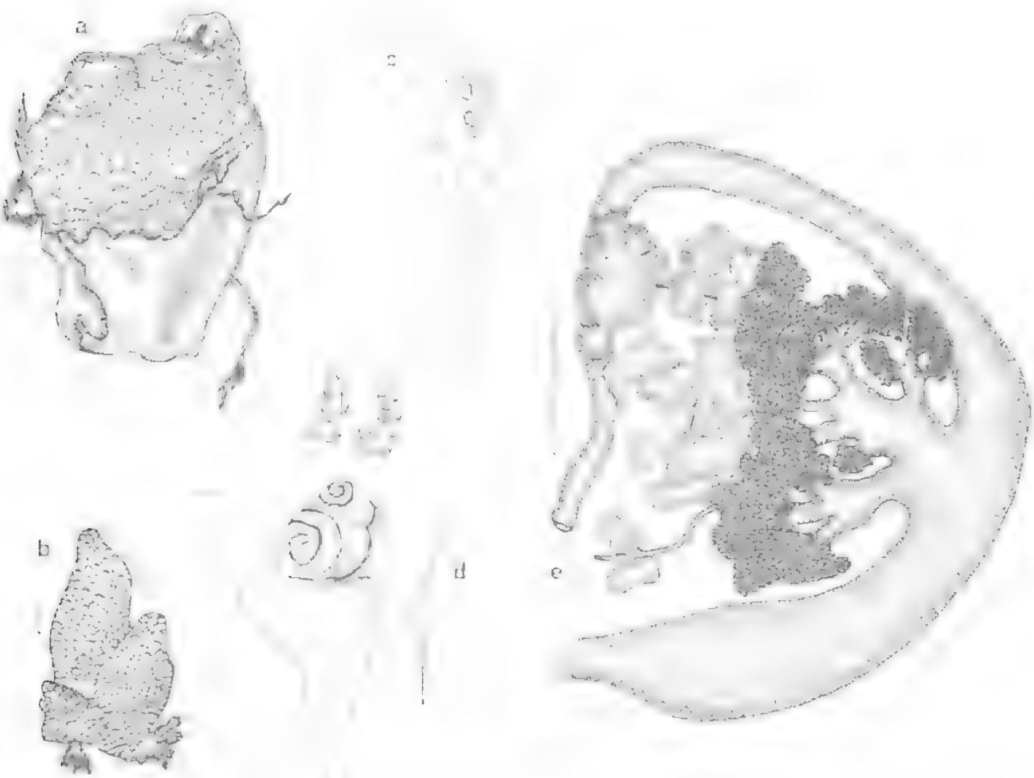


FIG. 137. *Pyura abradata* n.sp. — **a**, **b**, external appearance (QM GH1001, G9327); **c**, **d**, dorsal tubercles (QM G9301, G9327); **e**, gut and gonad, showing large liver (QM G9327). (Scales: **a**, **b**, **e**, 5.0 mm; **c**, 1.0 mm; **d**, 0.5 mm).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals up to 3 cm long are recorded. The body is upright, usually narrowing anteriorly to a short terminal branchial siphon, which is curved ventrally. The atrial siphon is also short and projects forwards from about halfway down the body. Contracted individuals are round, with broader body and shorter siphons, and with horizontal wrinkles around the base of the siphons.

The test is extemely hard, leathery, opaque and thin, although posteriorly it is often thicker and slightly cartilaginous in section. The surface is extremely rough, with shallow wrinkles and creases. These are generally parallel, either horizontal or longitudinal; their orientation may depend on the contraction of the body. Fine, horizontal wrinkles occur especially around the anterior part of the body. The surface test contains small, hard, circular, scale-like thickenings.

Epiphytes and foreign particles adhere to the test, but never form a continuous coat. Posteriorly, the test is produced into irregular, sometimes branching, holdfasts. Irregular aggregates of this species often occur.

Minute (0.01 to 0.02 mm), overlapping scales with rounded anterior borders are present in the outer part of the siphonal lining and continue externally over the small lobes surrounding the apertures.

INTERNAL STRUCTURE: The body wall is very muscular and opaque, with thick, wide and crowded longitudinal muscle bands radiating from the siphons and extending over the sides of the body. An external layer of circular bands becomes stronger around the base of the siphons. Although circular muscles are present posterior to the siphonal muscles, they are less conspicuous than the longitudinal bands. At the base of the branchial siphon, just in front of the tentacles, there is a muscular sphincter that projects into the lumen. The branchial tentacles are not bushy: they have only short primary and minute secondary branches. The very deep but wide peritubercular area extends about one-third to halfway along the dorsal mid-line (approximately the same length as the dorsal lamina). The dorsal tubercle is usually in the middle of the open, anterior end of this area. It is large and protruberant. Its conspicuous, C-shaped slit is turned to the left or right, with both horns spiralling inwards. The large neural gland, which is posterior to the tubercle, causes a swelling in the peritubercular area. The dorsal ganglion is long. The dorsal lamina overlies a large, conspicuous sinus and extends well posteriorly. The pointed dorsal languets, curving to the right, are present to the left of the sinus. A single or double row of large, accessory languets, sometimes with short, pinnate branches, is present along the right side of the sinus. The languets increase in size posteriorly.

There are always 9 branchial folds on each side. They are only moderately broad, and do not overlap. The folds terminate posteriorly around the sides and posterior rim of the oesophageal opening. The internal branchial vessels of a specimen 2.5 cm in diameter are arranged according to the following formula: DL5(15)1(16)1(15) 1(15)1(14) 2(14)2(13)1(10)1(8) 2E.Never more than 3 vessels lie in the interspace. There are 6 relatively short stigmata per mesh.

The gut forms a very wide, simple loop in the postero-ventral corner of the left side of the body and the rectum does not turn anteriorly. There are some very small liver diverticula along the long, proximal part of the gut loop. The main liver diverticulum branches about 4 times before dividing into groups of terminal liver lobules. The anal border is bilabiate.

The gonads are separate, irregularly lobed, polycarp sacs with sharp, almost right-angled, borders. The sacs extend along both sides of the gonoducts. The left gonad is in the gut loop, which does not have endocarps, although there are many on the lobed polycarp sacs. Both the gut and gonads are only very lightly attached to the body wall by thin ligaments and are readily detached.

REMARKS: Of the other Australian species of this genus with rounded siphonal scales, *P. confragosa* n.sp., *P. elongata* and *P. fissa* have similar small, scale-like thickenings in the surface test. *Pyura abradata* is distinguished from the former by the absence of endocarps on the gut and from the latter two species by its more numerous branchial folds. *Pyura rugata* Brewin, 1948 from New Zealand (OM A63.3) also has scale-like thickenings of the test and lacks endocarps on the gut loop. It is distinguished from the present species, however, by its bushy tentacles and fewer (7) branchial folds.

The species is characterised by its relatively thin, rough, wrinkled, scaly, hard, opaque but largely naked test; terminal branchial siphon; mid-dorsal atrial siphon; large dorsal tubercle in the centre of the wide anterior end of a long and wide peritubercular area; double row of dorsal languets; large numbers of branchial folds with relatively few internal longitudinal vessels in the interspaces; gut without endocarps on it; and large and irregularly lobed polycarp sacs with sharp borders.

Pyura arenosa (Herdman, 1882)
(Figs 138a,b, 139)

Cynthia arenosa Herdman, 1882, p.140.
Cynthia jacatrensis Sluiter, 1890, p.331
Halocynthia jacatrensis: Sluiter, 1904, p.47.
Tethyum (Pyura, Halocynthia) jacatrensis: Sluiter, 1913, p.66.
Pyura jacatrensis: Monniot and Monniot, 1974b, p.723. (Not: Hartmeyer, 1919, p.8. Hartmeyer and Michaelsen 1928, p.431. ? < *P. scortea* n.sp. Kott, 1952, p.273, < *P. tabella* n.sp.; 1954, p.127. Millar, 1960b, p.125).

Distribution

New Records: Western Australia (Houtman's Abrolhos, WAM 2.75 1119.84). Queensland (NW of Bowen, QM GH734 GH1467 GH1469–79; Townsville, QM GH750 GH1457 GH1468; Mission Beach, QM GH1808).

Previously Recorded: Indonesia (Sluiter 1890 1904). Torres Strait, Arafura Sea (BM 1887.2.4.52/4 Herdman 1882, Sluiter 1913).

The species is a common component of the shallow-water benthic fauna of sandy substrates off Abbot Point (Bowen) and in Cleveland Bay (Townsville). It is confined to tropical waters.

Description

External Appearance: Individuals are evenly egg-shaped to spherical, and are usually slightly flattened dorso-ventrally. The test is thin, but has fairly short hair-like processes amongst which sand is densely packed to form a hard, rigid sandy coat. The apertures, both of which are sessile, are on the upper surface, about one-third of the body length apart. Owing to the investment of sand, the small apertures are difficult to see. The specimens from north-eastern Queensland are all free-living, apparently lying on a sandy substrate. Individuals are never more than 2.5 cm long. The entire length of the siphonal lining has small (0.04 to 0.06 mm), sharply pointed, overlapping spines. Spines near the apertures are conical and slightly curved, with an open, oval base that becomes longer in the spines toward the base of the siphon. These conical spines continue onto the outer surface of the test around each aperture and onto the anterior part of the body, where they are obscured by the sand. Their open base can be observed only in the spines in the terminal part of the siphon, for those that line most of the length of the siphon are flattened and leaf-shaped. The flat part of these spines is transversely striated, conferring a characteristic pearly white iridescence to the siphonal lining. The edges curve inwards to form a concavity along their undersurface. A small notch appears to bisect the narrow posterior end.

Internal Structure: Internally, the branchial siphon, which is longer than the atrial siphon, is directed anteriorly. The atrial siphon is directed upwards and is on a conical prominence. The body wall is thin and transparent. Longitudinal muscle bands radiate from both siphons, breaking up around the periphery of the upper surface into very fine branches that continue over the rest of the body. Strong, circular muscle bands are present around the siphons and around the base of the siphons, but they are very fine and relatively sparse on the rest of the body.

About 8 branchial tentacles are thick and fleshy with rather swollen main stems and a narrow constriction at the base of their posterior edge. Primary branches are pinnate, and there are regular secondary branches. The branches arise from each side of the posterior edge of the tentacle. The muscular tentacular ring projects inwards as a sort of velum, with the branchial tentacles supported on its free rim. The dorsal tubercle is a moderately sized cushion enclosed in, or in front of, the relatively shallow peritubercular area with a U-shaped slit, directed anteriorly and to the right, with both horns turned in. The dorsal lamina is long, the oesophageal opening being almost at the posterior end of the branchial sac.

There are 6 wide, overlapping branchial folds on each side of the body. They are not very deeply curved. There are up to 25 internal longitudinal vessels on the folds and up to 11 in the interspace (Sluiter 1913). There are 3 to 5 stigmata per mesh crossed by parastigmatic vessels. The branchial formula for a 2 cm specimen is: E4(11)5(11)5(15)5(15)4(11)3(13)3DL. A juvenile specimen (GH1808) has only a single internal longitudinal vessel in each interspace and 6 or 7 on the folds.

The gut is long and voluminous. It forms a quite wide, but closed, loop around the whole of the posterior and ventral borders to the left of the mid-line. The rectum curves anteriorly, parallel to the descending limb of the loop, to open in the base of the atrial siphon. There is a row of small, delicate, liver lamellae from the cardiac end of the pyloric part of the gut. Distal to these rudimentary structures is a single, large, arborescent diverticulum with terminal lamellae, finger-like lobules, and occasional minute papillae on the free edge of the lamellae. These terminal branches of the liver diverticulum are packed together in clumps. There are also a few small diverticula from the gut distal to the main stalk. The anal border is finely scalloped with minute, rounded lobes.

The primary gut loop encloses the left gonad. The gonads are unusual in that the polycarp-like sacs do not separate from the ovarian tube, but

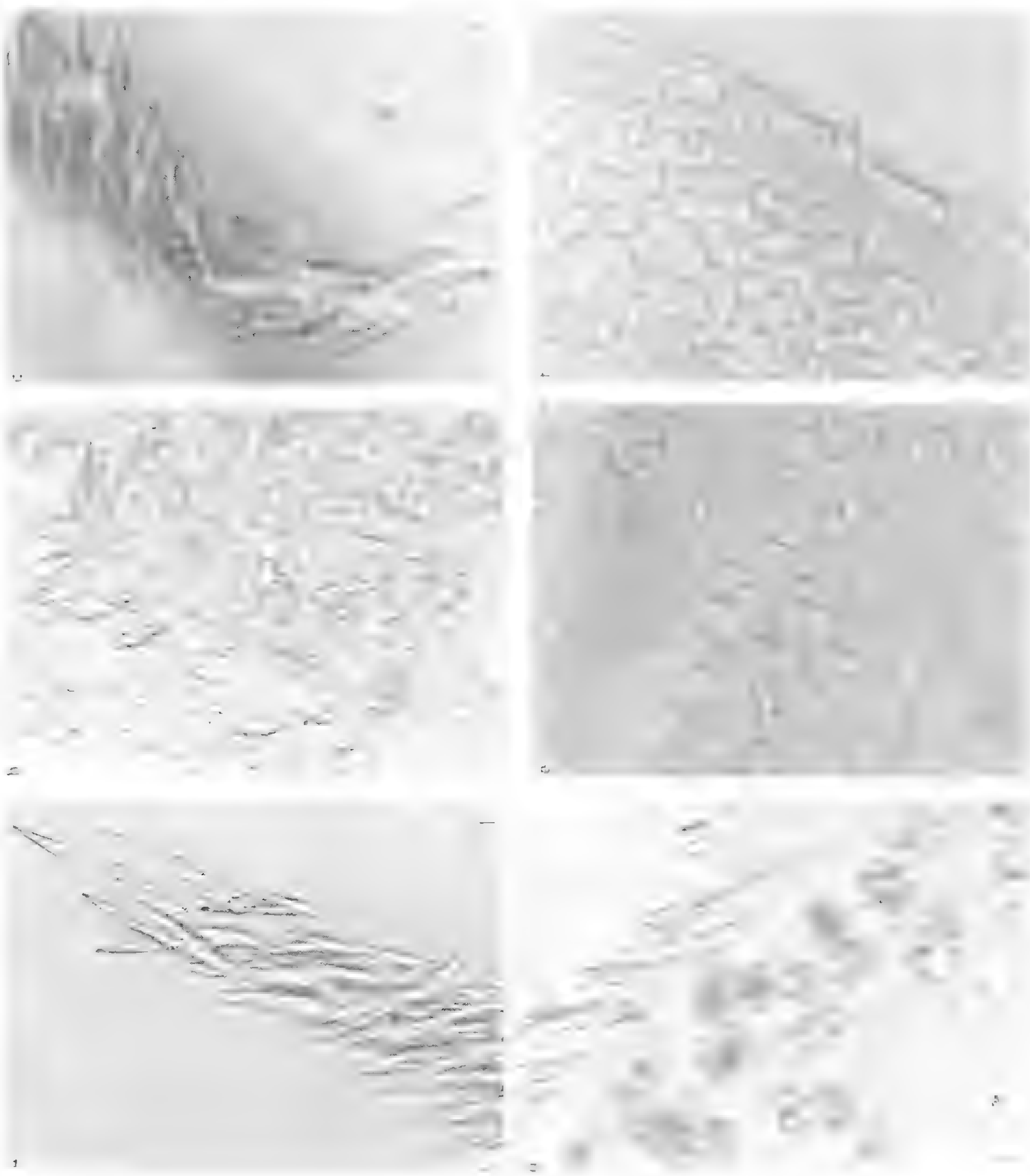


FIG. 138. *Pyura arenosa* siphonal scales — **a**, mature individual (QM GH1468); **b**, juvenile (QM GH1808). *Pyura australis* — **c**, siphonal spines; **d**, spicules. *Pyura confragosa* — **e**, siphonal spines. *Pyura crassacapitata* — **f**, siphonal spines. (Scales: 0.01 mm).

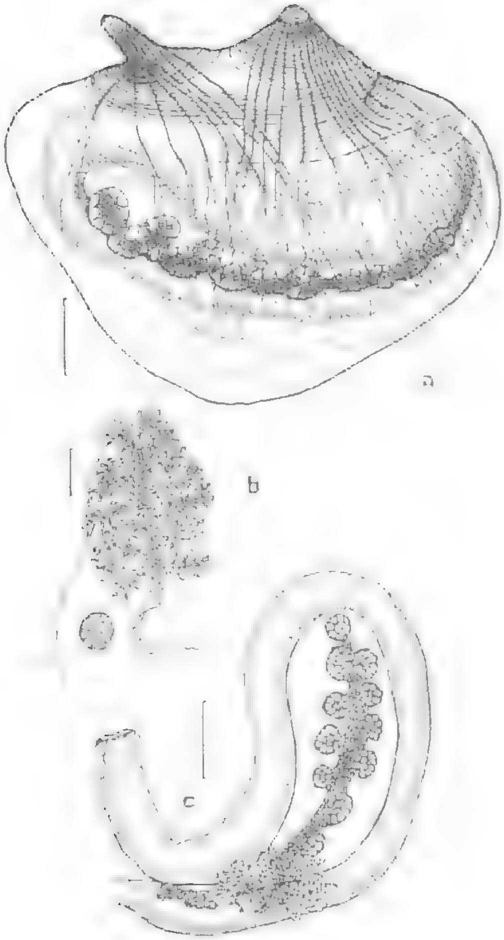


FIG. 139: *Pyura arenosa* — a, body removed from test; b, branchial tentacle, showing circular muscle in section (diagrammatic); c, gut and gonad. (Scales: a, c, 2.0 mm; b, 0.2 mm).

remain as side pouches alternating from side to side down the length of the tube. The whole gonad is firmly attached to the body wall. The male follicles are grouped around the end of each side pouch and their ducts join a common vas deferens that extends along the middle of the ovarian tube. The very small endocarps on the surface of each side-pouch are sometimes pointed, and sometimes associated with a vessel connecting the body wall and branchial sac. There are no endocarps on the gut.

REMARKS: The species is characterised by its sandy test, siphonal spines, long gut loop and zig-zag gonad (see Sluiter 1890). There is a marked similarity between this species and *Pyura baliensis* Millar, 1975. Millar's species is distinguished only by its longer siphonal spines and the presence of a stalk.

The type specimen of *P. jacatrensis* was redescribed by Monniot and Monniot (1974b). Unfortunately the siphonal spines were not described. The body (with long internal branchial siphon), sand-embedded test, gonad pouches (and long gut loop) is identical with that of the present specimens. Although the branchial vessels of the type specimen (DL0(21)3(13)6(25)4(17)7(11)7(6)E) are more numerous than those of the present specimens, the species appear to be conspecific. The specimen from Aru I. (Sluiter 1913) is 5 cm long, more than twice the size of the type specimen. It has a greater number of internal longitudinal vessels (9 to 11) in the interspace, but is otherwise similar to the type.

Pyura jacatrensis: Hartmeyer, 1919, from northwestern Australia differs from the present species in having a leathery test, papillae in the branchial siphon and on the atrial velum, siphonal spines less than 0.03 mm long, separate gonad sacs, and wart-like external siphons. It appears to be distinct from the present species. Hartmeyer and Michaelsen (1928) specimens from Shark Bay are reported to be conspecific with Hartmeyer's specimens (see *P. scortea* n.sp.).

Pyura lanka (Herdman, 1906) from Sri Lanka has many similarities to *P. arenosa* but is distinguished by the thick anterior ridge of test.

Pyura molguloides, which has a thick, sandy coat, like the present species has more branchial folds and rounded siphonal scales (rather than pointed spines). Individuals are also larger and more robust.

Pyura australis (Quoy and Gaimard, 1834)
(Figs 138c,d, 140)

Ascidia australis Quoy and Gaimard, 1834, p.614.
Boltenia australis: Herdman, 1891, p.571. Hartmeyer, 1909, p.1341.
Pyura australis: Hartmeyer and Michaelsen, 1928, p.413. Kott, 1952, var. typica p.226; var. parvispinatis p.268; 1972a, s.sp. *australis* p.39; 1972b, p.186; 1975, p.14; 1976a, p.77. Millar, 1963, p.739.
Boltenia gibbosa: Herdman, 1899, p.19.

DISTRIBUTION

NEW RECORDS: Western Australia (Dongara, WAM 1256-8.83; Cockburn Sound, WAM 581/2.31 16.75 197.75(1) 1259-64.83; Albany, WAM 119.75). South Australia (Port Noarlunga, QM G9308; Onkaparinga, QM G9360; Pearson I., QM GH1324). Tasmania (Orford, QM GH1332; Hobart, TM D92; Roches Beach, TM D1810 D1816; Ralphs Bay, TM D716; Tinderbox, QM G9997; Maria I., QM GH2056). Victoria (Portsea; Flinders, QM G10178; Bass Strait, QM G12746, NMV H783 F51581; Woodside, QM GH233; Gabo I., QM G12746). New South Wales (Ulladulla, QM G8574; Shell Harbour; Arrawarra). Queensland (Lizard I., QM GH2187).

PREVIOUSLY RECORDED: Western Australia (King George Sound — Quoy and Gaimard 1834; Geraldton, Cottesloe, Fremantle, Bunbury, Busselton — Hartmeyer and Michaelsen 1928, Kott 1952). South Australia (Great Australian Bight, St Vincent Gulf, Spencer Gulf, Kangaroo I., Investigator Strait — Kott 1972a,b 1975). Victoria (Port Phillip Bay — Millar 1963, Kott 1976a; Western Port Bay — Kott 1976a).

The species has been taken in subtidal waters down to 20 m. It has a wide range in Australian temperate waters. The record from Lizard I. is perplexing, since most records indicate a strictly temperate range for this species (see Remarks).

DESCRIPTION

EXTERNAL APPEARANCE: Spherical to oval heads (up to 4 cm long) are supported on narrow stalks of up to 30 cm in length. The head is sometimes slightly compressed laterally. Its upper free surface (which is the posterior end of the body) is usually smooth and rounded. At its anterior (lower) end, the body sometimes narrows abruptly to the stalk, but in other specimens it narrows gradually. The head is widest at the upper end. The apertures are on short siphons on the dorsal side of the head, slightly more than one-third of the body length apart, and directed away from one another. The atrial siphon is uppermost, quite close to the upper end of the head; its aperture is directed upwards, away from the substrate. The branchial aperture, which is toward the lower (anterior) end of the dorsal surface, faces in the opposite direction to the atrial aperture - down toward the substrate. This orientation of the apertures is caused by the differential growth of the siphonal walls, so that their facing sides are long, curve out and away from one another, and lie more or less parallel to the long axis of the head. There are, sometimes, longitudinal furrows on each side of the head, with rounded or pointed tubercles along the ridges between the furrows. In other specimens, similar tubercles are present on an otherwise smooth head. The longitudinal furrows are curved, parallel to the convex ventral border of the body. The dorsal border is either convex or straight.

The stalk is tough and horizontally wrinkled, narrowing toward the base. In section, the stalk has an outer, thin cuticular layer with softer internal test. There is a layer of crowded spicules inside the cuticle. Two large vessels extend along the centre of the stalk, surrounded by vacuolated, parenchymatous test, which often causes the stalk to be flattened in preserved material. The test of the head is very tough, with stellate spicules (up to 0.03 mm in diameter) embedded in it. A few dumbbell-shaped spicules like those of *P. gibbosa* are also present.

Living specimens are orange or maroon. Preserved specimens are usually some shade of beige or pinkish white.

Conical, slightly curved, pointed spines 0.02 to 0.05 mm long line the siphons. However, the rather thick, conical and pointed projecting part of the spine is only about half of the total length. Its outer surface projects backwards to form a long, open base. The longest spines are found toward the border of the apertures.

INTERNAL STRUCTURE: The body musculature is strong, and the body wall is usually opaque. The branchial tentacles are bushy with long primary

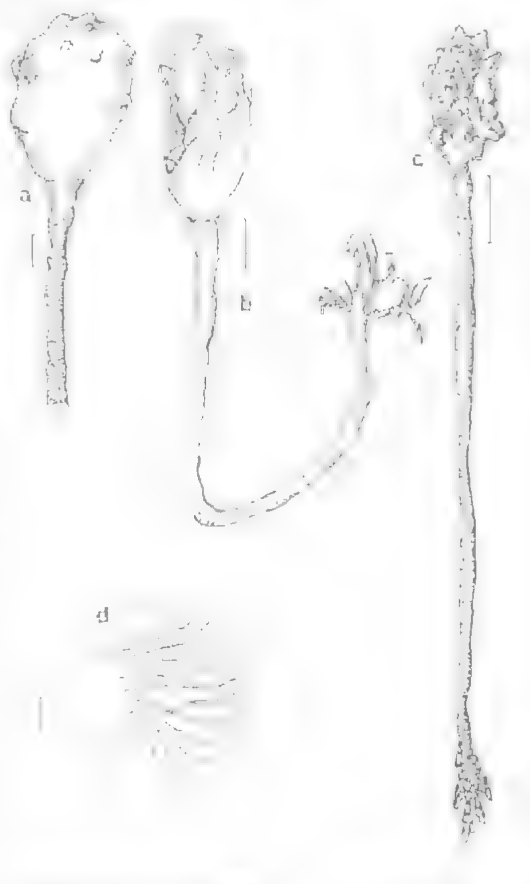


FIG. 140: *Pyura australis* — a - c, variable external appearance (QM G12746, G9308, G9360); d, anal lobes. (Scales: a, 5.0 mm; b, c, 2.0 cm; d, 0.5 mm).

and secondary but minute tertiary branches. The dorsal tubercle has a U-shaped slit with both horns rolled inwards. The dorsal lamina is long and the languets long, tapering and pointed. The oesophageal opening is at the posterior end of the body. The branchial folds are only slightly curved, and terminate posteriorly along the sides of the oesophageal opening (except for the most ventral fold, which terminates behind it).

There are 6 wide folds on each side of the branchial sac. Up to 8 internal longitudinal vessels are present on the folds and 3 or 4 in the interspace. There are about 8 long, rectangular stigmata in each mesh, crossed by a parastigmatic vessel. A typical branchial formula is: DL5(13)3(18)3(15)4(14)3(12)4(10)3E.

The gut follows the ventral border of the body, curving upwards at its proximal end to form a long, J-shaped loop. About 5 paired, arborescent liver diverticula branch off the gut in the pyloric region. Ridges projecting into the lumen of the distal part of the rectum extend into long, flattened anal lobes with rounded and rather spatulate tips. In some specimens, the anal border is not lobed, although the sharp ridges are present in the distal part of the rectum (see *P. australis* var. parvispinatis: Kott, 1952 and *P. australis*: Kott, 1972b). Kott (1972b) concluded that the separation of these specimens from those with a lobed anal border was not justified.

Each gonad consists of a single row of transversely elongate polycarp sacs on the anterior side of the male and female ducts. The left gonad is in the loop of the gut. The right gonad is in a corresponding position on the opposite side of the body wall. Each polycarp sac is firmly fixed to the body wall by the whole of its base. Endocarps are present along both limbs of the gut loop and on the gonads.

REMARKS: The species closely resembles *Pyura gibbosa*, *P. spinifera* and related species of the *pachydermatina* group in its general shape, stalk, orientation of the body and branchial sac. It can be distinguished by its siphonal armature, dorsal tubercle, test spicules, stalk structure and anal border. Variations in the length of the anal lobes can cause confusion with *P. gibbosa gibbosa*; from which it is distinguished externally only by the slight ventral curvature of the body. A cross-section of the stalk can be examined to a reliably indicate identity. Generally, where tubercles are present, their arrangement along longitudinal ridges can be used to distinguish specimens from *P. spinifera*. However, rounded specimens without tubercles must be dissected for reliable determination.

In one specimen lot (WAM 581/2.31), two individuals are joined to one another along the length of their heads, but only one of them has a stalk. Michaelsen and Hartmeyer (1928) describe the same phenomenon for *Pyura australiensis* (< *P. spinifera*). In each case, the tests of host and commensal appear to be confluent, rather than merely adhering. The length of the stalk in stalked species may be affected by environmental rather than genetic pressures. However, it does not seem reasonable to assume that the stalk does not develop when the need for it is satisfied by a commensal relationship with a stalked host. There is no apparent explanation of the phenomenon.

The record from Lizard I. (intertidal) is of a single specimen. It is right outside the normally recorded range of this species. The head is 2 cm long, and the stalk about the same length. The specimen has the spicules and siphonal spines characteristic of this species. The gonads, which are not divided into sacs, form very large masses embedded in the body wall. Their development appears to be abnormal.

Pyura confragosa n.sp.
(Figs 138e, 141)

DISTRIBUTION

TYPE LOCALITY: Queensland (Moreton Bay, Moreton I., 15 m, coll. A. Rozefelds, 20.4.81, holotype QM GH366).

FURTHER RECORDS: Queensland (Mudjimbah, paratype QM GH1149; Hervey Bay, paratype QM G9332; Heron I., QM GH2184 GH2990 GH3022 GH3069; Wistari Reef, QM GH2976; Lizard I., QM GH21[illegible]).

The species is found from shallow subtidal depths down to about 60 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are tough, very hard and irregular. Preserved specimens sometimes have flat surface depressions surrounded by hard ridges. The test sometimes has narrow horizontal ridges, but often appears to be too hard to be wrinkled. Spherical vesicles or hard, scale-like thickenings are present in the surface layer. In smaller specimens the test is thicker, more cartilaginous and with irregular processes over its surface (QM G9332). In larger individuals, the test is thin and rigid, with fewer processes and more flat, depressed areas separated by sharp ridges. The apertures are on short, conical siphons on the upper surface, the branchial aperture about one quarter of the body length from the anterior end of the body and the atrial aperture about the same distance from the posterior end. Individuals up to 9 cm are known. The ventral test is produced into

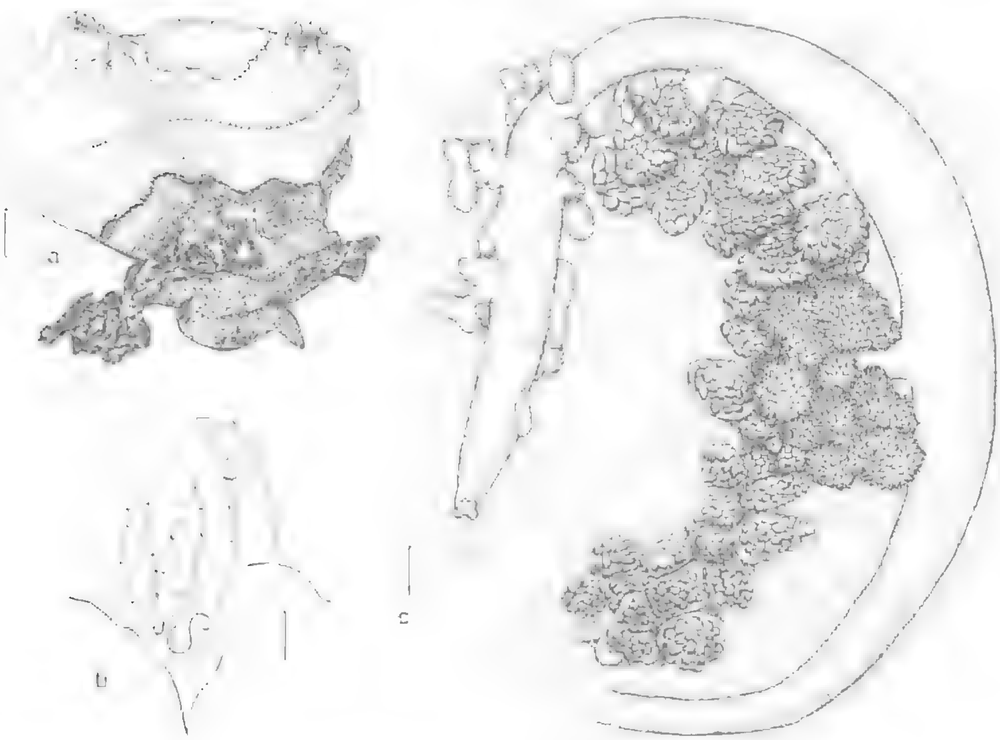


FIG. 141: *Pyura confragosa* n.sp. (QM GH366) — a, external appearance; b, dorsal tubercle; c, gut, gonads and endocarps. (Scales: a, 1.0 cm; b, c, 1.0 mm).

irregular roots and holdfasts, to which shell and rock particles are attached. A few foreign bodies are attached to other parts of the test, but it is generally naked. Minute (0.025 mm long), curved spines line the outer part of each siphon.

The test of living specimens is maroon, cinnamon rufous (Ridgeway 1886) to bright orange, but this colour is lost in preservative. The colour is most intense around the apertures and in the siphon linings.

INTERNAL STRUCTURE: The body wall is very muscular. Strong longitudinal muscle bands extend from each of the siphons onto the ventral surface. There are external circular bands around each siphon and some circular bands around the anterior border of the body at the base of the siphons. There are no other circular muscle bands: the musculature of the ventral two-thirds of the body consists entirely of longitudinal bands. In fresh material, the body wall is blue-grey, with orange siphons.

The branchial tentacles have only short primary branches and minute secondary branches. The prebranchial area is shallow. There is a wide, V-shaped peritubercular area with the dorsal tubercle, a conspicuous circular cushion, in the centre of this area. The slit is large and U-shaped, sometimes with both horns turned out. The dorsal lamina is long, with finely pointed, crowded languets.

There are 8 to 9 branchial folds on each side of the body. With the exception of the rudimentary ventral fold on each side, they are wide and overlapping. The internal longitudinal vessels are widely spaced both on and between the folds. There are up to 25 internal longitudinal vessels on the folds, and up to 8 in the interspace, but fewer in smaller specimens. A branchial formula of a 9 cm long individual is: E0(4)2(17)3(18)5(20)6(21)6(22)6(22)6(17)7(14)3DL. Sometimes orange blood cells outline the branchial vessels. There are 6 stigmata per mesh. The branchial folds are not very curved and, with the exception of the dorsal folds (which terminate each side of the oesophagus), they extend between the prepharyngeal and retropharyngeal grooves.

The gut forms a very wide, simple, D-shaped loop and the rectum does not turn anteriorly. There are no liver diverticula on the proximal part of the gut, but the main stem of the liver, arising from about halfway along the ascending limb of the loop, is large, and branches 4 times before dividing into bunches of elongate, terminal, liver lobules. The anal border has shallow, irregular indentations.

The single gonad on each side consists of very numerous, crowded, often subdivided, polycarp sacs along the sides of the gonoducts. The left gonad is curved around inside the ascending limb of the gut loop. The right gonad is in a corresponding position on the right side of the body. The polycarp sacs are only very lightly attached to the body wall by fine ligaments and are readily dislodged. There are endocarps on the gut loop.

REMARKS: The species is similar to *Pyura irregularis*, *P. crassacapitata* n.sp., *P. abradata* n.sp., *P. fissa* and *P. elongata*, all of which have curved scales lining the outer part of the siphons and very tough tests. *Pyura irregularis* further resembles *P. confragosa* in having a similar number of branchial folds, endocarps on the gut loop and a long dorsal lamina. The former species is distinguished by its dorsal tubercle crowded in the posterior end of a deep, narrow peritubercular area, and fewer, non-proliferating rounded polycarp sacs.

Pyura confragosa n.sp. is similar to the New Zealand species *P. rugata* Brewin, 1948 (OM A63.3) in external appearance, position of apertures, course of gut and gonads, position of liver, and numbers of internal branchial vessels. However, the New Zealand species is distinguished by having only 7 branchial folds on each side, and no endocarps on the gut loop.

Pyura crassacapitata n.sp.
(Figs 138f, 142)

DISTRIBUTION

TYPE LOCALITY: Queensland (Maroochydore, Mudjimbah, on black beacon, reef edge, coll. A. Rozefelds, 9.2.78, holotype QM G11910).

FURTHER RECORDS: Western Australia (Cockburn Sound, paratype QM G9665). South Australia (Onkaparinga, paratype QM G9361).

The species has been taken in shallow sublittoral water down to 10 mm.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are rounded to elongate, slightly flattened laterally, and fixed by a large part of the ventral surface. The surface is very hard and rigid and is covered with a mosaic of large, flat, circular to polygonal depressions with sharp raised ridges of test between them. The apertures are on small prominences at opposite ends of the upper surface, with a thick ridge of test extending between them in the dorsal mid-line. The test is thick and

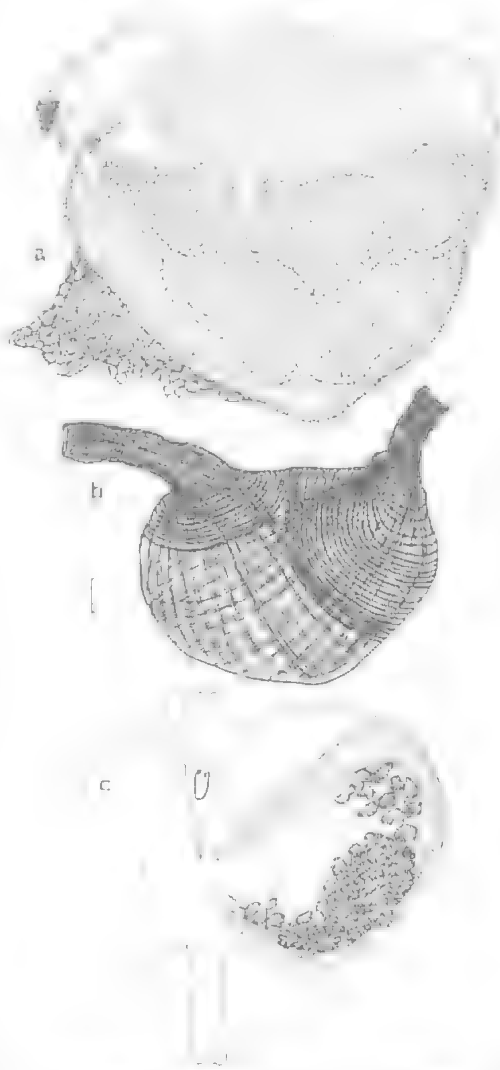


FIG. 142: *Pyura crassacapitata* n.sp. (QM 9665) — a, external appearance; b, body removed from test showing muscles; c, internal body wall. (Scales: 1.0 mm).

cartilaginous in section, without foreign particles, although some sand is included in the small South Australian specimen. There are minute, rounded scales in the outer part of the siphonal lining.

INTERNAL STRUCTURE: The body wall is muscular and opaque. The internal longitudinal muscles radiating from each siphon are strong and wide, crossing one another on the sides of the body. External circular muscles are present around the siphons and around the base of the siphons, forming a wider circle around the base of the atrial siphon than around the branchial siphon. Circular muscles are also present ventral to the siphonal muscles, although they are usually less conspicuous. There is a very strong sphincter muscle at the base of both the atrial and branchial siphons. The branchial sphincter, which is just anterior to the base of the tentacles, projects into the lumen.

The branchial tentacles (about 8) have primary, secondary and very minute tertiary branches. The internal siphons are extremely long, the atrial siphon being the larger. They are directed away from one another. The small, inconspicuous dorsal tubercle is in the base of a deep, narrow, V-shaped peritubercular area that occupies almost half of the dorsal mid-line of the pharynx, the dorsal lamina accordingly being relatively short. The slit on the dorsal tubercle is U-shaped.

The 7 branchial folds on each side of the body have up to 4 internal longitudinal vessels in the interspace and up to 16 on the folds. A branchial formula is: DL3(12)3(12)2(16)3(16)4(12)2(10) 2(5)0E (AM G11910). There are 8 narrow stigmata per mesh.

The gut loop forms a D-shaped or wide and sometimes curved loop. There is only one compact arborescent liver diverticulum. It is present about halfway up the ascending limb of the loop and is fixed to the gut and body wall by very numerous, fine ligaments. There are rudimentary diverticula on the proximal part of the gut. The anal border has about 6 shallow, rounded lobes.

The single gonad on each side consists of about 12 rather small, irregular polycarp sacs on each side of central gonoducts. These sacs are crowded, cuboid and often wider than they are long. They are only lightly attached to the body wall by fine ligaments. There are no endocarps on gut or gonads.

REMARKS: The species is readily confused with *P. elongata*, which also has widely separated apertures directed away from each other. The hard, irregular test appears very like that of *P. confragosa* n.sp. It is distinguished from the former species by the outer surface of the test and by its very numerous polycarp sacs. The latter species is distinguished by having endocarps on the gut loop. A conspicuous characteristic of *P. crassacapitata* n.sp. is the thickened ridge of test along the upper surface. This ridge of test holds the apertures in position and accommodates and strengthens the long siphons. *Pyura lanka* (Herdman, 1906) from Sri Lanka has a similar ridge-like thickening across the anterior part of the body between the siphons. However, it has a sandy test, only 6 branchial folds and a deep body and its polycarp sacs are only partly separated from the gonoducts.

Pyura curvigona Tokioka, 1950
(Figs 143a,b, 144)

Pyura curvigona Tokioka, 1950, p.147; 1967a, p.199. Millar, 1975, p.313. (Not: Kott and Goodbody, 1982, p.539, < *P. sacciformis*).

DISTRIBUTION

NEW RECORDS: Western Australia (Dirk Hartog I., WAM 2166.83). Queensland (Heron I., QM GH1395; Lizard I., QM GH2186 GH2342).

PREVIOUSLY RECORDED: Palau Is (Tokioka 1950 1967a). Indonesia (Millar 1975).

This beautiful tropical western Pacific species has been recorded on very few occasions. It has been taken from depths of from 5 to 37 m. It is one of the few species of *Pyura* with a range that extends into the western Pacific (see also *P. sacciformis* and *P. elongata*).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are laterally flattened, with a smooth, cartilaginous to rough, and leathery test. In some of the preserved specimens, the external test is pink to white, and the siphonal lining is often red. Tokioka (1967a) records traces of red, brown, and yellowish green in his specimens. The largest individuals recorded are 5 cm long (Tokioka 1950). Attachment to the substrate is by all or part of the right side or of the ventral or posterior aspects of the body. Apertures are sessile, on only slight elevations of the test. The border of the apertures is divided into large, triangular lobes.

Minute spines cover the external surface of the branchial and atrial lobes and continue down into the siphonal lining. These spines are 0.15 to 0.2 mm long and sharply pointed. About halfway along their length, on the outer side, there is a large, flat scale, its base extending around the spine like a collar (Fig. 4). This scale, which lies just under the surface test, is brilliantly opalescent. A groove extends along the inside of the distal tapering part of the spine in front of the collar.

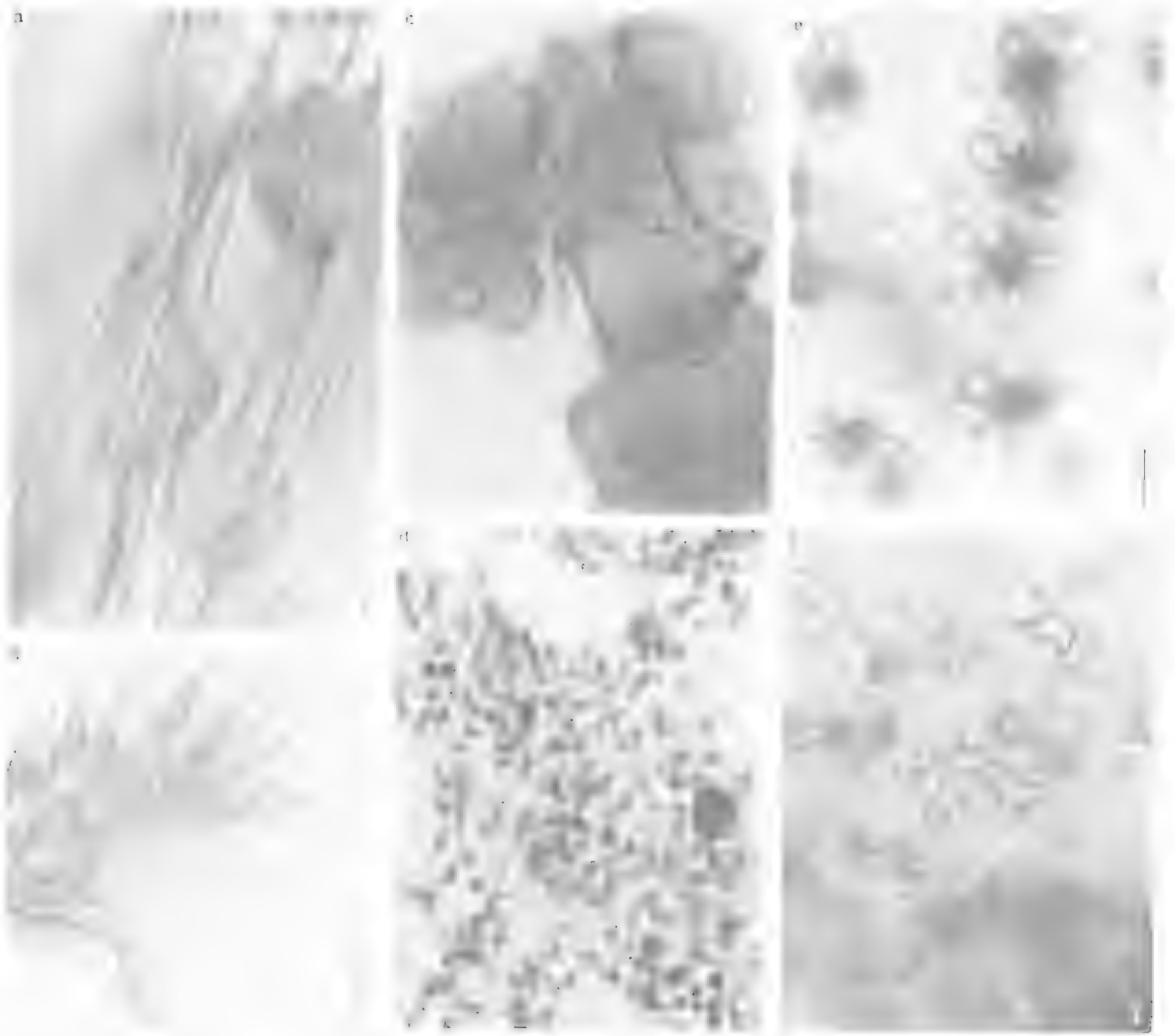


FIG. 143: *Pyura curvigona* — **a**, **b**, siphonal spines. *Pyura elongata* — **c**, scale-like thickenings in test. *Pyura gibbosa gibbosa* — **d**, siphonal spines and spicules; **e**, spicules from the stalk. *Pyura gibbosa draschii* — **f**, dumbell-shaped spicules. (Scales: **a**, **e**, **f**, 0.01 mm; **b** - **d**, 0.1 mm).

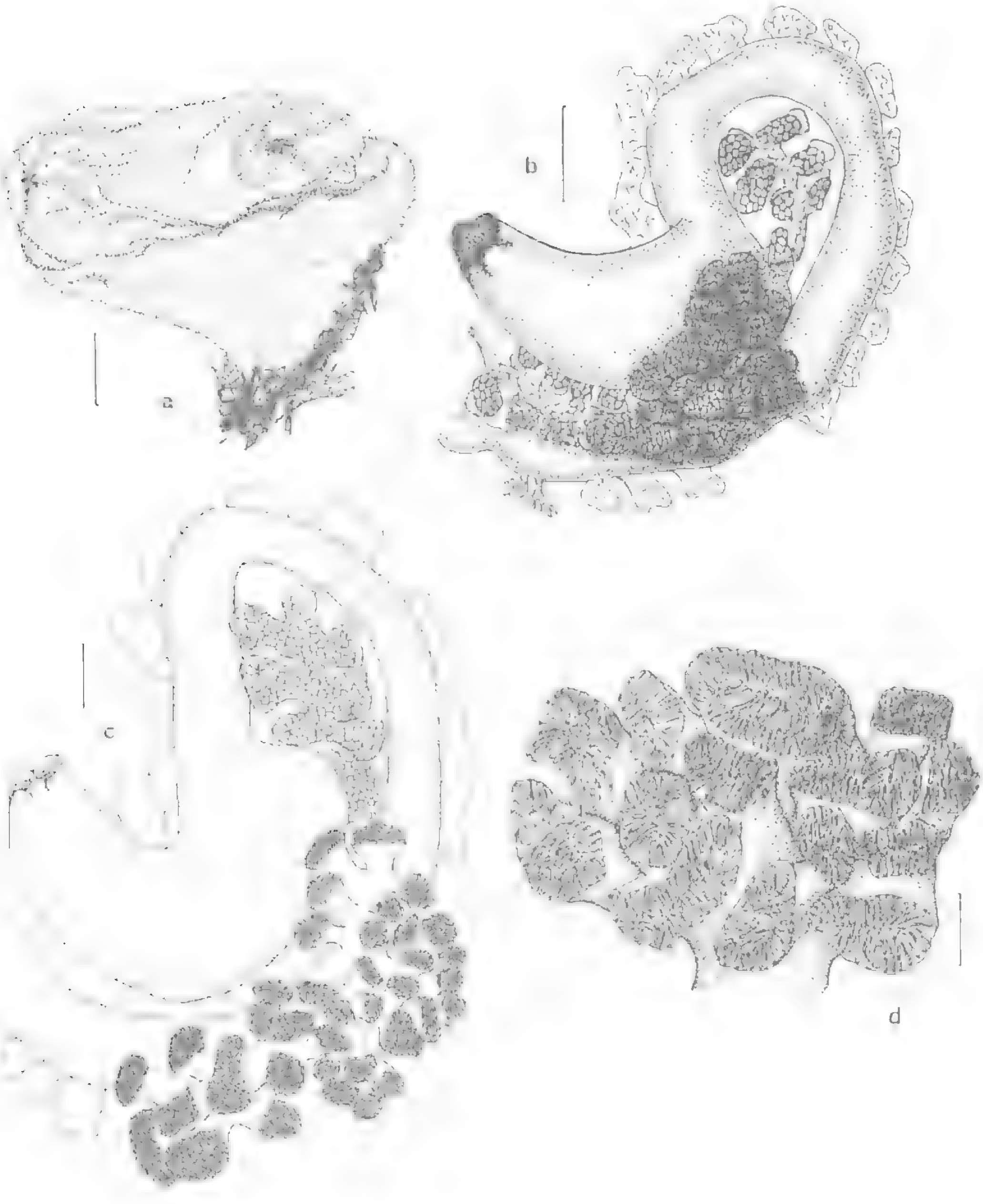


FIG. 144: *Pyura curvigona* — **a**, external appearance (QM GH790); **b**, **c**, gut and gonads (QM GH1395, G2186); **d**, part of liver. (Scales: **a**, 5.0 mm; **b**, **c**, 2.0 mm; **d**, 0.5 mm).

The proximal part of the spine is rather solid, with an indented end. The outer, free, pointed shaft is longitudinally striated, but is not iridescent.

INTERNAL STRUCTURE: The body wall is rather thin and delicate, although the muscles are strong, especially on the anterior part of the body. Longitudinal muscles radiate from each siphon, subdividing into branches that form a fine mesh ventrally. Circular muscles are confined to the siphonal area.

The branchial tentacles (12), with their moderately long primary branches and only minute secondary branches, are not bushy. The dorsal tubercle is small with a U-shaped slit. There are 6 branchial folds on each side of the body. The Heron I. specimen has no more than 15 internal longitudinal vessels on the folds and 6 in the interspace. There are 6 stigmata per mesh, crossed by parastigmatic vessels. The Palau Is specimens have a similar number of branchial vessels, although specimens from Indonesia have up to 26 vessels on the folds. The branchial formula for the Heron I. specimen is: E6(14)6(15)5(12)5(12)4(10) 4(7)3DL.

The gut forms a curved loop, open at the pole. The rectum is greatly swollen with sand and mud. There is a row of small, branched liver diverticula from along each side of the cardiac end of the pyloric region. At the pyloric end, a single, large, branched liver diverticulum hangs free in the peribranchial cavity. The liver lobules are short and oval to round. They are crowded together on the free ends of the terminal branches of the liver diverticula, where they form compact, mushroom-like caps. The liver is pale green, blue-black, olive brown or brownish. Delicate endocarps are spaced rather regularly all along the outer curve of the gut loop. The anal border is divided into rounded lobes: 5 in the Heron I. specimens; or 7 to 11 (Tokioka 1967a).

The polycarp-sacs are rounded and crowded together along both sides of the gonoducts. The left gonad is in the gut loop. Each polycarp sac has a rather long endocarp rising from its surface. The gonad sacs are firmly attached to the body wall. They are often incompletely separated, remaining as pouches on each side of the central ducts.

REMARKS: The musculature is similar to that of *P. sacciformis*. The spines are positioned around the apertures much as in *P. obesa*, which also has endocarps on the gut. However, the siphonal spines, loose liver lobules, swollen rectum, and the regular series of endocarps over the gonads and along the gut are characteristic of the present species. The branchial spines appear to be related to those of *P. sacciformis*, in which the base is swollen but not produced out into a scale-like flap.

Pyura elongata Tokioka, 1952
(Figs 143c, 145)

Pyura elongata Tokioka, 1952, p.136. Millar, 1975, p.311. Kott and Goodbody, 1982, p.539.
Pyura lepidoderma: Kott, 1966, p.299; 1976a, p.84.
?*Pyura pulla*: Vasseur, 1967a, p.118.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 961.83 979.83; Shark Bay, WAM 2149.83; Cape Preston, WAM 2148.83; Cockburn Sound, WAM 2150.83). Tasmania (Hobart, TM D1882). Victoria (Hobson's Bay, QM G11866; Bass Strait, NMV H525, QM GH2692). New South Wales (Port Kembla, QM GH2002). Queensland (Moreton Bay, QM GH2749; Hervey Bay, QM G9354-7; Heron I., QM GH2721 GH2750 GH3020; Townsville, QM GH1386; Mossman, QM GH792).

PREVIOUSLY RECORDED: Victoria (Port Phillip Bay — Kott 1976a). Queensland (Hervey Bay — Kott 1966). Arafura Sea (Tokioka 1952). Indonesia (Millar 1975). Hong Kong (Kott and Goodbody 1982). ? Indian Ocean (Mascarene Archipelago — Vasseur 1967a).

The species has been recorded intertidally and down to 15 m. It is difficult to collect, as it adheres tightly to undersurfaces and is wedged in crevices. Its range may be greater than present records suggest.

DESCRIPTION

EXTERNAL APPEARANCE: Dome-shaped or dorso-ventrally flattened specimens are fixed by a large part of the flat ventral surface. More or less spherical ones are fixed by the postero-ventral surface. When the animal is relaxed, the branchial aperture is at the anterior end of the upper surface, the atrial aperture at least two-thirds of the body length distant from it. When contracted, the apertures are drawn closer together on the upper surface of the body, while the test forms rounded swellings around each aperture. The test is rather thick and tough. It is white and cartilaginous in preserved material. The surface usually has a mosaic of flat-topped polygonal or circular scale-like thickenings separated from one another by shallow creases. These thickenings are often present over the whole surface, but in other, less regular, specimens these surface features are more patchy, and are sometimes obscured by adherent particles or wrinkles and folds on the surface. The siphons are variable. They are conspicuous and have longitudinal furrows alternating with ridges in which the test contains scale-like thickenings in specimens from temperate waters. The apertures are often almost sessile in specimens from the tropics. The test in the dorsal mid-line between the

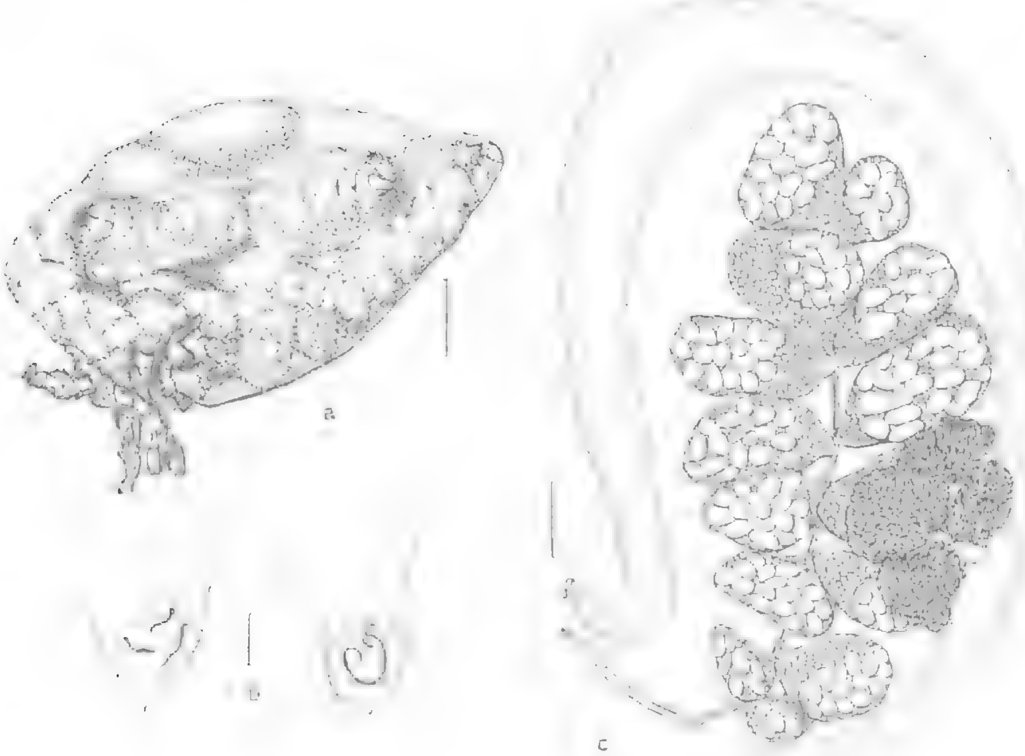


FIG. 145: *Pyura elongata* — a, external appearance; b, dorsal tubercles; c, gut and gonads. (Scales: a, 5.0 mm; b, c, 0.5 mm).

apertures is often thick and swollen. When the short siphons are extended, they are bright vermilion, contrasting vividly with the reddish brown or buff colour of the test. In preservative, patches of red colour may persist in the external layer of test, but generally the test fades to white. The bright vermilion persists in the siphonal lining and in the anterior part of the body wall. The test around the apertures is divided into smooth, rounded and rather conspicuous lobes. Immediately around the rim of the apertures, there are small lobes covered with the minute (about 0.02 mm long) curved scales that continue into the terminal part of the siphonal lining.

INTERNAL STRUCTURE: The body wall adheres closely to the test. It is moderately muscular, with wide bands radiating from the siphons and crossing each other to form rectangular meshes. Circular bands are present around the base of each siphon and along its length. The radiating longitudinal bands terminate on each side of the ventral mid-line. A muscular sphincter at the base of the branchial siphon projects into the lumen just in front of the branchial tentacles. The branchial tentacles have slender primary branches and only minute secondary branches. The dorsal tubercle is a large cushion that fills the base of a wide but deep peritubercular area, which is from a quarter to half the length of the dorsal lamina. The slit is roughly U-shaped, with horns turned in or out. In one specimen, the left horn is divided, one branch turning in and the other out. In another, the slit is divided into 3 separate, oblique openings (QM GH1386). The dorsal ganglion is very long, extending between the siphons.

The branchial folds, 6 on each side, are high, overlapping and curved, terminating posteriorly around the oesophageal opening which is a short distance from the posterior end of the body. There are up to 30 internal longitudinal vessels on the folds and up to 8 in the interspace. These vessels are rather evenly spaced on the folds and in the interspace. There are 4 to 6 stigmata per mesh, crossed by parastigmatic vessels. A characteristic branchial formula is: E5(17)6(18)5(15)3(28)2(27) 2(19)3

The gut forms a rather wide, curved loop with parallel limbs, extending from the oesophageal opening to occupy most of the ventral curve of the body. Small, rudimentary liver diverticula are present proximal to the single, large diverticulum which is about one-third of the distance along the ascending limb of the gut loop. The lobules are all small and rounded, but not very crowded. The anal border is smooth.

Each gonad consists of a row of 7 or 8 pairs of large, rounded polycarp sacs extending along each side of the central gonoducts. The left gonad is in the gut loop. The polycarp sacs are only very lightly attached to the body wall by fine ligaments.

There are no endocarps on the gut or gonads.

REMARKS: Kott and Goodbody (1982) have drawn attention to the similarity between this species and *P. gangelion* (Savigny) from the Persian Gulf. Despite the similarity in body shape, *P. gangelion* can be distinguished by its smaller number of internal longitudinal branchial vessels and the presence of endocarps on the gut loop (Monniot 1973).

Pyura pulla: Vasseur, 1967a appears to be identical with the present species, and distinct from the New Zealand *P. pulla* Sluiter, which has long, needle-like spines and a narrow gut loop.

Pyura abradata n.sp., *P. confragosa* n.sp. and *P. fissa* have similar scale-like thickenings in the surface test. The former species is readily distinguished from *P. elongata* by its more numerous branchial folds; the last two by the endocarps on their gut-loops.

Pyura elongata is characterised by the large number of internal longitudinal vessels in the interspace; the position of its apertures at opposite ends of the upper surface; its long neural ganglion; large, rounded polycarps; the absence of endocarps; and the scale-like thickenings on part, at least, of the surface.

Pyura fissa (Herdman, 1882)
(Fig. 146)

Cynthia fissa Herdman, 1882, p.137.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H477).

PREVIOUSLY RECORDED: Victoria (Bass Strait — holotype BM 1887.2.4.48-9 Herdman 1882).

DESCRIPTION

EXTERNAL APPEARANCE: The body is fixed by a small part of the ventral surface. It is about 3 cm long, and curves upwards to a terminal branchial aperture. The anterior half of the body is narrow. The atrial aperture is on a wide cone produced from the posterior half of the dorsal surface. It usually projects away from the body The ventral surface is convex. The test is very hard and has small, round swellings on the surface, each containing two or three scale-like thickenings of the outer cuticle. Narrow horizontal wrinkles and longitudinal creases curve along the long axis of the body. Around each aperture are sharply pointed projections of the test. The test is orange in preservative; this colour is still present in the holotype specimen.

Minute (0.01 to 0.02 mm) flattened scales, with a rounded border, line the terminal part of each siphon.

INTERNAL STRUCTURE: The body wall is muscular and adheres closely to the test. A conspicuous muscular sphincter projects into the lumen at the base of the branchial siphon, just anterior to the base of the tentacles. There are about 12 branchial tentacles, with only very short papilla-like primary branches and a few minute secondary branches. The peritubercular area is a deep V-shape, about half the length of the dorsal lamina. The dorsal tubercle, with a conspicuous, sometimes slightly irregular, U- or S-shaped slit, is a large oval cushion occupying the wide upper part of the peritubercular area. The oesophageal opening is at the posterior end of the branchial sac. The branchial folds are slightly curved posteriorly and terminate around the oesophageal opening. The long dorsal lamina has only a single row of languets.

The branchial sac has 7 folds on each side of the body, with internal longitudinal vessels arranged according to the following formulae: DL0(8)4(16)4(14)4(12)4(10)3(10)2(8)1E (holotype); E0(2)3(9)3(12)3(18)4(20)3(9)3(12)1DL (NMV H477). In the latter specimen, the ventral fold consists of only 2 internal longitudinal vessels close together. There are about 6 relatively short, oval stigmata in each mesh.

The gut forms a wide, open loop across the posterior end of the body, with only a short rectum curving dorsally to the atrial aperture. There is a single, much branched liver diverticulum about halfway up the ascending limb of the gut loop. The terminal lobules are elongate and rather loose. The anal border is divided into 6 to 12 rounded lobes. The gut is covered by a membrane that firmly attaches it to the body wall.

Each gonad consists of numerous, crowded, irregularly shaped polycarp sacs. The left gonad is in the gut loop; the right is in a corresponding position on the opposite side of the body. The sacs

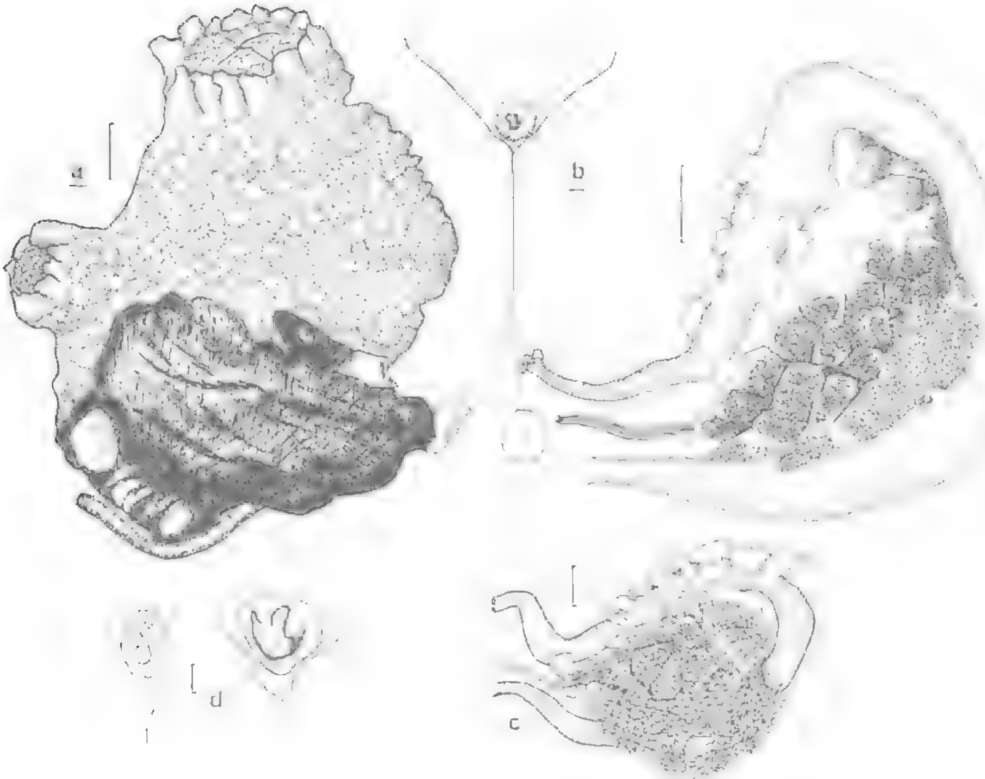


FIG. 146: *Pyura fissa* — **a**, external appearance (NMV H477); **b**, **c**, gut gonads and endocarps (NMV H477, BM 1887.2.4.48–9); **d**, dorsal tubercles (NMV H477, BM 1887.2.4.48–9, NMV H477). (Scales: a – c, 2.0 mm; d, 0.5 mm).

are attached to the body wall and to one another by very fine ligaments. They are readily dislodged.

Large, conspicuous endocarps are present on the descending limb of the gut loop and on the gonads.

REMARKS: The species resembles *P. elongata* in its body shape, scale-like thickenings of the test and position of the liver. It is, however, readily distinguished by the endocarps on the gut loop. These endocarps, together with a lesser number of branchial folds, distinguish the species from *P. abradata* n.sp. *Pyura irregularis* is distinguished from the present species by the position of its dorsal tubercle (in the base of the peritubercular area). *Pyura confragosa* n.sp. (which also has crowded polycarp sacs) can be distinguished by its more numerous branchial folds. *Pyura pantex*, from the Red Sea, is also a closely related species, apparently differing from *P. fissa* only in its larger cuticular thickenings and its body shape.

Pyura gibbosa (Heller, 1878) **gibbosa** Heller, 1878
(Figs 143d,e, 147a,b; Pl. VIIb)

Cynthia gibbosa Heller, 1878, p.27.
Pyura gibbosa: Hartmeyer and Michaelsen, 1928, p.410.
Boltenia pachydermatina: Drasche, 1884, p.371. ? Carter, 1885, p.198. Traustedt, 1885, p.25. Herdman, 1899, p.16. Herdman and Riddell, 1913, p.875. Anderson *et al.*, 1975, p.205.
Pyura pachydermatina: Kott, 1952, var. intermedia p.264; 1964, p.140.
Boltenia spinifera: Michaelsen, 1905, p.72 (part, one of 2 specimens from Bass Strait — see Hartmeyer and Michaelsen 1928).

DISTRIBUTION

NEW RECORDS: Tasmania (Cape Barren I., TM D1177; Roches Beach, TM D189; Western Tasmania, TM D937; Kingston, TM D705; Ralph's Neck Bay, TM D715; Bruny I., QM G8575). New South Wales (Solitary I., QM G9584).

PREVIOUSLY RECORDED: Victoria (Bass Strait — Heller 1878, ? Carter 1884, Michaelsen 1905, Hartmeyer and Michaelsen 1928, Kott 1952). New South Wales (Coffs Harbour, Wreck Bay, Port Jackson, Port Hacking, Kiama — Drasche 1884, Herdman 1899, Herdman and Riddell 1913, Hartmeyer and Michaelsen 1928). Queensland (Moreton Bay — Kott 1964).

This species has temperate range from western and eastern Tasmania and up the eastern coast of Australia to Moreton Bay.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals consists of an elongate head joined at the anterior end to a long, narrow stalk. The heads (up to 5 cm in length) usually have sharp, vertical ridges down each side on which tubercles, usually pointed, are supported. These tubercles, variable in length and in number, are sometimes absent altogether, and the longitudinal ridges may be rounded. The head is almost rectangular, narrowing abruptly to the stalk at its anterior end and with a rounded posterior or upper, free end. The head of this species is relatively long and narrow, without any curvature on the longitudinal axis and with dorsal and ventral borders more or less parallel to one another. Branchial and atrial apertures are on the vertical dorsal side. Differential development of the siphonal walls ensures that the apertures are directed away from one another. The lower and upper rim of the branchial and atrial apertures, respectively, are sessile, while the opposite rim in each case is produced across the opening. There are longitudinal swellings along the external wall of each siphon.

Living specimens are maroon, and retain some red colouring in preservative.

The test of the head is firm, solid, leathery, and white in cross section. The many calcareous spicules in the surface layer of test are dumbbell-shaped or, less often, stellate. The shaft of the dumbbell-shaped spicules is only about 0.02 mm long, and about one-third as thick. There are 4 or 5 short rounded tubercles at each end. Rounded tubercles are often present along the length of the shaft, tending to obscure the dumbbell-shape of the spicules. A shortened shaft produces a more stellate-shaped spicule.

The stalk is of variable length and thickness, usually long and narrow. The surface of the stalk has a thick, brownish, translucent cuticle, but internally the test is white. Stellate, rather than dumbbell-shaped, spicules crowd in a layer beneath the cuticle. Short, radial extensions of this layer project toward the centre of the stalk. There are no spicules in the centre of the stalk, through which extend two very large longitudinal vessels.

Crowded, overlapping spines line the siphons. They are 0.05 to 0.06 mm long overall; however, the pointed, projecting, overlapping part is only about one-quarter of that length, as is the open, oval base. The long, narrow, posterior extension of the outer side of the spine is about half of the length of the spine.

INTERNAL STRUCTURE: The body wall is rather transparent between the meshwork of muscles that radiate from each siphon. The branchial tentacles are bushy. The dorsal tubercle is conspicuous and dome-shaped, broken on its surface by the very convoluted opening of the neural gland. The dorsal lamina is very long, but the dorsal languets are of moderate length, although quite conspicuous. The oesophageal opening is at the posterior end of the branchial sac.

There are 6 branchial folds on each side of the body. They are wide, overlapping and rather straight, terminating posteriorly just anterior to, and along each side of, the oesophageal opening. There are up to 15 internal longitudinal vessels in the folds and 1 or 2 in the interspace. A typical branchial formula is: E3(8)1(12)2(15)1(11)2(15) 2(11)1DL. Each mesh has about 6 stigmata.

The gut loop is moderately narrow, forming a J-shaped curve around the ventral border of the body, almost reaching to the prepharyngeal groove. There are endocarps along both limbs of the gut. There are three pairs of arborescent (cauliflower-like) liver diverticula, one of each pair on opposite sides of the ascending limb of the gut loop. The over 20 rounded anal lobes are small, but well defined.

A single series of up to 8 polycarp sacs are enclosed in the gut loop on the left; and in a corresponding position on the right. The polycarp sacs, which are upright and transversely elongate, are firmly fixed to the body wall. The common ducts extend close to the posterior side of the row of gonad sacs.

REMARKS: The differences between the present subspecies and *P. gibbosa draschii* are discussed below. The anal borders of both are unique, and help to distinguish them from one another and from other species. However, their external appearance is very similar, and confusion with *P. australis* is also possible. *Pyura gibbosa* is characterised by the large numbers of dumbbell-shaped spicules, the relatively fewer internal longitudinal branchial vessels in the interspace, and its relatively long, narrow body with vertical, more or less parallel, dorsal and ventral borders.

Kott (1952) regarded the Australian *P. gibbosa* as a subspecies of the New Zealand *P.*

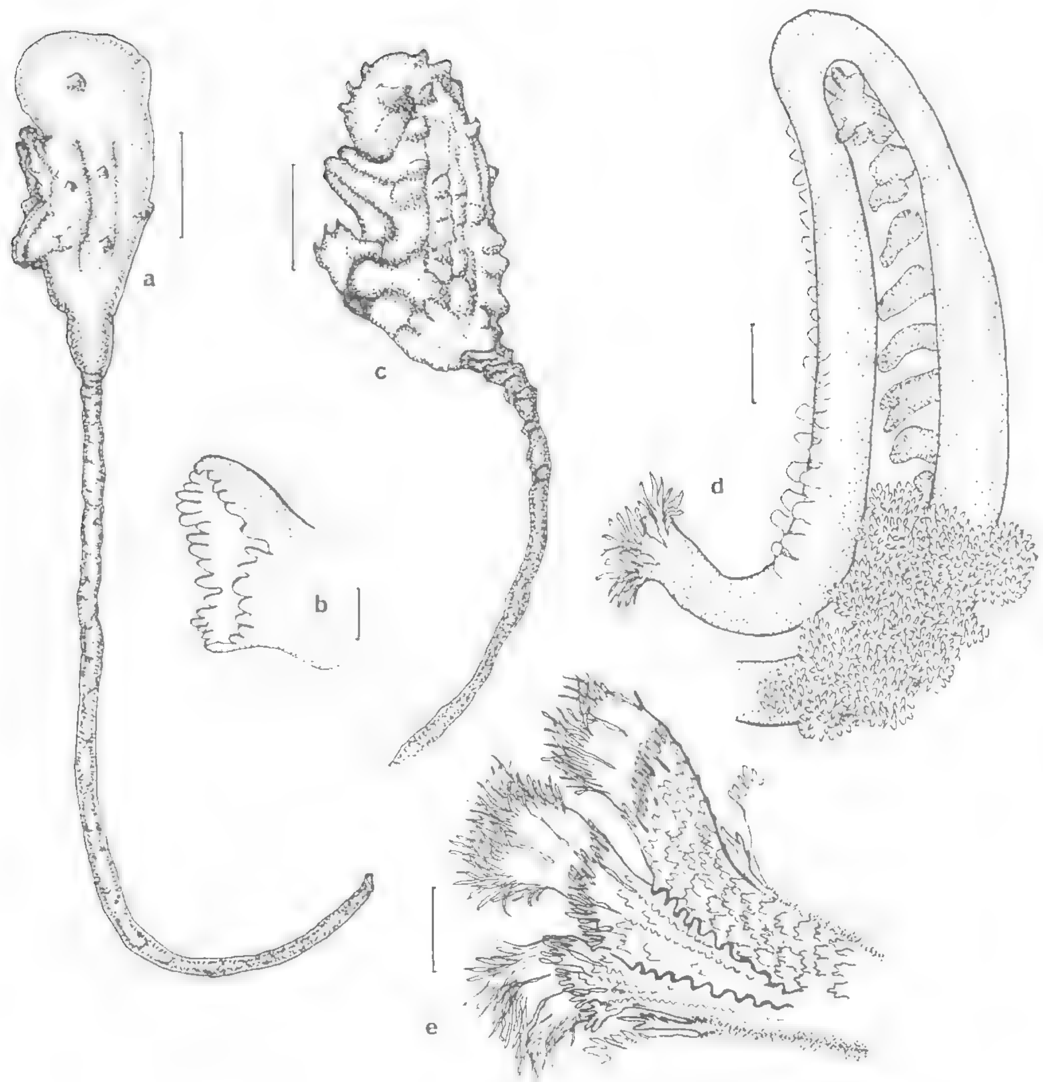


FIG. 147: *Pyura gibbosa gibbosa* — **a**, external appearance; **b**, anal border. *P. gibbosa draschii* — **c**, external appearance; **d**, gut and gonads; **e**, anal border. (Scales: **a**, **c**, 2.0 cm; **b**, 0.25 mm; **d**, 5.0 mm; **e**, 0.2 mm).

pachydermatina, which has similar spicules. There are differences in the structure of the stalk, however, as well as a different anal border, and in the present work the New Zealand and Australian populations are regarded as distinct species.

Pyura gibbosa (Heller, 1878) **draschii** Kott, 1972
(Figs 143f, 147c–e; Pl.VIIa)

Pyura pachydermatina: Millar, 1966, p.371. Kott, 1952, var. gibbosa p.265; 1972b, s.sp. *draschii* p.187.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, WAM 1246.83 1248.83). Tasmania (Bruny I., QM G8575). Victoria (Portsea, QM G10171; Port Phillip Bay, QM G10173).

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound, Hamelin Bay — Kott 1952). South Australia (St Vincent Gulf — Kott 1952; Great Australian Bight — Kott 1972b). Victoria (Port Phillip Bay — Kott 1952, Millar 1966).

The range is temperate, from Cockburn Sound into the Great Australian Bight and to Port Phillip Bay. It may just overlap the range of *P. gibbosa gibbosa* in Bass Strait.

DESCRIPTION

REMARKS: Individuals of this subspecies have similar variations to those of *P. gibbosa gibbosa* (see above). The subspecies are different in the following respects:

1. In *P. gibbosa draschii*, the long lobes of the anal border have fine, pointed fringes that form a long, tangled mop around the opening.
2. The siphonal spines of *P. gibbosa draschii* are smaller, being only 0.03 to 0.04 mm in total length.
3. The dumbbell-shaped spicules are the same length in both subspecies, but in *P. gibbosa draschii* the shaft is less often reduced in length, and seldom has secondary tubercles on it.
4. *P. gibbosa draschii* has 5 or 6 pairs of large liver diverticula, one of each pair on opposite sides of the gut, while *P. gibbosa gibbosa* has only 3 pairs.

Pyura irregularis (Herdman, 1882)
(Figs 148a, 149)

Cynthia irregularis Herdman, 1882, p.141.
Pyura irregularis: Kott, 1952, p.271 (part., specimens from d'Entrecasteaux Channel); 1976a, p.80. Millar, 1963, p.739; 1966, p.370.

DISTRIBUTION

NEW RECORDS: Tasmania (Hobart, TM D1816; d'Entrecasteaux Channel, TM D251; Pt Davey, QM GH2001). Victoria (Bass Strait, NMV H453 H911; Western Port, QM GH3057).

PREVIOUSLY RECORDED: Tasmania (d'Entrecasteaux Channel — Kott 1952). Victoria (Port Phillip Bay Millar 1963 1966; Western Port — Kott 1976a). New South Wales (Port Jackson — Herdman 1882).

The species is taken at depths of from 5 to 60 m off the eastern coast of Tasmania to Port Jackson. Its range suggests that it is a temperate indigenousspecies.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are broad basally, tapering to a rather long terminal branchial siphon that is turned ventrally or to one side. The atrial siphon is also long. It arises from halfway down the dorsal surface and either diverges from the body or is bent over to the same or opposite side of the body to the branchial siphon. The variation in orientation of the siphons probably results from the fact that individuals form large, irregular aggregates. The surface of the thin, but rigid and tough, test is a mosaic of large, irregular, flat depressions, separated by sharp ridges. The siphons have longitudinal furrows. Occasionally there is a short stalk posteriorly. There are minute (0.01 to 0.02 mm), overlapping scales with rounded anterior borders in the outer part of the siphonal lining.

INTERNAL STRUCTURE: The branchial tentacles have primary branches, but the secondary branches are small and tertiary branches are not apparent. A very long, narrow perituberculat area extends about one-quarter of the length of the dorsal mid-line of the pharynx. The dorsal tubercle is crowded in the posterior end of this deep, V-shaped area. It has a long, U-shaped slit (which is sometimes interrupted to form separate openings). The dorsal lamina is very long, the oesophageal opening being at the posterior end of the branchial sac. The tapering languets of the dorsal lamina are relatively long. Similar languets are present at the dorsal end of the transverse vessels to the right of the primary row.

The 7 or 8 branchial folds terminate posteriorly around the oesophageal opening. A branchial formula for a fairly large individual (7 cm) is DL2(20)5(18)6(24)7(20)4(12)4(14)3(10)2(3)1E. In this case, the ventral fold is rudimentary. There are 6 to 8 stigmata per mesh.

The gut loop is wide and open, forming a D-shape. The descending limb is straight. The rectum does not curve anteriorly. There is a large, branched liver diverticulum halfway up the curved ascending limb. Small rudimentary diverticula are present on the proximal part of the ascending limb. The anal border has irregular, rounded lobes.

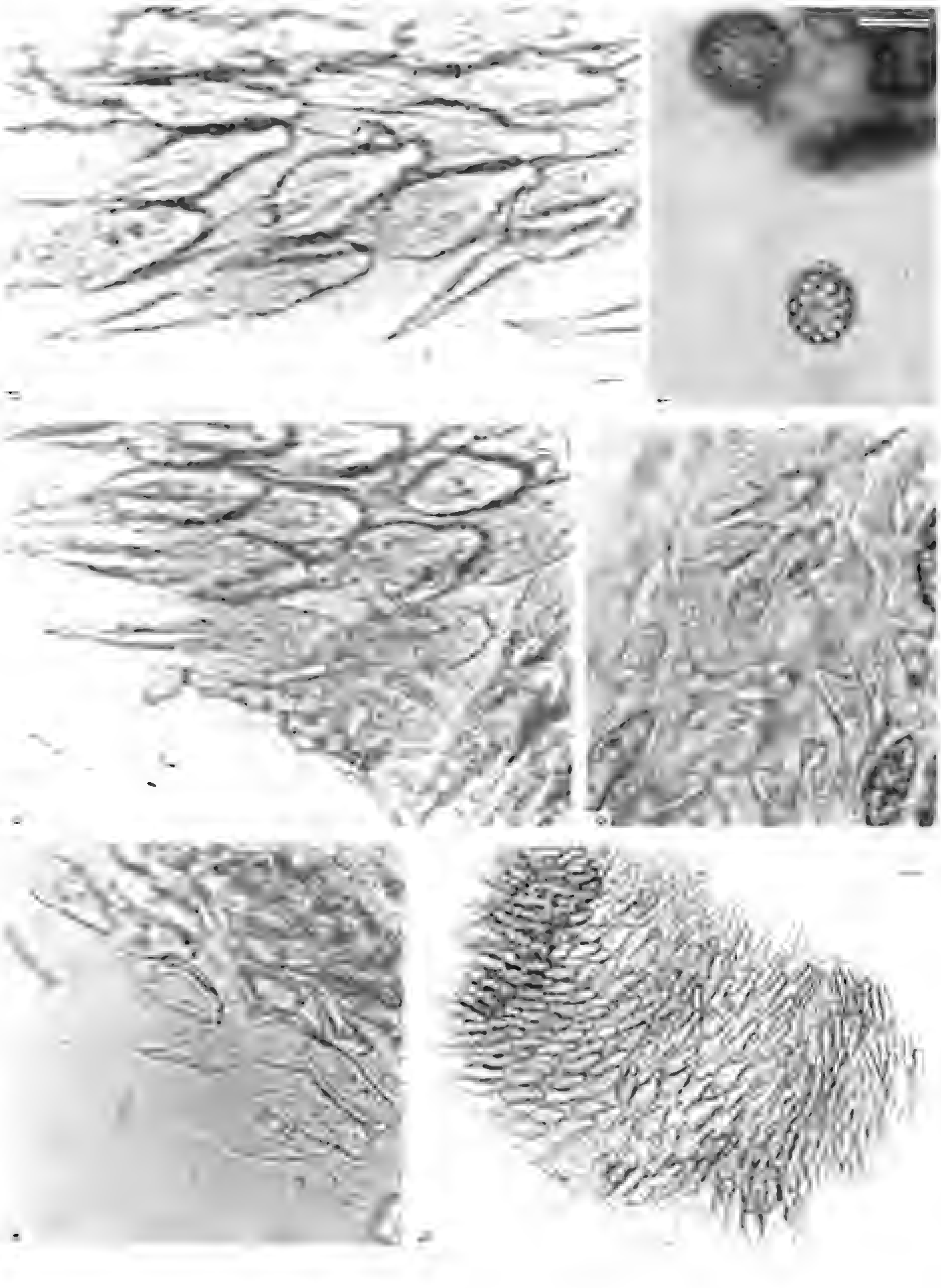


FIG. 148: *Pyura irregularis* — **a**, siphonal scales. *Pyura isobella* n.sp. — **b**, siphonal spines; **c**, outer surface of spines; **d**, inner surface of spines showing partially closed base. *Pyura littoralis* — **e**, siphonal spines; **f**, spicules. (Scales: **a**, **b**, **e**, **f**, 0.01 mm; **c**, **d**, 0.1 mm).

FIG. 149: *Pyura irregularis* – a, b, external appearance (TM D1814, NMV H417); c, peritubercular area showing opening of neural gland in base of peritubercular area; d, gut with endocarps and gonads (NMV H417). (Scales: a, b, 1.0 cm; c, d, 0.5 mm).

There are 8 to 10 polycarp sacs along each side of the central gonoducts, attached to the body wall by very fine ligaments. The sacs are more or less cuboid, with sharp borders but no lobes. The left gonad lies along the inner curve of the ascending limb of the gut loop.

There are endocarps on both the gut loop and gonads.

REMARKS: This species bears a close resemblance to *P. confragosa*, n.sp. which has the same hard test, its surface sometimes marked with sharp ridges, and endocarps on the gut loop. However, in *P. confragosa* the body is not as narrow anteriorly, the dorsal tubercle is not in the base of the peritubercular area, and the gonads are very much proliferated. *Pyura abradata* n.sp. from South Australia, like the present species, has an accessory row of dorsal languets. However, its test is hard, with small elevations and fine wrinkles, but without the flat surface depressions of the present species. Further, in *P. abradata*, the dorsal tubercle is at the top of a very wide peritubercular area (rather than at the base of the deep, narrow V, as in the present species); the extensive polycarps sacs are very much lobed; and there are no endocarps on the D-shaped gut loop. *Pyura fissa* from Bass Strait also has endocarps on the gut loop, but, like *P. abradata* has its dorsal tubercle on the top, rather than at the base of the peritubercular area.

Characteristics of *Pyura irregularis* are the hard test with sharp ridges and depressed areas; the body shape with long, usually curved, siphons; the deep, narrow peritubercular area with the tubercle in the base of the V; the long, dorsal lamina; the large number of longitudinal vessels between branchial folds; the curved gut loop and the unlobed polycarp sacs.

Pyura isobella n.sp.

(Figs 148b–d, 150)

Pyura jacatrensis: Kott 1952, p.273.

DISTRIBUTION

TYPE LOCALITY: New South Wales (Ulladulla, on rocks, intertidal, coll. I. Bennett, 25.10.73, holotype QM GH1448, paratypes QM G8576).

FURTHER RECORDS: Western Australia (Cottesloe, WAM 196.75(1)). New South Wales (Port Jackson, paratype QM G10102).

The recorded distribution is discontinuous. It is likely that the species is temperate and may be expected to occur across the southern coast of Australia.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are more or less spherical, or dome- or top-shaped, narrowing to a thin stalk from the middle of the ventral surface. They are sometimes solitary, but most often occur in solid, sandy aggregates. The apertures are always close together on the upper surface in a depressed area that is surrounded by a hollow elevation of test bordering the upper surface. This ridge is sometimes divided into 6 separate, rounded swellings (WAM 196.75(1)). The atrial aperture is in the centre of the upper

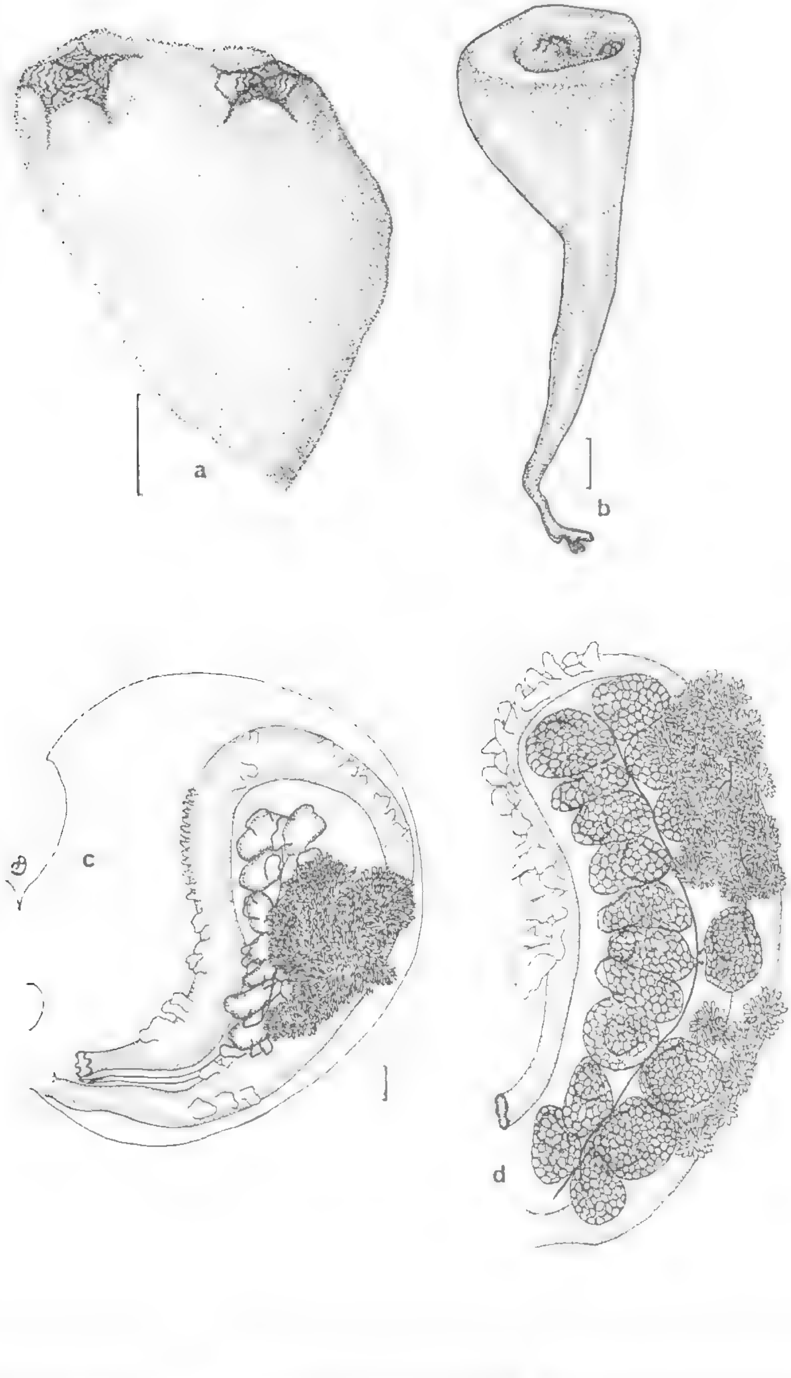


FIG. 150: *Pyura isobella* n.sp.: **a**, **b**, external appearance (WAM 196.75, QM G8576); **c**, **d**, gut and gonads (QM G8576, WAM 196.5). (Scales: **a**, **b**, 5.0 mm; **c**, **d**, 1.0 mm).

surface, and the branchial aperture is toward the periphery. Each aperture is on a small, wart-like siphon. Small lobes around the apertures are free of sand, but are covered with overlapping, iridescent spines that continue down into the siphon lining. The remainder of the thin, white test, including the siphons and stalk (when present), has fine, irregular processes to which sand adheres to form a firm sandy coat of variable thickness (up to 1 cm) enclosing the animal. When aggregates are formed, the sandy coat of each individual mingles with that of its neighbours. In these aggregates, each individual is upright. As their upper surfaces are level with each other, they form a flat platform, interrupted only by the depressed anterior end of each individual with its naked, wart-like siphons. Here, the sandy casing is always thinner than on other parts of the body, probably allowing some flexibility around the base of the siphons. Specimens up to 3 cm diameter and 3.5 cm high are recorded.

In living specimens, the bare areas around each aperture covered with iridescent spines have transverse pink and white bands. In the preserved material, there are bands, sometimes faint, of blue-green opalescence formed by bands of opalescent spines that alternate with transparent spines. These continue down into the siphonal lining as horizontal bands. The crowded, overlapping siphonal spines extend the whole length of the internal siphonal lining. In the base of the siphon they are small, and flattened, tapering to a fine point. Further up, the narrow horizontal bands that alternate with the opalescent band have slightly curved, transparent, pointed spines with a short groove in their distal tip. The opalescent spines have a long, oval, proximal (basal) expansion that becomes progressively larger further up the siphon, the spines at the top having their whole basal half conspicuously inflated. The blue-green opalescent bands in the siphonal lining of the preserved material is caused entirely by the crowded, opalescent, inflated basal half of these spines. Siphonal spines of both types are the same length in the one population. However, there is some variation in the length of the spines, *viz.*: 0.09 mm (QM G10102); 0.12 mm (WAM 196.75(1)). The siphonal lining is drawn up into fine longitudinal folds, which may be the result of contraction; possibly they flatten out when the aperture is fully expanded.

INTERNAL STRUCTURE: The body wall is firmly adherent to the test anteriorly. It is very muscular. The longitudinal muscle bands extend the whole length of the deep body. They are covered by a layer of circular bands that are also conspicuous over the whole length of the body. Both circular and longitudinal muscles are especially strong around the anterior part of the body. The circular bands, especially, branch and anastomose where the body wall adheres closely to the test in the vicinity of the raised rim around the upper surface. There is also a very strong sphincter muscle internal to the longitudinal muscle bands at the base of the atrial siphon. A branchial sphincter muscle extends around the base of the branchial siphon, just anterior to the branchial tentacles, in a muscular velum that protrudes into the lumen.

The branchial tentacles have short primary branches, but only small secondary and, occasionally, minute tertiary branches. The dorsal tubercle is conspicuous and protruberant, with the horns of a U-shaped slit spiralling inwards. The dorsal lamina is relatively long, extending the whole length of the upper surface from the branchial aperture at one end to the oesophageal opening at the opposite end. The ventral mid-line of the pharynx is deeply curved, extending down into the tapered body.

There are 6 overlapping branchial folds on each side of the body. The thick internal longitudinal and transverse vessels project into the pharynx. The parastigmatic vessels are also thick and projecting. There are up to 25 internal longitudinal vessels on the folds and up to 6 between. Internal longitudinal vessels of the type specimen are arranged according to the following formula: E4(11)4(18)3(21)3(20)2(19)2(19)2DL. The meshes between the longitudinal vessels are wide, with 6 to 8 stigmata per mesh.

The gut forms a long, J-shaped loop extending around to the left of the postero-ventral border. The rectum curves up toward the atrial aperture, but the anal opening is separated from the atrial opening by about half the length of the upper surface. There are small liver diverticula at the proximal end of the gut. The main liver diverticulum is a single, arborescent stalk with bunches of elongate, terminal lobules. The anal border, which is turned back, has 4 shallow, rounded lobes. There are crowded, irregularly branched endocarps on the outer curve of the gut loop, especially on the distal part of the descending limb.

The gonads consist of rather irregularly lobed polycarp sacs along both sides of the central gonoducts, to which they are connected by relatively long ducts. The left gonad is in the gut loop. There are irregular endocarps on the polycarps.

REMARKS: This species is reminiscent of *P. curvigona* with endocarps on both gut loop and gonads. Further, the opalescent scale on the spines of *P. curvigona* may have evolved from the similarly opalescent, inflated basal half of spines like those occuring in the present species. However, unlike *P. curvigona*, the apertures of the present species are close together, the rectal part of the gut is not swollen, its endocarps are branched and its gonads lobed.

This species also resembles *Pyura zansibarica* Michaelsen, 1905 from the western Indian Ocean and eastern Atlantic. Vasseur (1969) reports two types of siphonal spines from the specimen of *P. zansibarica* he examined; and the spines from the outer test appear to have swollen bases similar to those of the Australian material. Further, the apertures of *P. zansibarica* are close together (as in the present species), occasionally specimens with a thick, sandy coating have been recorded (Millar 1956), and the rectal part of the gut is swollen as in *P. curvigona*. However, the endocarps of *P. zansibarica* are not branched, the siphonal spines are very much larger (0.275 mm) than those of the present species, and the anterior rim of test is not present. Therefore despite similarities in many characters, the western Indian Ocean *P. zansibarica* appears to be distinct from the Australian species.

The characteristics by which *P. isobella* can be identified are: the close, wart-like siphons in a depressed area on the upper surface; the thick coat of sand and thin, white test; the strong body musculature; the horizontal, opalescent bands in the siphonal lining; the form of the siphonal spines; the very robust and projecting internal branchial vessels; the branched endocarps on gut and gonads; and the irregularly shaped polycarp sacs.

The spines of *Pyura vittata*: Tokioka, 1950 from the Palau Is have not been described. Other characters are similar to those of the present species; it is possible these species are conspecific.

Pyura littoralis (Kott, 1956)
(Figs 148e,f, 151)

Culeolus littoralis Kott, 1956, p.59.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Tasmania (Hunter I. — paratypes AM Y1745, QM GH2311 Kott 1956).

The species has been taken only from the intertidal zone at this location.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are more or less top-shaped. The upper surface is circular and almost flat, and the body narrows toward the substrate. They are found in aggregates, adhering to one another along the sides of their bodies. The apertures are on very short siphons a little distance apart on the upper surface. The atrial aperture is directed upwards and the branchial aperture is directed more or less horizontally, away from the atrial opening. The test is wrinkled and furrowed, possibly as a result of contraction, and is beige to whitish in preservative. There are sparse, but conspicuous, pointed papillae, about 1 mm long and tipped with brown, over the surface of the body. They are about 3 mm apart on the upper surface, but are less crowded around the sides of the body, and are squashed against the surfaces where individuals adhere to one another. Papillae are absent from the siphons. The borders of the apertures are raised into 4 rounded swellings.

The test is leathery, tough and very hard and granular from the calcareous spicules embedded in it. The spicules are large (up to 0.1 mm in diameter), mulberry-like and globular. Smaller spicules in the superficial layer of test are more stellate in outline, with separate rays.

Minute (0.04 mm long), hollow, curved spines line the siphons and continue onto the external test of the anterior surface. The base of these spines is open, the outer surface being produced backwards into a rounded, scale-like expansion. Brown, oval bodies are also present in the test around the rim of the apertures.

INTERNAL STRUCTURE: Longitudinal muscles radiate from each siphon, bend sharply down onto the sides of the body beneath a sharp rim of outer body wall around the perimeter of the upper surface, and fade out about halfway down the body. Circular siphonal muscles are present inside and outside the longitudinal bands and around the base of each siphon, but circular musculature on the remainder of the body is very delicate indeed.

About 12 branchial tentacles of varying size alternate with rudimentary tentacles. They are very bushy but regular, with long primary branches, short secondary branches and minute tertiary branches. The small, oval dorsal tubercle, with its long, inverted, S-shaped slit, is in the shallow prebranchial area close to the base of the tentacles. The dorsal lamina is long, the oesophagus opening from the posterior end of the branchial sac. The dorsal languets are long and curved, but are not very crowded.

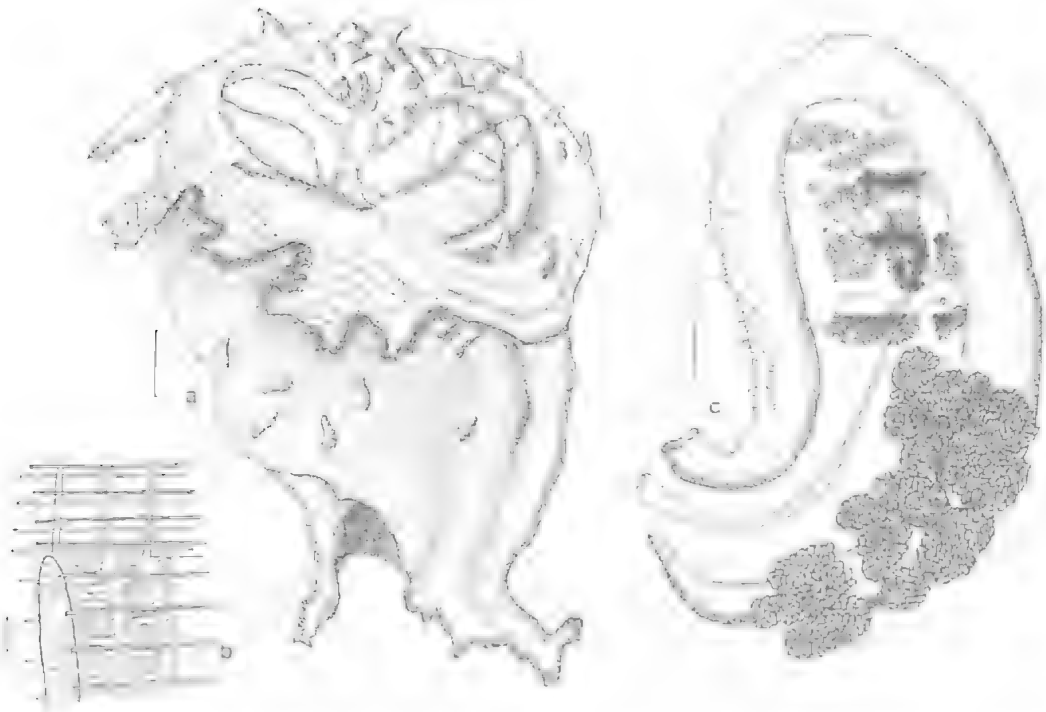


FIG. 151: *Pyura littoralis* (QM GH2311 — part AM Y1745) — a, external appearance; b, part of branchial fold (diagrammatic); c, gut loop and gonads. (Scales: a, c, 2.0 mm; b, 0.1 mm).

The branchial sac has 6 overlapping branchial folds on each side of the body. The stout and projecting internal longitudinal vessels of a typical specimen are arranged according to the following formula: DL1(13)1(13)1(15)1(12)1(10)1(5)2E. The longitudinal and transverse vessels of each branchial fold extend out beyond the margin of the fold of the perforated pharyngeal wall. Thus, the outer half of each branchial fold is an open mesh of longitudinal and transverse vessels without stigmata. The stigmata are oval, separated from one another by relatively wide, unperforated expanses of the pharyngeal wall. There are 3 to 5 stigmata per mesh in the centre of the branchial sac. In the ventral part of the pharynx, near the endostyle, the transverse vessels are irregular, as are the stigmata. Stigmata are also irregular in the folds. Parastigmatic vessels are often present and occasionally divide the stigmata.

The gut forms a quite wide, J-shaped loop, the rectum curving anteriorly at its distal end. There are about 4 pairs of arborescent liver diverticula in the pyloric region. Pointed papillae are present on the descending limb of the gut loop. The anal border is not lobed.

The left gonad is enclosed by the gut loop, while the right gonad is in a corresponding position on the opposite side of the body. The gonads consist primarily of paired polycarp sacs in which male follicles cover the mesial surface of a sac-like ovary. However, although the male glands have a common duct, which receives branches from each sac, each ovarian sac opens separately into the peribranchial cavity on a short oviduct. There is thus only a single male gonad on each side of the body, but numerous female gonads. The latter also proliferate and are often found without associated male follicles. The female gonads may cover a considerable area of the ventral body wall, especially on the right side where up to 40 ovarian sacs, each with its own short duct, have been observed. Endocarps are often present on the hermaphrodite sacs, but are usually not present over the solely female glands.

REMARKS: The pointed test papillae resemble those of *Pyura spinosa*. However, *P. spinosa* has test papillae around the apertures (in *P. littoralis* they are absent from the immediate vicinity of the siphons). The present species and *P. spinosa* also have similar paired liver diverticula, bushy tentacles and siphonal spines. Their test spicules are the same, although smaller in *P. spinosa*. The two species appear to be closely related. *Pyura littoralis* is, however, distinguished from all other species by its remarkable gonads and modified branchial folds.

Kott (1956) suggested that the short oviducts were an adaptation for a viviparous habit. If this is so, it would be the only known viviparous species of this genus. The species apparently has a very limited range and a viviparous habit could have resulted in the isolation of this population from the closely related *P. spinosa*, which occurs in adjacent waters of southern Australia, Bass Strait and eastern Tasmania.

Pyura molguloides (Herdman, 1899)
(Fig. 152)

Cynthia molguloides Herdman, 1899, p.27.
Pyura tenlata Kott, 1972b, p.187; 1975, p.14.
Pyura cancellata: Kott, 1972d, p.254.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H382; Western Port, QM G9362; Lakes Entrance, NMV H415 H901 F51589; Portland, NMV F51598).

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — Kott 1975; Investigator Strait — Kott 1972b). New South Wales (Port Jackson — Herdman 1899; Port Hacking — Kott 1972d).

The species is recorded from 22 m down to 220 m from the southern coast and around the southeastern corner of Australia. It appears to be a temperate indigenous species.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are completely encased in a thick, sandy, outer layer of test, and sometimes occur in aggregates. They are up to 5 cm long. One specimen (Lakes Entrance, NMV F51589) is 12 cm in diameter across the wide flat base. Most of this diameter consists of a thick, sandy outer coat, which varies in thickness (up to 1 cm in places). The test is thin and flexible. Between it and the sandy outer casing is a space that is traversed by the fine, crowded test hairs. The outer ends of these hairs fuse with one another and sand adheres to and is enmeshed by them to form the sandy outer casing. The sand casing of the animal may result in its being overlooked, and hence seldom recorded.

The body narrows anteriorly to a terminal branchial aperture. The atrial aperture is postero-dorsal. The terminal portion of each siphon is turned down into the siphon so that the aperture is at the base of a funnel-like depression in the tip of the siphon. In smaller specimens the space between the test and the outer layer opens to the exterior around the siphons, but in larger

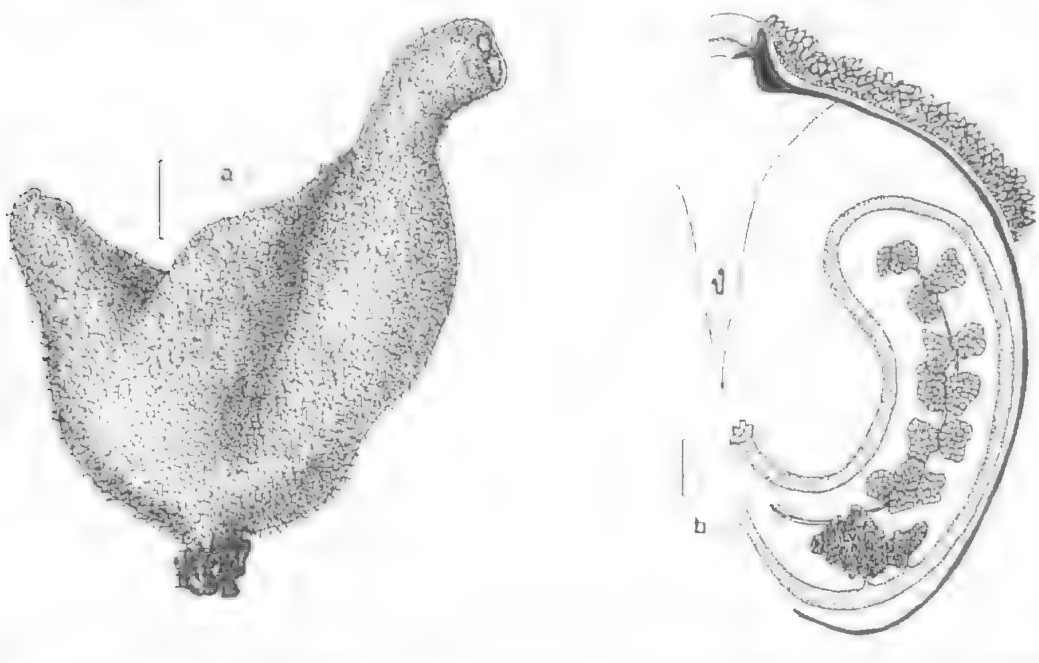


FIG. 152: *Pyura molguloides* (QM G9362) – a, external appearance; b, inner body wall, left side of body. (Scales: a, 5.0 mm; b, 2.0 mm).

specimens, the outer sand layer with its fused test hairs closes this gap around the outside of the siphons. Siphons vary in length according to the thickness of the sandy coating that they must extend through for access to the exterior. Where the sandy coating is thick, the atrial siphon may project upwards to open on the outside of the sand more or less level with the branchial aperture (Kott 1972b) and apparently close to it. When the external sandy coat is removed, however, the posterior origin of the atrial siphon can be observed. In other specimens, the atrial siphon projects back from the posterior end of the body (QM G9362). The space between the sandy coat and the surface of the test is often irrigated by commensal crustaceans and other organisms.

Small (0.01 mm), overlapping scales with rounded borders are present in the outer part of the siphon lining.

INTERNAL STRUCTURE: The body wall is very muscular. The strong longitudinal muscles from the branchial aperture extend the whole length of the body, and are crossed posteriorly by radiating bands from the atrial aperture. They are surrounded externally by a layer of circular bands. At the base of the branchial siphon, just anterior to the branchial tentacles, there is a large, muscular sphincter. The inner siphonal lining forms a wide, flat, fibrous velum inside this sphincter. The branchial tentacles, which branch 2 or 3 times, are not bushy. The dorsal tubercle is a small round, oval or elongate cushion, with a simple, U-shaped aperture, deep in a very long and narrow peritubercular area that extends about halfway down the branchial sac. Sometimes one of the horns of the neural gland opening is turned inwards. The dorsal ganglion is also very long, extending posteriorly behind the dorsal tubercle. The dorsal lamina, which extends along the posterior half of the dorsal mid-line, is represented by crowded languets. Some features of the morphology are affected by the posterior position of the atrial aperture. These include the attenuation of the dorsal ganglion and peritubercular area, the position of the dorsal tubercle and the course of the 3 or 4 most dorsal branchial folds, which originate from the margins of the peritubercular area, rather than from the prepharyngeal groove at the anterior end of the body.

There are 8 or 9 branchial folds on the left and 7 or 8 on the right. In larger specimens up to 22 fine, internal longitudinal vessels are present on the folds, with up to 3 in the interspace. The branchial formula for a large (5 cm, QM G9362) specimen is E0(3)1(9)2(11)3(13)3(17)3(16)3(16)3(15)3(15) 3DL. The branchial formula for a specimen of 2.5 cm is: DL2(15)2(18)1(18)2(18)2(16)2(12)2(12)1(2) 3E. The stigmata are elongate. The longitudinal vessels in the interspace are not always evenly spaced, the most dorsal row of meshes having up to 10 long stigmata per mesh, while the ventral rows have 6. In juvenile specimens (in which gonads are not developed, NMV H382), there are only 2 or 3 rounded stigmata per mesh, with no more than 8 vessels per fold and 1 or none, in the interspace. The branchial folds are curved, terminating around the sides and posterior rim of the oesophagus.

The gut forms a simple, D-shaped or open, curved loop that occupies the posterior two-thirds of the length of the left side of the body. The very compact liver arising from a limited pyloric region consists of a single main stem and some unpaired accessory diverticula proximal to it. The distal tip of the rectum sometimes bends up through the fibrous velum across the base of the atrial siphon, with the anus opening into the lumen of the siphon beyond this velum. The anal border has 9 shallow, rounded lobes.

Each gonad consists of 7 or 8 rounded polycarp sacs that alternate with an equal number on the opposite side of central common ducts. The left gonad is in the gut loop. The polycarp sacs are only very lightly attached to the body wall by fine ligaments. There are no endocarps on the gut.

REMARKS: The distinctive characters of this species are its shape (with a long posterior atrial siphon), its thick, sandy outer casing with anastomosing test hairs, its long peritubercular area and long dorsal ganglion, the position of its dorsal tubercle and presence of a fibrous siphonal velum. The musculature, long peritubercular area and long dorsal ganglion are probably adaptations associated with the position of the atrial aperture.

In *Pyura mirabilis* (Drasche), a boreal species extending south to the South China Sea (Kott and Goodbody 1982), the atrial aperture is also at the posterior end of the body. But *P. mirabilis* has a more specialised morphology, associated with this posterior position of the atrial opening, than the present species.

Pyura ambonensis Millar, 1975 closely resembles the present species in all characters except its long siphonal spines.

Pyura elongata also has small siphonal scales and a posterior atrial siphon, but it does not have a distinctive siphonal velum and its test is naked and mammillated. As well, the outer part of its siphons do not invaginate into the lumen as they do in the present species.

The species resembles the New Zealand species *Pyura cancellata* Brewin, 1948, *P. carnea* Brewin 1948 and *P. trita* Sluiter, 1900a in having an outer layer of test formed by fusion of the long test processes. Further, the rampart-like structures around each aperture of *P. cancellata* appear to be homologous with the rim of the inverted siphon in the present species. However, the strongly developed siphonal velum has not been reported in any of the New Zealand species, which also differ in having a larger number of internal longitudinal branchial vessels in the interspace, quite shallow peritubercular areas and pointed, conical (rather than scale-like) siphonal spines.

The velum at the base of the branchial siphon is apparently analagous with a similar structure in sand-living species of the Molgulidae. It is, therefore, probably a convergent adaptation for a sandy habitat rather than a character indicative of phylogenetic affinity.

Pyura navicula n.sp.
(Fig. 153)

[illegible]

TYPE LOCALITY: Queensland (Moreton Bay, Moreton I., Cowan Cowan, 20 m, coll. A. Rozefelds, 20.4.81, holotype QM GH369).

DESCRIPTION

EXTERNAL APPEARANCE: The single specimen is more or less boat-shaped, broad and rounded posteriorly, narrowing anteriorly and slightly dorso-ventrally flattened. There is a short stalk from the ventral surface. The apertures are both on the upper surface on short siphons directed upwards. The branchial siphon is near the anterior end of the body, and the atrial siphon is about halfway along the upper surface. The body is 3 cm long.

The test is extremely hard and rigid. Evenly spaced and crowded, short, irregular processes or papillae arise from the surface, being absent only from an area around the siphons. Sand is embedded in the test, adhering to its surface and obscuring the shape of the surface papillae. There are small, pointed processes around the branchial aperture. The outer part of each siphon is lined with small, curved scales 0.02 mm long, with rounded anterior borders.

INTERNAL STRUCTURE: The body wall adheres closely to the test. In the fresh material, it is bright vermilion with a blue tinge. The colour is especially intense around the siphons. The musculature is strong. The usual longitudinal bands extend onto the ventral surface. There are external circular bands around each siphon and around the base of each siphon. Circular bands also extend horizontally around the body ventral to the siphonal muscles. The branchial tentacles are not bushy and have small primary and secondary branches only. The peritubercular area is a wide V, and the small, circular dorsal tubercle has a U-shaped opening with both horns turned in. The dorsal lamina is long, with crowded and finely pointed languets. The branchial folds terminate around the opening of the oesophagus at the posterior end of the branchial sac.

There are 7 broad, overlapping branchial folds on each side of the body. The internal longitudinal vessels are arranged according to the following formula: E2(12)4(16)4(20)3(20)3(19)3(16)2(15) 1DL. The 4 to 6 long, oval stigmata per mesh are crossed by a parastigmatic vessel.

The gut forms a wide, almost circular, loop in the postero-ventral half of the body, and the rectum does not curve anteriorly. The single, large, branched liver diverticulum has elongate terminal lobules and some accessory diverticula proximal to it. The anal border has about 6 rounded lobes.

Each gonad consists of about 5 irregularly lobed, transversely lengthened, rectangular polycarp sacs on each side of central gonoducts. The left gonad extends around in the curve of the ascending limb of the gut loop. There are endocarps on the gonads. The polycarp sacs are only very lightly attached to the body wall with a few, very fine, ligaments; their principal attachment is by means of their gonoducts, which are joined to the central common ducts embedded in the body wall. There are no endocarps on the gut.

REMARKS: The species belongs to the *irregularis* group with curved siphonal scales. It is distinguished from other species in the group by the sand embedded in its test, rather than forming a sandy outer coating (attached to test hairs) as it does in *P. molguloides*; by its large and relatively few polycarp sacs; and its conspicuous circular muscles passing horizontally around the body posterior to the circular siphonal muscles (as in *P. irregularis*).

Pyura subuculata: Tokioka, 1950, from the Palau Is, closely resembles the present species in all characters except the sandy papillated test and the number of branchial vessels. (*Pyura subuculata* Sluiter is a New Zealand species not related to *P. navicula*).

Characteristics of *Pyura navicula* are its test papillae and sandy coat; strong body muscles,

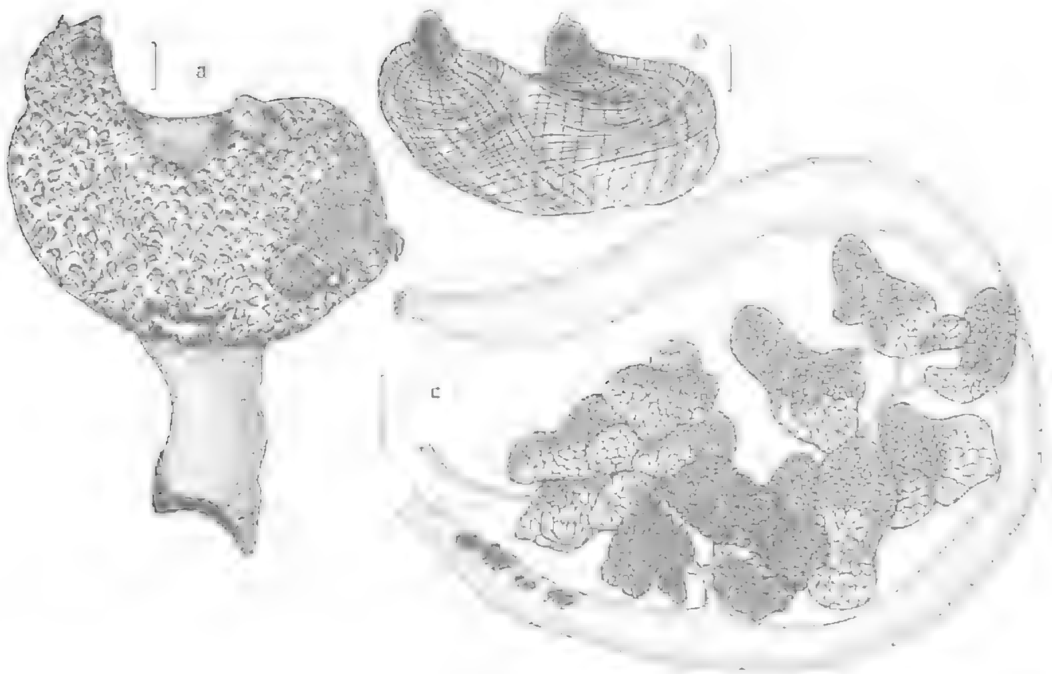


FIG. 153: *Pyura navicula* n.sp. (QM GH369) — a, external appearance; b, body removed from test showing muscles; c, gut and gonads. (Scales: a, b, 2.5 mm; c, 2.0 mm).

scale-like siphonal armature; small dorsal tubercle, rectangular, block-shaped and slightly lobed polycarp sacs; and the absence of endocarps on its gut.

Pyura obesa Hartmeyer, 1919
(Figs 154a,b, 155)

Pyura obesa Hartmeyer, 1919, p.14.
Pyura albanyensis Hartmeyer and Michaelsen, 1928, p.435. Kott, 1976a, p.80.
Pyura vittata: Tokioka, 1950, p.146; 1952, p.135. Kott, 1964, p.142; 1966, p.300; 1972a, p.37; 1972c, p.242.
Pyura scoresbiensis Kott, 1972a, p.36; 1972b, p.187; 1975, p.14; 1976a, p.78.

DISTRIBUTION

NEW RECORDS: Western Australia (Dampier Archipelago, WAM 876.83 1247.83; Shark Bay, QM GH1812). South Australia (St Vincent Gulf, QM GH1816-7; Spencer Gulf, QM GH2690). Victoria (Bass Strait, QM G11878 G12749). Queensland (Hervey Bay, QM GH2185 GH2221; Gladstone, QM G9723; Heron I., QM GH2209 GH3092; Wistari Reef, QM GH3097; NW of Bowen, QM GH748 GH1819; Lloyd Bay, QM GH815; Barrow Point, QM GH791 GH1822; Fair Cape, QM GH1820; Cleveland Bay, QM GH1378; Cape Melville, QM GH2344).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert — Hartmeyer 1919; Albany — Hartmeyer and Michaelsen 1928). South Australia (St Vincent Gulf — SAM E876 E892 E912 Kott 1972a; Upper Spencer Gulf — Kott 1972b; Investigator Strait, Pearson I. — Kott 1975). Victoria (Western Port — Kott 1976a). Queensland (Moreton Bay — Kott 1964 1972c; Hervey Bay — Kott 1966; Townsville, Innisfail — Kott 1964; Arafura Sea — Tokioka 1952). Palau Is (Tokioka 1950).

The species appears to have a range around the Australian coast and into the western Pacific.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens from 0.5 to 12 cm (excluding the stalk) in maximum dimension have been examined. Occasionally aggregates occur. The body varies in shape. Rounded and slightly dorso-ventrally or laterally compressed individuals have both apertures on the dorsal surface. Upright and more or less cylindrical individuals either have the branchial and atrial apertures on opposite sides of a slight terminal projection; or have a terminal branchial aperture with the atrial aperture on the dorsal surface behind it, never more than one third of the body length away and often closer. These upright individuals sometimes narrow to a long and narrow or a short and thick posterior stalk. In some South Australian specimens, an oblong head up to 3 cm long is supported on a stalk up to 20 cm long. The stalk, like the remainder of the test, has sand embedded in it; only a very small central core, perforated by 2 long vessels, is free of sand.

The apertures are sessile, surrounded by an greenish black to mustard-green (in preservative) area of thickened test that is always bare of encrusting or embedded sand but is covered with minute iridescent spines that continue down into the siphon lining for most of its length. The smaller spines (0.1 mm) are scattered among the larger ones (0.25 to 0.275 mm). These spines are more or less straight, with a slightly expanded cup-shaped concavity at their basal end. Where they project out of the test, they flatten and expand before tapering to a very long, sharp point. Black bands (caused by localised distribution of large pigment patches beneath the overlapping spines) radiate from the apertures across the bare areas surrounding each aperture. They also continue down the siphon lining. These black bands fade in preservative and are not always readily observed. The radii of the bare areas around each aperture are variable; sometimes they are so wide that they become confluent with one another in the mid-line between the apertures.

Juveniles (0.5 to 1.0 cm) are white in preservative, with a smooth-surfaced, cartilaginous test, but larger individuals have a relatively thin test hardened with embedded sand. Occasionally, large specimens (5 to 12 cm: QM G5028, WAM 876.83 1247-83) are completely without embedded or encrusting particles and have a leathery, smooth-surfaced test with some furrows and creases.

A living specimen from Heron I. (QM GH3092) was brick red with black siphons.

Internal Structure: The body wall is thin; body organs can be seen through it, especially on the left. However, the musculature is well developed. The body wall adheres closely to the test around the anterior end of the body. There are strong, circular muscle bands around the whole length of the body, although they are least conspicuous over the gut on the left and posteriorly, where they are reduced to very fine fibres. The circular muscles overlie longitudinal bands that extend, almost parallel to one another, from both siphons toward the posterior end of the body to form a rather irregular mesh-work with the circular fibres. Only in the centre of the body do the longitudinal bands cross one another. The internal siphons arise very close together at the anterior end of the body, and then diverge. In contracted specimens, the diameter of the body is abruptly increased posterior to the base of the siphons.

Branchial tentacles have a solid, sickle-shaped main stem. They are not very bushy. The primary branches are short, and there are only small or minute secondary branches. The dorsal tubercle is a round cushion of moderate size, with a U-shaped opening that always has both horns spiralling inwards, although the orientation of the aperture is variable. The dorsal lamina is short and the pointed languets are crowded.

Owing to the height of the body and its short dorsum, the branchial sac has a deep, ventral curve and the 6 wide, overlapping branchial folds on each side of the body are deeply curved. Posteriorly, the branchial folds terminate along each side of the oesophageal opening. The internal longitudinal vessels are fairly evenly spaced on the folds and in the interspace. There are up to 40 on the folds and up to 16 between. Typical branchial formulae are: E5(12)6(22)5(24)7(22)8(21)9(16)8DL (4 cm specimen); DL12(30)14(36)14(44)16(40) 12(32)12(32)12E (12 cm specimen). There are 4 to 6 stigmata per mesh.

The gut loop is very deeply curved into a U-shape. It is slightly wider at the pole than at the dorsal end, where it is narrow and closed. Sometimes the whole loop is very narrow, crowding the enclosed gonad between the two limbs. A short series of small liver diverticula with elongate lobules is at the cardiac end of the pyloric region. Further along, a large, arborescent diverticulum with elongate, branched, terminal lobules extends in a tight, cauliflower-like mass over a considerable extent of the gut. The anal border has about 3 shallow indentations. There are large endocarps along both limbs of the gut loop and on the gonads, and in very large specimens, minute papillae cover the gut, liver and body wall between the endocarps.

The usual pyurid polycarp sacs are crowded together on both sides of the central ducts. The left gonad is in the primary gut loop. The right gonad is in a corresponding position on the right side of the body. The individual ducts from each sac are short, and when the female ducts are filled with eggs, the ovary appears to be a continuous, rather sinuous, lobed tube with male follicles around the outside of the lobes. The whole gonad is firmly embedded in the body wall.

Remarks: The species is distinguished by its mixture of large and small siphonal spines; close, sessile apertures with radiating stripes of pigment

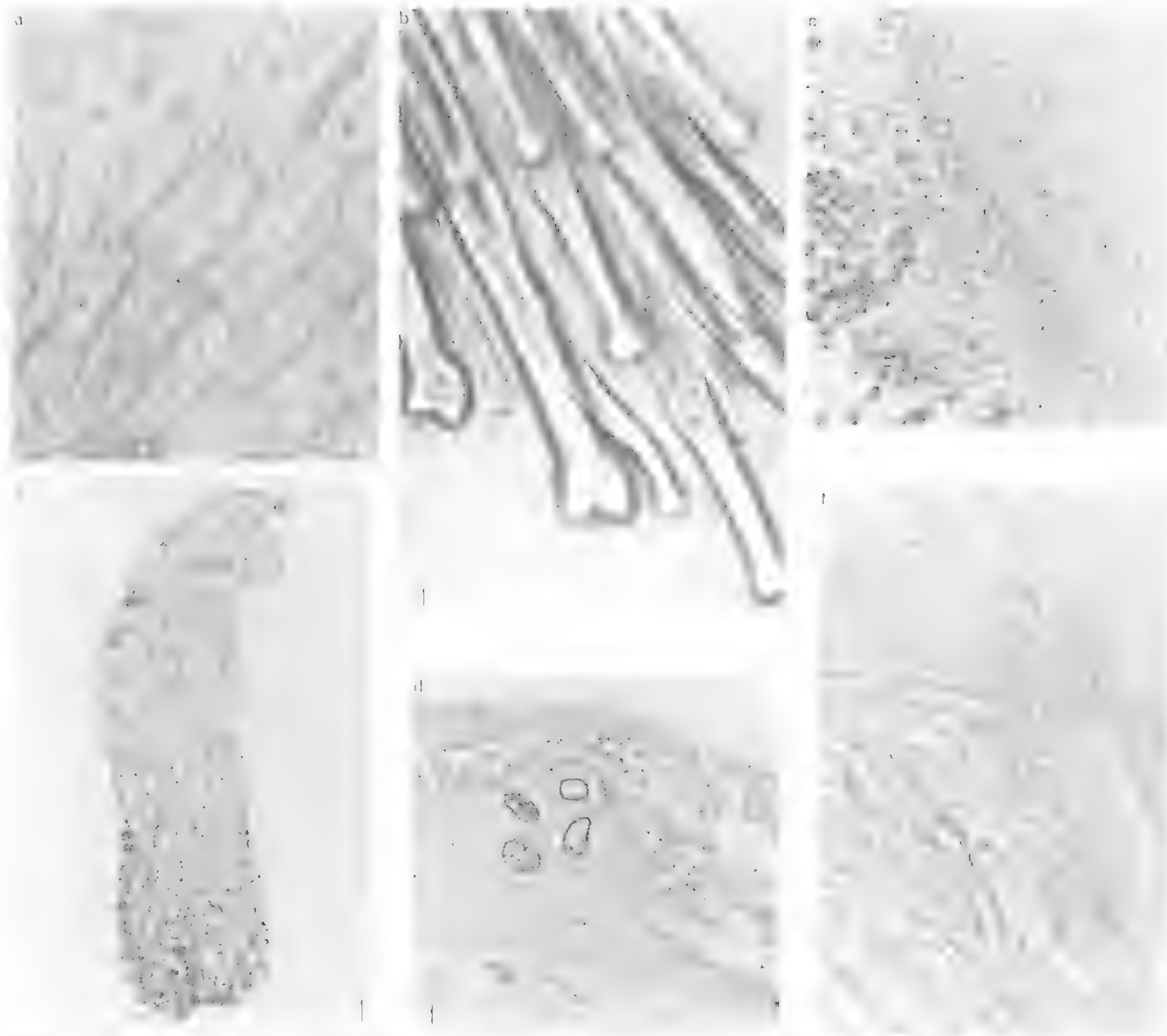


FIG. 154: *Pyura obesa* — **a**, siphonal lining spread out showing short and long spines; **b**, basal part of crowded spines. *Pyura ostreophila* — **c**, test (right) and associated sponge (left); **d**, test vessels entering an incipient stolonic outgrowth; **e**, longitudinal section through terminal end of stolon showing branching test vessels; **f**, siphonal spines. (Scales: **a, d, e**, 0.1 mm; **b, c, f**, 0.01 mm).

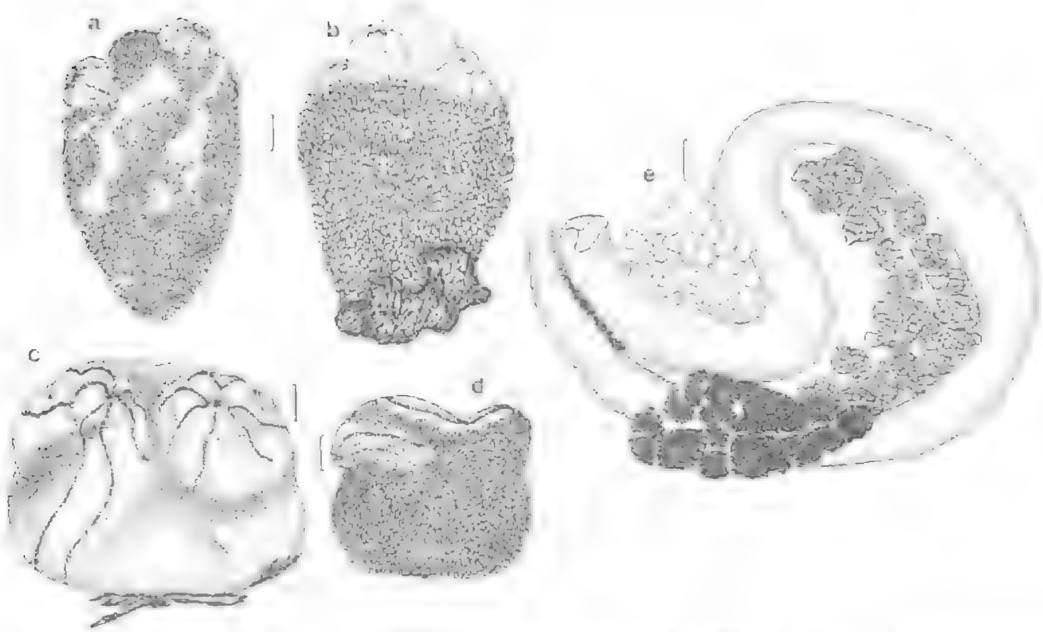


FIG. 155: *Pyura obesa*: a – d, external appearance (QM GH1814, GH1817, GH748, G6127); e, gut loop and gonads (QM GH1816). (Scales: **a**, **b**, **d**, 5.0 mm; c, 1.0 cm; **e**, 2.0 mm).

across the bare anterior part of the body; short dorsal lamina; numerous internal longitudinal vessels in the interspace; wide, deeply curved, overlapping branchial folds; deeply curved gut loop; embedded gonads; many endocarps on the gut loop; and its conspicuous layer of posterior siphonal circular body muscles. Specimens from South Australia with a dramatically long stalk (SAM E892, E912) are from mixed populations of stalked, non-stalked and intermediate forms.

The confused taxonomy of this and related species (*P. albanyensis*: Kott, 1976a) has resulted largely from the fact that the unique siphonal armature has been overlooked, the smaller spines being obscured by the larger ones and not always observed.

Microcosmus solanoides Herdman, 1899 from Port Jackson (AM U360) resembles the present species in the shape, position and form of its apertures, its body musculature, and in its characteristically close and diverging siphons when it is removed from the test. However, unlike *P. obesa*, it has no dorsal lamina (in this resembling *P. stolonifera*). It also has a characteristic pyurid liver. Its siphonal armature is similar to that of *P. stolonifera*. However, the type specimen of *Microcosmus solanoides* is in a poor condition, and it was not possible accurately to determine its identity.

Pyura ostreophila Hartmeyer and Michaelsen, 1928
(Figs 154c-f, 156)

Pyura ostreophila Hartmeyer and Michaelsen, 1928, p.424.

DISTRIBUTION

NEW RECORD: Victoria (Bass Strait, QM GH1399).

PREVIOUSLY RECORDED: Western Australia (Albany — Hartmeyer and Michaelsen 1928).

Although this remarkable species has been recorded only twice, the records suggest a distribution across the southern coast of Australia. Both Albany and Bass Strait records are from relatively shallow water (down to 5 m).

DESCRIPTION

EXTERNAL APPEARANCE: Aggregates of small individuals are covered by an encrusting *Halisarca* sponge to form irregular colonies with rounded surface swellings where the sponge covers the projecting surfaces of the ascidians. The sponge is so closely associated with the surface of the test of each individual that it is difficult to separate; in section, the base of the sponge is seen to be entirely contiguous with the test of the ascidian. The ascidian individuals are held together by the sponge and do not adhere to one another directly. The sponge forms an almost continuous, smooth, firm and slippery surface over the aggregate, interrupted only by the apertures of each individual. Only a very few small patches of test

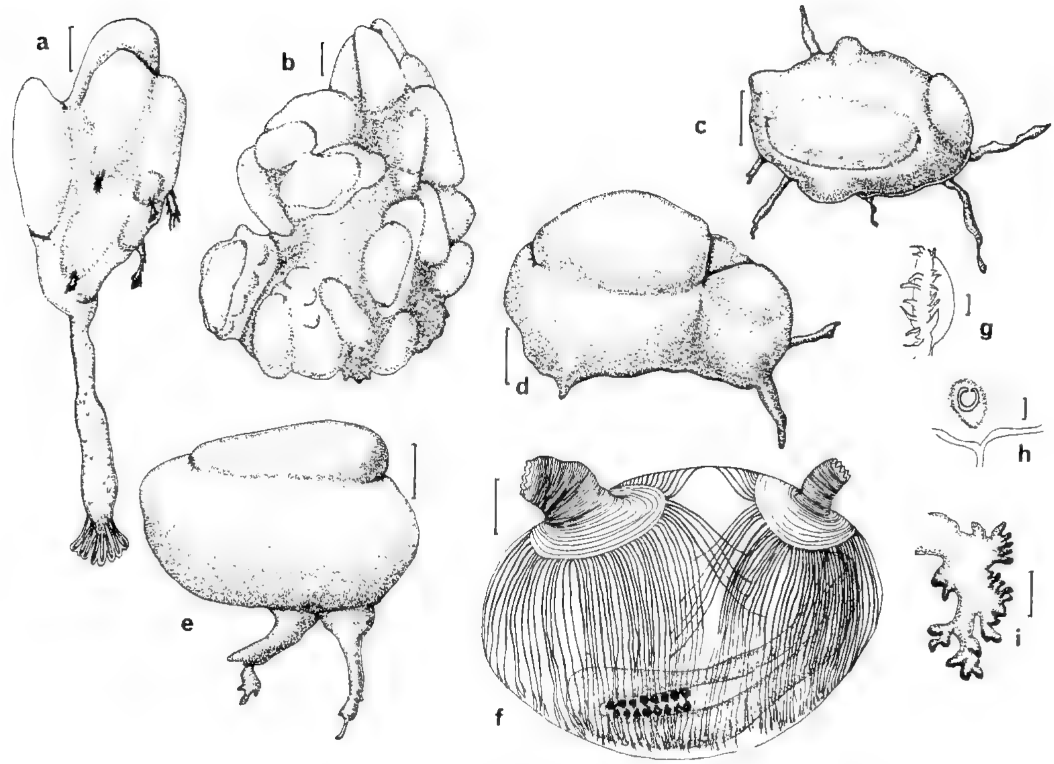


FIG. 156: *Pyura ostreophila* (QM GH1399) — **a, b,** aggregates of zooids in sponge (long stolon from a single zooid); **c – e,** separate zooids removed from sponge; **f,** zooid removed from test; **g,** branchial tentacle; **h,** dorsal tubercle; **i,** liver diverticulum from pyloric part of gut. (Scales: **a – e,** 2.0 mm; **f,** 1.0 mm; **g – i,** 0.2 mm).

are not covered by sponge. In an aggregate 3 cm long 2 cm wide and about 1.5 cm maximum thickness, from Bass Strait, 40 individuals were dissected from the surrounding sponge. Individuals are from 2 to 10 mm in length.

Each individual is more or less dome-shaped, slightly longer than wide. The basal surface is flat; the apertures are at opposite ends of the upper surface. The basal test is thin, but elsewhere it is firm, cartilaginous and translucent. Occasional thickenings of the test form swellings on the surface. Between the apertures, the test is always thickened to form a long, raised prominence, beneath which the apertures can be withdrawn. The border of each aperture is produced into 10 small, pointed lobes.

There are small, rounded, yellow spots on the test, which are more intense in those areas not covered by the sponge. From 1 to 5 stolonic test extensions, of various lengths, arise from almost any part of the test, but especially from around the lower half of the body and around the periphery of the thin basal test. These stolons contain numerous, very fine, test vessels, apparently generated in the stolon, and not always continuous along its whole length. Some terminate along its length; others extend into side branches. Those vessels that terminate at the end of the stolon spread out slightly from one another within the terminal lobes of test. Growth of the stolons appears to be a continuous process. They extend through the surrounding sponge, and each stolon is covered with its own layer of sponge. The vessels in the stolons have thin epithelial walls and contain blood cells.

There are 4 parallel ridges extending down the inside of each short siphon. Overlapping siphonal spines, 0.07 mm long, are present in the terminal part of the siphon lining and extend further down along these ridges. The protruding part of each spine is hollow and slightly curved. The long outer surface of the spine is flat and scale-like posteriorly.

INTERNAL STRUCTURE: The body wall is thin and transparent. Circular muscles are present around each siphon and around the base of each siphon. Longitudinal muscles extend down the siphons beneath the circular muscles and radiate over the sides of the body. The longitudinal muscles of the respective siphons do not overlap, and there are no intersiphonal muscles.

The branchial tentacles are thick and fleshy, with short primary branches and only very few minute secondary branches. The dorsal tubercle is a simple, circular cushion with a C-shaped, almost closed, slit. The peritubercular area is very shallow. There is an extensive prebranchial area. The dorsal lamina is long, with pointed languets.

There are 6 wide branchial folds, with internal longitudinal vessels arranged according to the following formula: E4(9)3(9)2(11)1(10)1(10) 2(9)1DL. The gut forms a narrow, J-shaped loop to the left of the ventral border of the body, enclosing the left gonad. About 4 pairs of liver diverticula branch from each side of the proximal one-third of the ascending limb of the gut loop. The anal border has 9 or 10 broad, shallow and slightly irregular lobes.

Each gonad consists of 8 polycarp sacs along each side of the central ducts. Each sac is upright and firmly fixed to the body wall. There are no endocarps on the gut loop, but there are minute, pointed papillae.

REMARKS: The individuals from Bass Strait are at most only one-third of the size of the specimens described by Hartmeyer and Michaelsen (1928). They have the same shape, the same multiplicity of stolons and the same thickening of the test between the apertures. Michaelsen regarded the largest stolon of the many on each individual as homologous with the single stolon of the bolteniform species *Pyura pachydermatina, P. gibbosa, P. australis* and *P. spinifera*. There is no indication from the structure of the stolons of the Bass Strait specimens that this is so.

The vascular stolons, the small size of the individuals and their close association with one another, all suggest the hypothesis that the species reproduces vegetatively. However, although heavily vascularised, the stolons extend between the individuals in the aggregate, embedded in the enveloping sponge, and do not adhere to adjacent individuals. They may help to anchor individuals in the sponge, and there is no evidence of a vegetative process.

The small, pointed papillae on the gut loop resemble those of *Pyura obesa* Hartmeyer 1919 and *P. sacciformis*. They may be homologous with endocarps.

Pyura pantex (Savigny, 1816)

Cynthia pantex Savigny, 1816, p.90.
Pyura pantex: Hartmeyer 1909, p.1340. Michaelsen, 1918, p.21. Hartmeyer and Michaelsen, 1928, p.439.

DISTRIBUTION

NEW RECORDS: None

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Hartmeyer and Michaelsen 1928). Red Sea (Savigny 1816, Michaelsen 1918).

This is one of the few Indian Ocean species recorded from Australia.

DESCRIPTION (after Michaelsen 1918, Hartmeyer and Michaelsen 1928)

EXTERNAL APPEARANCE: Individuals are more or less elliptical but irregular, and up to 8.0 cm long. They are fixed by their left and ventral sides. The surface is uneven, broken up into an irregular mosaic of brown, cushion-like swellings. The pale, narrow creases between the swellings are more or less parallel to the dorsal line. The test is tough. The apertures are on the upper surface, more than half the length of the body apart. They are on broadly based conical elevations.

Minute (0.02 mm), rounded scales line the siphon.

INTERNAL STRUCTURE: The body wall is closely adherent to the test. It is muscular, the muscle bands crossing one another to form a regular mesh. A siphonal sphincter muscle projects into the lumen at the base of the branchial siphon, just anterior to the tentacles. The dorsal lamina is long, the oesophagus opening at the posterior end of the branchial sac, which has 7 folds on each side. There are 6 stigmata per mesh. The branchial formula for an Australian specimen is: DL2(16) 3(16)5(15)3(12)3(9)3(7)1(5)0E. A Red Sea specimen has the following arrangement of vessels: DL2(20)3(21)3 (21)1(23)2(17)3(12)3(8)0E.

The gut forms a wide, open, straight loop that always reaches the anterior end of the branchial sac. It has the usual liver diverticula on the ascending limb. The anal border is bilabiate, with some slight indentations on the inner lip. The gonads are numerous, proliferated and crowded polycarp sacs.

REMARKS: The species is not very different from *P. elongata*, which also has a mosaic of scale-like thickenings on the surface but more internal longitudinal vessels and fewer branchial folds. Of other species that have 7 branchial folds per side, *P. navicula* n.sp. and *P. viarecta* n.sp. have a sandy test and (like *P. crassacapitata* n.sp.) do not have the scale-like thickenings of the present species. *Pyura fissa*, a species recorded only from Bass Strait, appears to be similar to the present species in having scale-like thickenings in the test and crowded polycarp sacs. However, endocarps that are conspicuous on the gut of *P. fissa* do not appear to be present in *P. pantex*, and the former species has long siphons that are not present in *P. pantex*.

Pyura sacciformis (Drasche, 1884)
(Figs 157a–c, 158; Pl.VIIc)

Cynthia sacciformis Drasche, 1884, p.376.
Pyura sacciformis: Tokioka, 1967a, p.197. Nishikawa, 1980, p.79. Kott, 1981, p.203.
Cynthia japonica Traustedt, 1885, p.30.
Cynthia sanderi Traustedt and Weltner, 1894, p.11.
Halocynthia sanderi: Hartmeyer, 1906, p.5.
Pyura sanderi: Tokioka, 1953a, p.275. Rho, 1966a, p.214; 1966b, p.367; 1968, p.97; 1971, p.122; 1975, p.144.
Halocynthia michaelseni Oka, 1906, p.46.
Cynthia michaelseni: Oka, 1935, p.437.
Pyura michaelseni: Tokioka, 1949b, p.54; 1954b, p.90. Kott, 1964, p.140.
Pyura aspersa Tokioka, 1949a, p.10.
Pyura masuii Tokioka, 1949b, p.57.
Pyura subuculata: Tokioka, 1950, p.149.
Pyura plicata Kott, 1952, p.278.
Pyura curvigona: Kott and Goodbody, 1982, p.539.

Distribution

New Records: Tasmania (Maria I., QM GH2013 GH2084). New South Wales (Wattlewood, QM G9711; Port Stephens, QM G10174). Queensland (Moreton Bay, QM G12716 GH2182; Heron I., QM GH2181 GH2557; Wistari Reef, QM G11914; Euri Creek, QM GH1458; Lloyd Bay, QM GH790; Cape Kimberley, QM GH1459).

Previously Recorded: Western Australian (Hamelin Bay — AM Y1856 Kott 1952). Queensland (Heron I. — Kott 1964). Japan (Drasche 1884, Traustedt and Weltner 1894, Hartmeyer 1906, Tokioka 1949a,b 1953a 1954 1967a). Korea (Rho 1966a,b 1968 1971 1975). Fiji (Kott 1981).

The species has a wide range in the western Pacific, from the temperate waters of Korea to the eastern and western coasts of Australia.

Description

External Appearance: The body is robust and rounded. It is often (but not always) covered with sand or sponge, and often has irregular projections from the surface test. Basally, it is usually produced into irregular holdfasts. Sand is sometimes present adhering to, or embedded in the surface of, the white, cartilaginous test.

The apertures are on the upper surface, separated by about one-third of the body length. The structure of the upper surface of the body and the disposition of the apertures are both very variable. Sometimes they are in depressions, surrounded by thickened test; or they are surrounded by a variable number of large, projecting lobes; or the apertures are at each end of a longitudinal ridge of test. The lobes, which may be rounded or pointed, occasionally have secondary tubercles. One or two series of smaller projections are produced forwards from around the rim of the apertures. These are also very variable. Sometimes they are relatively numerous, long and conspicuous, and occur in an inner and outer ring, but occasionally they are only swellings around each aperture. The specimens from Tasmania (QM GH2013, GH2084) are small, spherical juveniles (1.5 cm diameter) without lobes around the apertures. Their test is mostly thin and flexible, but thick and cartilaginous posteriorly.

The external test around the apertures is covered with overlapping, curved, pointed spines that continue down into the outer half of the siphonal lining. These are about 0.13 mm to 0.2 mm in total length along their outer borders. The anterior or inner curve of the projecting point is about 0.07 mm to 0.1 mm. There is a wide, flat flange around the open base of the spine. The spines cause a bluish iridescence in the siphonal lining. They are present only in the outer half of the siphon. The siphon linings are red in living specimens. Sometimes the preserved specimens have regular, oval bodies of orange pigment in the surface test around the apertures.

In some specimens, the upper half of the body appears to be articulated to the lower half by a horizontal strip of thinner test that extends around the animal. The strip makes it possible to contractdorsal half of the body into a sort of cup of solid test.

Internal Structure: In a juvenile specimen from Heron I. (QM GH2557), the body wall is produced into long, tongue-like projections that fit into the lobes around the apertures. These are less conspicuous in larger specimens. The body wall is very thin, except anteriorly, where there are strong muscle bands. It is very closely associated with the inner surface of the white, cartilaginous test. Very strong longitudinal muscle bands radiate from both siphons across the upper half of the body, but divide on the sides and posterior end of the body to form a fine, irregular mesh. Muscles are quite inconspicuous on the lower half of the body. Circular muscle bands are present only around the siphons, which are directed away from one another.

FIG. 157: *Pyura sacciformis* — **a** – **c**, siphonal spines (QM G12716, GH2181, GH1458). *Pyura spinifera* — **d**, siphonal spines. *Pyura spinosa* — **e**, siphonal spines; **f**, spicules. (Scales: **a**, 0.006 mm; **b** – **e**, 0.01 mm; **f**, 0.1 mm).

FIG. 158: *Pyura sacciformis* — a, b, external appearance (QM G11914, G12716); c, lobes fringing rim of apertures (QM GH2181); d, gut and gonads (QM GH790). (Scales: a, c, 2.0 mm; b, 1.0 cm; d, 0.25 mm).

The branchial tentacles have long primary branches, but only small secondary branches. Tertiary branches are minute or absent. Curved, branching spicules are often present in parts of the body wall. The dorsal tubercle has a large slit, with both horns rolled inwards to form a double spiral cone in larger individuals. Sometimes one of the horns is branched. The slit is often slightly convoluted. The dorsal lamina is long, with long, curved languets.

The branchial folds are wide and overlapping, and there are 6 or 7 on each side of the body. The seventh folds are rudimentary, on either or both sides of the endostyle. The internal longitudinal vessels are well spaced, with up to 20 vessels on the folds. However, the interspaces are narrow, with only 2 or 3 vessels. There are 4 to 6 stigmata per mesh in the interspace. A typical branchial formula is: E6(12)3(14)3(15)2(17)2(13)2(7)3DL.

The gut forms a pronounced J-shaped loop around the postero-ventral part of the left side of the body enclosing the left gonad. The loop is open in its distal half. The end of the rectum curves up sharply to the atrial aperture. The liver, which is usually well developed, comprises 4 pairs of arborescent diverticula. Those at the cardiac end are usually smaller, and sometimes consist of 2 or 3 pairs of rather flat rudimentary lamellae broken up into lobes along their borders; more often, the accessory diverticula are aborescent and almost as large as the distal pair. The branching stems of the latter are often long, lying free in the peribranchial cavity. The terminal lobules are also loose and separated, not crowded closely together. The anal border has about 6 rounded lobes.

Each gonad consists of a row of polycarp sacs along each side of the central gonoducts. The polycarp sacs are close to, and almost continuous with, the central ducts. They are firmly embedded in the body wall.

One large specimen from Moreton Bay has a fine fur of short, pointed processes all over the descending limb of the gut; they may be homologous with endocarps.

REMARKS: The species is distinguished by its cartilaginous test with a very irregular surface; protective processes around the apertures; circular muscles confined to the siphons; paired liver diverticula; double spiral coil of the dorsal tubercle; large, curved siphonal spines extending only halfway down into the siphons; and the wide basal expansion or flange on the spines. The number of internal longitudinal vessels in the branchial sac and the rather narrow interspace, the narrow gut loop with its open pole, and the variations in test thickness also help to distinguish the species.

The protective test processes (sometimes present around the apertures) are often similar in form, and probably in function, to those of *P. spinosa*, which is, however, readily distinguished by its spherical spicules. The minute processes over the gut of the large specimen from Moreton Bay have been previously observed in this species by Tokioka (1967a). They are present only in larger specimens and may be homologous with similar processes that occur in *P. ostreophila* and some individuals of *P. obesa* (see Hartmeyer 1919). The latter species is distinguished by its large number of branchial vessels. Identical branched spicules are embedded in the body wall of *Pyura stolonifera*. *Pyura obesa* has a similar thick cartilaginous test. Thus, many of the features of this species are shared with others in the genus, but this does not necessarily indicate a related phylogeny.

Nishikawa (1980) has suggested a relationship with *P. stolonifera*; however, the latter species has a very short dorsal lamina, less well-developed siphonal spines that have no basal expansion and do not extend onto the external test, apertures very close together, and an external test that is even, without marked irregularities.

This species is one of the few occurring in Australia that has a wide range in the western Pacific (see also *P. elongata*).

Pyura scortea n.sp.
(Fig. 159)

?*Pyura jacatrensis*: Hartmeyer 1919, p.8. Hartmeyer and Michaelsen, 1928, p.431.

DISTRIBUTION

TYPE LOCALITY: Western Australia (Cockburn Sound, coll. D. Heald, 1974, holotype QM G9666).

DESCRIPTION

EXTERNAL APPEARANCE: The single specimen is large (6 cm long) and upright. The posterior half of the body is about 3 cm in diameter, but it narrows anterior to the sessile atrial aperture, which is halfway down the dorsal side of the body. The terminal branchial siphon curves dorsally. The surface of the test is tough and leathery, with irregular creases, and with horizontal wrinkles around the apertures. Foreign particles are attached to the posterior part of the left side, but the remainder of the test is more or less naked. The test around each siphon is divided into wide, triangular lobes. In section, the test is moderately thick and translucent, but very tough. It is thicker toward the posterior end of the body. Small, curved, overlapping scales, with a rounded margin, line a very narrow strip of test around the rim of the apertures.

INTERNAL STRUCTURE: The branchial siphon is long and finger-like, while the atrial siphon is a short cone, directly slightly posteriorly. The musculature is very strong, and forms external circular bands around the siphons as well as around their bases. The latter extend over a wide radius, with the outer bands of each siphon meeting in the dorsal mid-line and reaching about halfway down the sides of the body. There are no horizontal bands around the body posterior to the siphonal muscles. The longitudinal bands radiating from each siphon are especially thick. They form an almost continuous layer over the sides of the body, branching and becoming slightly irregular on the ventral surface.

The branchial tentacles are long, but not very bushy. The peritubercular area is a wide V, completely filled by the large, protruberant and slightly lobed tubercle. The slit is a wide, somewhat irregular U, with the horns turned out, running parallel to the outer border of the tubercle. The dorsal lamina is a long, wide, ribbed and fleshy membrane over the dorsal sinus. The languets are long, but become shorter posteriorly.

There are 6 wide, overlapping folds on each side of the body. The internal longitudinal vessels are evenly spaced, crowded only on the edges of the folds. They are arranged according to the following formula: E5(18)6(20)7(20)7(18)5(22)3(20)0DL. There are about 6 stigmata per mesh.

The gut forms a long loop, curved dorsally only at the posterior end. The pole reaches to the prepharyngeal band. The limbs of the loop are almost parallel. There are about 4 unpaired liver diverticula with elongate terminal lobules. The anal border is primarily bilabiate, with some secondary indentations.

The gonads consist of up to 10, upright and almost cube-shaped polycarp sacs along each side of the gonoducts. The left gonad is enclosed in the gut loop. The polycarp sacs are attached very lightly to the body wall by their ducts and by very fine ligaments. They are easily dislodged. There are no endocarps on gut loop or gonads.

REMARKS: The species resembles *Pyura irregularis* and *P. confragosa* n.sp. in the irregular and largely naked surface test. However, their very hard test is different, when seen in section, from the cartilaginous test of the present species. Other characteristics by which *P. scortea* can be distinguished are the large number of internal longitudinal branchial vessels in the interspace and the cube-shaped, undivided polycarp sacs.

With the exception of *P. jacatrensis*: Hartmeyer 1919 and Hartmeyer and Michaelsen, 1928, *P. elongata* and *P. scortea* are the only species known with 6 branchial folds and small (not more than 0.03 mm) siphonal spines. *Pyura scortea* shares many characters with the former specimens: the general form of the body; the size of the siphonal spines; the length of the gut loop; the number of branchial folds and the number of internal

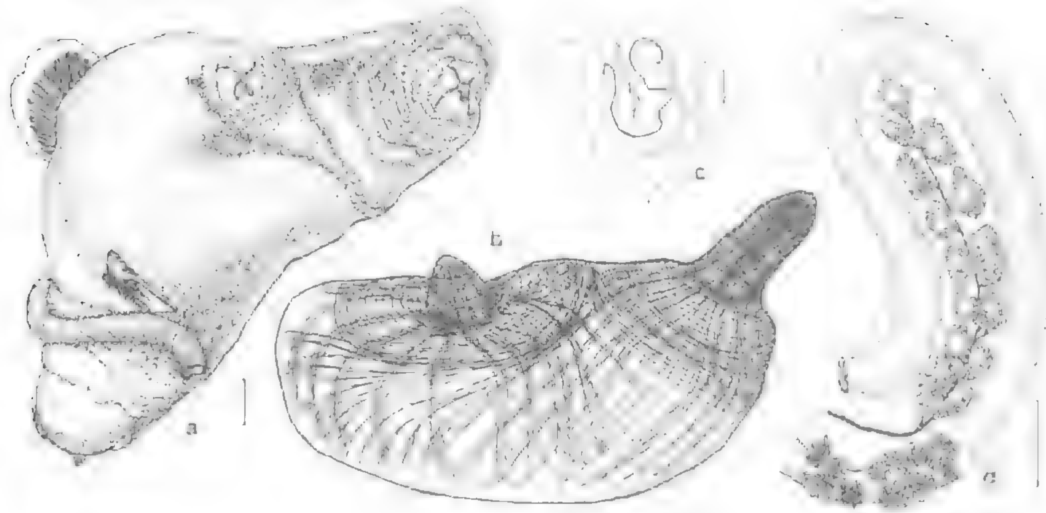


FIG. 159: *Pyura scortea* (QM G9666) — a, external appearance; b, body removed from test; c, dorsal tubercle; d, gut and gonads. (Scales: a, b, d, 5.0 mm; c, 0.5 mm).

longitudinal vessels on and between them; and the number of polycarp sacs. Hartmeyer and Michaelsen's (1928) description of the siphonal spines could refer to a profile view of the scale-like spines of the present species and the specimens (and those of Hartmeyer 1919) may be of *P. scortea*.

Pyura spinifera (Quoy and Gaimard, 1834)
(Figs 157d, 160; Pl.VIId)

Ascidia spinifera Quoy and Gaimard, 1834, p.617.
Boltenia spinifera: Herdman, 1891, p.571. Michaelsen, 1905, p.72 (part, not *B. gibbosa*).
Pyura spinifera: Hartmeyer, 1922, p.301. Kott, 1952, p.269; 1972a, p.39; 1972b, p.186.
Boltenia australiensis Carter, 1885, p.197.
Pyura australiensis: Hartmeyer and Michaelsen, 1928, f. typica p.410; f. busseltonensis p.429.
Cynthia multiradicata Herdman, 1899, p.30
Boltenia spinosa: Michaelsen, 1908b, var. intermedia p.231.
Boltenia gibbosa: Schmeltz, 1879, p.89.
Pyura gibbosa: Michaelsen, 1922, var. intermedia p.390.
Boltenia tuberculata Herdman, 1899, p.30.

DISTRIBUTION

NEW RECORDS: Western Australia (Carnarvon, WAM 1268.83; Cape Naturaliste, WAM 1267.83; Warnbro Sound, WAM 1269.83). South Australia (Cape Northumberland, QM G11894 GH1397). Victoria (Cape Woolamai, NMV F51593; Bass Strait, NMV 401 H403; Deal I., QM GH2180). New South Wales (Kingscliff, QM GH4925; Solitary Is, QM G9590).

PREVIOUSLY RECORDED: Western Australia (Busselton — Hartmeyer and Michaelsen 1928; King George Sound — Quoy and Gaimard 1834). South Australia (Backstairs Passage — Michaelsen 1908; St Vincent Gulf — Kott 1972a,b). Victoria (Bass Strait — Schmeltz 1879; Port Phillip Bay — Carter 1885). New South Wales (Port Jackson — Herdman 1899).

The species has a wide temperate range from southwestern to mideastern Australia, down to 80 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are robust, with a large (up to 12 cm long) kidney-shaped or top-shaped head, wider at the posterior (upper) end, and usually narrowing to a long, narrow stalk at the anterior end of the body. The head is rounded and only rarely slightly laterally flattened. Sometimes there are one to two longitudinal furrows down the side of the head, parallel to the rather conspicuous ventral convexity. More often the surface is smooth, with rounded tubercles, apparently randomly distributed, especially on the rounded anterior end of the body. The tubercles are very variable in both size and arrangement, and are sometimes absent altogether. The whole surface, including the stalk, is closely covered with an investing sponge (*Halisarca australiensis* Carter, 1885). Both apertures are on the dorsal side of the body, directed away from each other by differential development of the borders of the apertures. The

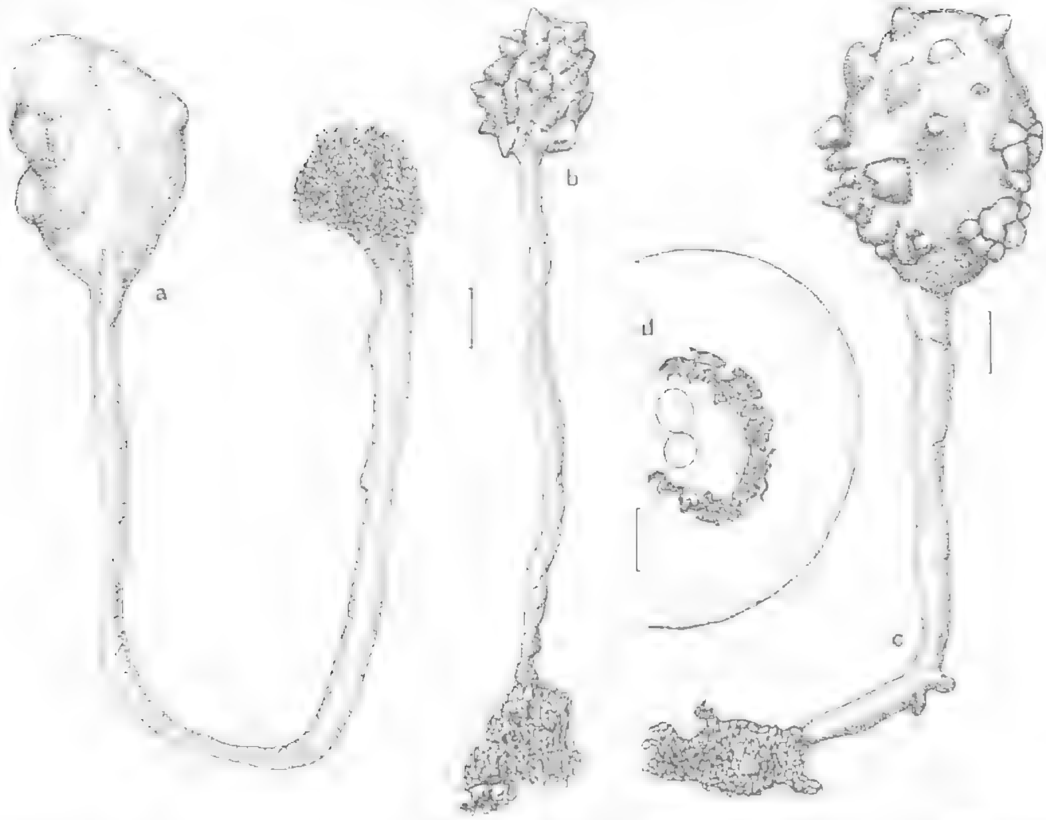


FIG. 160: *Pyura spinifera* — **a**, **b**, external appearance (QM GH1397); **c**, external appearance (QM GH925); **d**, cross section through stalk, showing horny cylinder and central blood vessels. (Scales: **a** – **c**, 2.0 cm; **d**, 2.0 mm).

atrial aperture is closest to the upper, free end of the head, about halfway down the dorsal surface; the branchial aperture is beneath it, closest to the stalk. Each aperture is surrounded by conspicuous, rounded lobes.

The cross section of the stalk shows a thin outer cuticle, a meshwork cylinder of brown, keratose material that encloses the central axial test and two large vessels that extend down the centre of the stalk. In small specimens, the meshwork cylinder is of relatively greater diameter and closer to the outer cuticle.

Minute, hollow conical spines, only slightly curved, 0.06 mm long, line the outer part of the siphons. There is no basal expansion of these spines, and they are only slightly longer along the outer (convex) surface than along the inner (concave) surface. The base of the spine is open, and circular to oval in shape. There are no spicules in the test.

INTERNAL STRUCTURE: The body wall is fleshy, muscular and opaque, with muscle bands radiating from each siphon to cross one another on both sides of the body. The dorsal tubercle has two shallow cones, each with a horn of the neural gland opening coiled inwards around it. The slit is slightly convoluted. The branchial tentacles are numerous and bushy. The dorsal lamina is short; the languets short and pointed.

The oesophageal opening is halfway down the branchial sac, which is strongly curved. The branchial folds terminate posteriorly behind the oesophageal opening. There are usually 6 branchial folds on each side of the body, although occasionally (in larger specimens) there are 7. Theinternal longitudinal vessels are not crowded; there are up to 30 or more on the folds and no more than 6 in the interspace. Each mesh has from 6 to 8 stigmata, crossed by parastigmatic vessels. A typical branchial formula for a specimen of 4 cm is: E12(21)5(22)6(26)5(30)5(32)5(30)12DL.

The gut forms a J-shaped loop around the posterior and ventral borders of the body. There are 3 pairs of liver diverticula, with clumps of slightly crowded terminal lobules, near the oesophagus. The anal border has 6 shallow lobes.

The gonads consist of a single row of transversely elongate polycarp sacs along the anterior side of the central ducts. The left gonad is in the gut loop. There are no endocarps, although in larger specimens both gut and gonads are firmly embedded in the body wall.

REMARKS: The species shares many characters with other bolteniform species such as *P. australis* and *P. gibbosa*. It can be distinguished by the absence of spicules; the hollow, conical, siphonal spines in which the open base is not attenuated; the slightly convoluted double-spiral opening of the neural duct; the cylinder of branched keratose fibres in the stalk; the deeply curved branchial sac; the shallow anal lobes; and the *Halisarca* sponge with which it is invariably covered. Further, in comparison with related species it grows larger, often has a smooth surface (whereas others are rough), the upper free end of its head is more swollen and rounded, its test tubercles are more conspicuously rounded and are randomly scattered (rather than being arranged in longitudinal rows) and the lobes around its apertures are more conspicuous and rounded. However, the external appearance of each species in this group varies so much that general appearance does not always provide a reliable guide to identity; internal features must be relied on for positive determination.

Pyura spinosa (Quoy and Gaimard, 1834) (Figs 157e,f, 161)

Ascidie spinosa Quoy and Gaimard, 1834, p.615.
Cynthia cerebriformis Herdman, 1882, p.136.
Cynthia cataphracta Herdman, 1899, p.31.
Pyura cataphracta: Kott, 1976a, p.77.
Pyura multiradicata: Kott, 1952, p.269 (part, not Herdman's type specimen of *C. multiradicata* < *P. spinifera*).
Pyura leeuwinia Kott, 1952, p.277.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, QM G11893 GH2183, NMV H639 F51827 F51588). Tasmania (NW Tasmania, TM D984).

PREVIOUSLY RECORDED: Western Australia (Triggs I., Albany — Quoy and Gaimard 1834, Kott 1952). Victoria (Western Port, Portland, Cape Grant — Kott 1976a). New South Wales (Port Jackson — BM 1887.2.4.47 Herdman 1882, 1899).

The species has been taken from intertidal to 275 m around the southern half of Australia. It is particularly well adapted for turbulent conditions off rocky coasts.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are upright, stalked or sessile, with apertures at opposite ends of the upper, free surface. Posteriorly there are root-like processes anchoring the animal to the substrate, or the body narrows abruptly to a thin stalk that is never longer than the head. Individuals are up to 5 cm high and 3 cm wide. The test around the apertures is produced into conspicuous, pointed processes that tend to close over the apertures when these are withdrawn. The surface of the test varies. It may be smooth with occasional small, pointed tubercles; or creased and wrinkled. Specimens from exposed intertidal locations (> *P. leeuwinia* Kott, 1952) occur in tight aggregates and have a very rough test, with pointed processes of the test helping to lock individuals together in the aggregate. Basal, root-like processes, often branched, help fix the animal to the substrate. Despite its irregularities, the test is not usually very thick, but it is very tough and hard. The surface feels especially hard and granular, owing to the large (0.30 mm diameter) calcareous spicules that are crowded in it. These spicules become slightly less crowded toward the inner surface. They are spherical and consist of tight, radially arranged, cylindrical rays with slightly projecting rounded ends. Rudimentary spicules, 0.04 mm in diameter and with a small number of well-separated rays, are packed in the test amongst the larger, spherical spicules.

The siphonal lining has minute, pointed, overlapping, hollow spines. The spines are 0.04 mm in overall length, including the scale-like posterior extension. The projecting curved point is only 0.01 mm long.

INTERNAL STRUCTURE: The body wall is very thin and adheres closely to the test. Strong longitudinal muscle bands radiate from both siphons, and break up into an irregular network over the posterior end of the body.

The branchial tentacles have primary, secondary and tertiary branches, and are rather bushy. The prepharyngeal area is narrow. The dorsal tubercle is large, with a U-shaped opening directed to the left. The dorsal lamina is long, but the languets are not crowded.

There are 6 branchial folds on each side of the body, with up to 21 internal longitudinal vessels on the folds, and 2 or 3 between. A typical branchial formula is: E1(11)2(10)2(12)2(12)2(12)1(11)1DL. There are 4 to 6 stigmata per mesh.

The gut forms a J-shaped loop, wide in its terminal half. Only the distal end of the rectum and oesophagus are curved. There are about 6

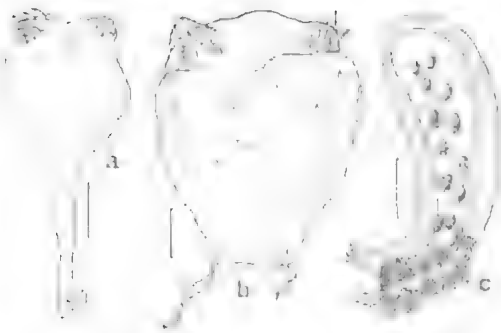


FIG. 161: *Pyura spinosa* — a, b, external appearance (after Kott 1976); c, gut and gonads (QM G11893). (Scales: a, b, 1.0 cm; c, 5.0 mm).

pairs of liver diverticula along the pyloric region of the gut. The liver lobules are slightly elongate and not very crowded. The anal border has 6 well-developed lobes.

The gonads consist of small, rounded polycarp sacs along both sides of the central gonoducts. The sacs are firmly attached to the body wall. The left gonad is in the gut loop.

There are very small and inconspicuous endocarps on the gut loop, and an occasional pointed endocarp on the free surfaces of the polycarp scas.

REMARKS: The very large, globular spicules are distinctive and known only in the present species and in *P. littoralis* (where they are smaller but otherwise identical). *Pyura littoralis* is readily distinguished by its multiple oviducal apertures and unusual branchial folds. The present species is not very closely related to others in the *pachydermatina* group, and is readily distinguished from them by the position of the apertures and stalk as well as by its spicules. The very hard, irregular test with tubercles and pointed spines and the well-separated apertures were noted by Quoy and Gaimard (1834).

Pyura stolonifera (Heller, 1878)
(Fig. 162; Pl. VIIIa,b)

Cynthia stolonifera Heller, 1878, p.10.
Pyura stolonifera: Hartmeyer, 1911, p.554; 1912, p.246; 1913, p.133. Michaelsen, 1915, p.370; 1921b, p.5; 1923, p.50; 1927, f. waia p.193. Hartmeyer and Michaelsen, 1928, p.433. Sluiter, 1927, p.56. Kott, 1952, p.274; 1964, p.141; 1976a, *praeputialis* p.82. Millar, 1962a, p.193. Monniot, 1965, p.100. Day, 1974, p.35. Griffiths, 1975, p.1. Driel, 1978, p.1.
Cynthia praeputialis Heller, 1878, p.12. Drasche, 1884, p.374. Traustedt, 1885, p.33. Herdman, 1899, p.27.
Cynthiopsis praeputialis: Michaelsen, 1905, p.91.
Pyura praeputialis: Hartmeyer, 1911, p.560. Millar, 1963, p.738; 1966, p.372. Anderson *et al.*, 1975, p.205.
Microcosmus coalitus Sluiter, 1898a, p.57.
Cynthiopsis coalitus: Michaelsen, 1904a, p.201.
Halocynthia vanhoeffeni Michaelsen, 1904a, p.201.
Cynthiopsis valdiviae Michaelsen, 1904a, p.201.
Cynthiopsis herdmani Michaelsen, 1904a, p.208.
Microscosmus herdmani: Herdman and Riddell, 1913, p.876.
Pyura bradleyi Van Name, 1931, p.221; 1945, p.334.

DISTRIBUTION

NEW RECORDS: Western Australia (Albany, WAM 1251.83). South Australia (St Vincent Gulf). Tasmania (Eaglehawk Neck, QM GH1804; Kingston, TM D707. SE Bruny I., TM D1856; Ralph's Bay, TM D720; Roches Beach, TM D1538 D1809 D1838 D1842, QM GH1804). Victoria (Ninety Mile Beach, QM G11869; Port Phillip Bay, QM G10051–2, NMV F51596). New South Wales (Arrawarra; Hastings Point QM G10104–5). Queensland (Noosa Heads; Point Cartwright, QM G10112; Alexander Headland, QM G10113; Caloundra, QM G10119; Currumbin, QM G2109; Moreton Is., QM GH360). Chile (Antofagasta, collection D.P. Abbot; Valparaiso, MHN).

PREVIOUSLY RECORDED: Western Australia (Shark Bay, Cockburn Sound — Hartmeyer and Michaelsen 1928). South Australia (St Vincent Gulf — Kott 1952). Tasmania (Spring Bay — Kott 1952). Victoria (Wilson's Promontory, Walkerville — Kott 1952; Port Phillip Bay — Kott 1952 1976a; Millar 1963; Western Port — Kott 1976a). New South Wales (Jervis Bay — Herdman and Riddell 1913; Port Jackson — Heller 1878, Drasche 1884, Traustedt 1885, Herdman 1899). Queensland (Cape Moreton — Kott 1952; Noosa — Kott 1964). Tahiti (Michaelsen 1923). Western Africa (Port Nolloth — Sluiter 1898a; Algoa Bay to Cape Town — Heller 1878, Drasche 1884, Michaelsen 1921, Griffiths 1975, Driel 1978; Numibia — Michaelsen 1915; Luderitz Bay — Hartmeyer 1913; Dakar — Monniot 1965; Morocco — Sluiter 1927). Tahiti (Michaelsen 1923). Eastern Pacific (Peru — Van Name 1931). Ecuador (Van Name 1945). Records for the Chatham Is. referred to by Monniot (1965) have not been traced.

The species extends into the tropics and north of the equator on the western coasts of both the African and South American continents. On the eastern Australian coast the species is not recorded north of Noosa (2625'S). The only record from the tropical central to western Pacific is from Tahiti (Michaelsen 1923), well north of its northern limits on the Australian continent. The affinities of the Tahitian populations are not known.

Populations off the eastern Australian and Numibian, South African and Peruvian coasts are crowded, forming extensive mats at low tide on rocky exposed shores. These populations extend into subtidal depths where rocky substrates are free of sediments (see also Day 1974). In protected waters, individuals can be found on wharf piles. They are also found on sandy substrates, where they are solitary rather than occurring in aggregates. In Australia and South Africa, the species has been reported down to 12 m.

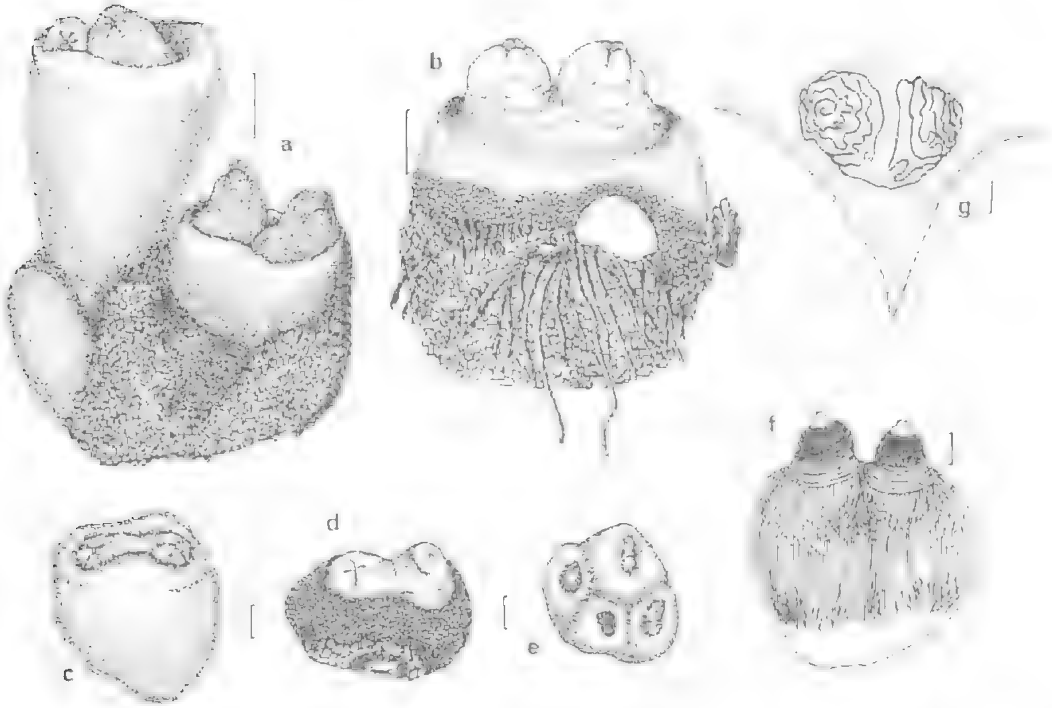


FIG. 162: *Pyura stolonifera* — **a** – **e**, external appearance (**a**, **b**, characteristic rocky shore form, QM G10105, G10051; **c**, **d**, Tasmanian locations, TM D707, D720; **e**, aggregate of juveniles, TM D720); **f**, body removed from the test (TM D707); **g**, dorsal tubercle (TM D707). (Scales: **a**, **c**, 1.0 cm; **b**, **d** – **f**, 5.0 mm; **g**, 0.5 mm).

During the winter, storms cast up very large numbers of this species along the coasts of New South Wales and Victoria.

Reproductive activity has been reported in April/May and September for 3 Australian populations in the vicinity of Port Jackson (Anderson *et al.* 1975).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are either upright and more or less cylindrical, or squat with an expanded base. They are up to 30 cm high and 10 cm in diameter around the upper surface. The apertures, their borders divided into large, triangular lobes, are close together and protrude as rounded hemispheres from the depressed upper surface. The apertures are surrounded by a rounded ridge bordering the the upper surface of the body. Populations from the intertidal zone of rocky shores consist of tightly aggregated, tall, cylindrical individuals in which the basal part of the animal is entirely solid leathery test, the animal itself being supported at the top of this column of test. In individuals from sandy substrates, the basal test is broken up into a long beard of root-like processes enmeshed with sand; there is no solid pillar of basal test.

The test is always thick and hard. It is sometimes covered with embedded sand. However, the rocky shore aggregates are more often leathery on the surface and have epiphytes. Individuals from Tasmania and South Australia are smaller than those from the central New South Wales coast. Epiphytes and sand are sometimes absent from the test immediately surrounding the apertures, but they usually are present elsewhere, except in Tasmanian populations, in which the anterior ridge of test is rounded, bare, smooth and yellow. This ridge is of varying width, sometimes flattening out so that the body gradually expands in diameter from the base of the siphons to about halfway down the side of the body. Juvenile specimens have an irregular surface with nodules, bumps and projections. These variations have also been observed in South African populations (Day 1974).

The atrial aperture is directed upwards, the branchial aperture slightly laterally. The test around the rim of the apertures is produced into small, hollow, tentacular processes of varying length that project down into the siphon when it is contracted. Corresponding processes of the body wall fit into these projections. The outer half of the siphonal lining has hollow, curved spines with slightly expanded bases, the outer surface flaring out posteriorly. Spines vary in length from 0.02 to 0.1 mm (see Kott 1976a). A range from 0.05 to 0.09 mm has been observed in the one individual

INTERNAL STRUCTURE: The body wall is soft and fleshy, but is muscular anteriorly. It is characteristically bright red-orange. Longitudinal bands extend from the siphons down the body wall, but unlike those in most species of this genus they do not cross one another to form a mesh. Circular muscles are conspicuous around the base of the siphons and the anterior part of the body. There are many short terminal branches of these circular muscles in the vicinity of the circular fold of test surrounding the anterior end of the body. Branched, horny spicules occur in the body wall, branchial tentacles and pharynx of some, but not all, specimens.

The branchial tentacles are very variable. They are sometimes bushy, sometimes almost pinnate with only minute secondary branches, and sometimes the tentacles themselves are quite rudimentary and inconspicuous. There are 16 tentacles, large and small alternating, with rudimentary tentacles between them. The large dorsal tubercle is close behind the ring of tentacles at the anterior end of the V-shaped peritubercular area. The slit forms a double spiral cone, which is more complex and convoluted in some specimens than in others. The open interval between the cones is anterior.

The dorsal lamina is very short, and in larger specimens is absent altogether. The folds of the branchial sac are deeply curved, and there are 6 or 7 folds on each side of the body. Up to 20 internal longitudinal vessels are present on the folds, and up to 4 between them. There are 5 to 8 stigmata per mesh. A branchial formula for a small Tasmanian specimen is E(14)2(16)3(18)2(18)1(23)1(21)6DL.

The gut forms a curved and rather wide loop around the postero-ventral border of the left side of the body. There are 2 unpaired, large, branched liver diverticula. The anal border has about 8 shallow, rounded lobes.

The gonads are always embedded in the body wall, but are otherwise very variable. They are broken up into block-shaped polycarp sacs, sometimes in paired rows, with up to 8 in a row, along each side of central ducts; or in a single row of large, flat topped blocks (in very large cylindrical specimens). The left gonad is primarily in the gut loop, although blocks of gonad often occur, embedded in fleshy endocarp, in the secondary curve of the gut loop, outside the primary loop.

REMARKS: Michaelsen (1923), Hartmeyer and Michaelsen (1928) and Kott (1952 and 1976a) have discussed the relationships of populations from South Africa known as *P. stolonifera* and those from Australia known as *P. praeputialis* and believe them to be conspecific. Millar (1962a, 1963) regarded the African and Australian populations as separate species on the basis of the branching spicules in certain specimens from Africa, and of the direction of coiling of the slit of the neural gland opening. In fact, the branching spicules occur in Australian populations (and also in specimens of *P. sacciformis*). The direction of coiling of the neural gland opening appears to be a stable character in each of the respective populations, and may indicate a degree of isolation. However, on its own it does not justify species status for each of the populations.

The relationship between this species and populations off the Chilean coast are also close (> *Pyura bradleyi*) and are based on the same variations in body shape and internal structure, including the presence of the branching spines.

There are some differences in breeding season, although egg sizes are remarkably similar in South African and Australian populations. Specimens from South Africa have eggs of 0.25 mm to 0.3 mm and breed from December to January (False Bay, Griffiths 1975; Driel 1978), or June and December (Capetown, Day 1974). Three populations around Port Jackson have eggs that are 0.23 mm in diameter (0.26 mm with chorion) and breed in April/May and September (Anderson *et al.* 1975). The larval trunk is 0.30 mm long in the Australian populations and 0.23 to 0.28 mm long in the South African specimens (Griffiths 1975).

Similarities between the populations off the African, Australian and South American continents are too dramatic to be regarded as other than significant. In addition to the morphological and ecological similarities, E.V. and Circular Dichroism spectra for Australian, Chilean and South African populations, demonstrating that the molecular structure of the blood pigments are identical (C.J. Hawkins *pers. comm.*), constitutes compelling evidence of a close phylogenetic relationship.

It seems unlikely that there is gene flow between the contemporary populations on these three continents. The only plausible explanation for their occurrence is that they are relict populations of a Gondwanaland species. This explanation conforms well with the present range of South American and Australian populations. The South African populations could have isolated earlier and may be expected to have diverged further. Prevailing west wind drift could explain why the range did not extend across the southern coast of Australia after its separation from the Antarctic continent. Since there is no evidence that the present populations have been isolated for long enough to have achieved the true biological isolation that could justify their separation from one another as distinct species, they are regarded here as conspecific; although their geographic separation suggests that each can be regarded as a subspecies (Kott 1976a).

Pyura stolonifera is characterised by its body shape and close apertures, orange-red body wall, specialised body musculature, siphonal spines, very short dorsal lamina and deeply curved branchial sac, double spiral of the neural gland opening, and block-shaped, embedded gonads. *Pyura sacciformis* has larger and more hooked siphonal spines with a wide basal flange. Nor does it have the shortened dorsal lamina, block-shaped gonads or body shape of the present species, and its apertures are further apart. *Cynthia arcuata* Heller, 1878, from New South Wales waters, may be a specimen of *P. stolonifera* in which the anterior rim of test had flattened out, as in some of the Tasmanian specimens that it closely resembles.

Pyura tasmanensis n.sp.
(Figs 163a–d, 164)

DISTRIBUTION

TYPE LOCALITY: Tasmania (Ralph's Bay, Neck Canal, coll. R. Hetherington, August 1983, holotype TM D1881, paratypes D720).

FURTHER RECORDS: Tasmania (Roche's Beach, TM D190 D1834 D1844 D1848 D1869; Tasman Head, TM D1189; Port Davey, QM GH2016).

Specimens have been taken from Tasman Head at 154 m. Large numbers are washed up on beaches after storms.

DESCRIPTION

EXTERNAL APPEARANCE: The species is robust, and occurs in large aggregates. Generally the body is upright and rounded, with both apertures on small siphons close together on the upper surface. The atrial aperture is just dorsal to the branchial aperture in the centre of the upper surface. The apertures are sometimes withdrawn into the upper surface, or are extended and diverging. Posteriorly, there is either a short stalk, or a dense beard of fine, sand-encrusted, root-like extensions of the test, which hold the aggregates together. The test is very hard, with fine horizontal wrinkles or a mesh of slight, rounded ridges over the surface. There is a fine encrustation of sand over most of the posterior third of the body. Individuals are generally about 3 cm in diameter.

The siphons are lined for most of their length with long (0.1 to 0.2 mm), overlapping, pointed spines, which cause a yellowish iridescence. They extend onto the outer surface of the anterior half of the body. The distal part of the inside surface of these spines has a groove.

INTERNAL STRUCTURE: The body wall is muscular, with strong circular bands around the siphons and around the base of the siphons. There is also a layer of circular muscles around the body posterior to the siphonal muscles. Internal longitudinal muscles cross one another over the sides of the body. The branchial tentacles (about 20) are especially long, giving a bushy appearance. However, their primary branches are of only moderate length, their secondary branches are small, and their tertiary branches are minute. The dorsal tubercle is in a V-shaped peritubercular area. It is a large and very protruberant cushion, often with a constriction around the base to form a stalk. The slit is deep and wide, basically U-shaped, with both horns turned in to form a double spiral cone. The dorsal lamina is long, the oesophageal opening being at the posterior end of the branchial sac.

There are 6 high, overlapping branchial folds on each side of the body. The dorsal folds are almost straight, but the ventral folds are curved in a semicircle, because of the deep convexity of the body. There are up to 20 internal longitudinal vessels on the folds and up to 6 in the interspace. A typical branchial formula is: E5(12)6(14) 5(20)5(22)5(24)4(22)3DL.

The gut loop is narrow and forms a J-shaped curve around the postero-ventral quarter of the left side of the body. The ascending and descending limbs are parallel. There is a large, arborescent liver diverticulum from about halfway along the ascending limb, and small accessory diverticula proximal to the main stem. The anal border is bilabiate. Densely crowded endocarps lie on the outer curve of the descending limb.

There are about 12 rounded polycarp sacs along each side of the common gonoducts on each side of the body. The sacs, which are sometimes continuous with the central ducts, are very firmly fixed to the body wall. There are also endocarps on the polycarp sacs.

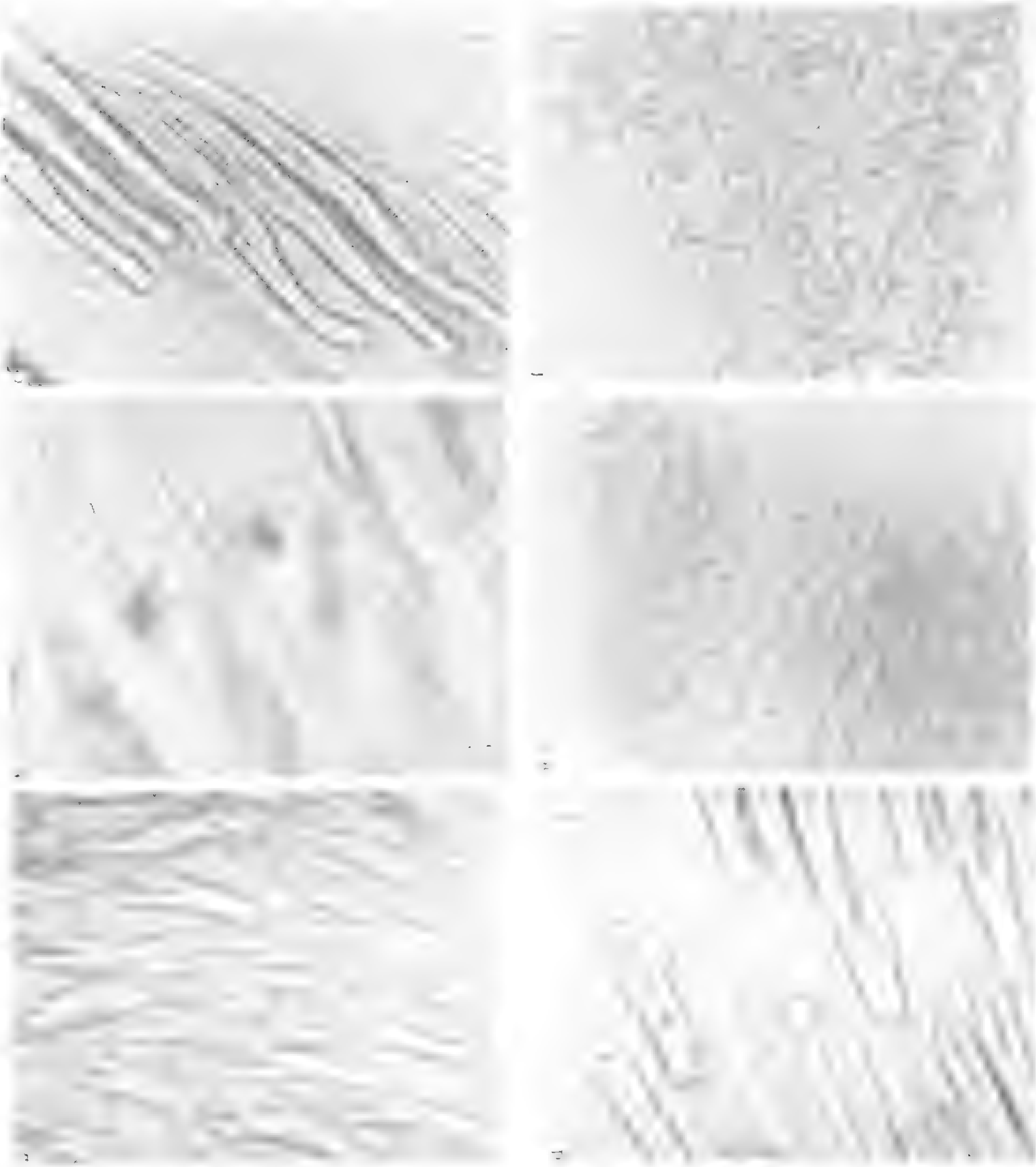


FIG. 163: *Pyura tasmanensis* n.sp. — **a** - **c**, siphonal spines from near base of siphon (**a**, from below; **b**, from above; **c**, profile); **d**, siphonal spines near top of siphon. *Pyura viarecta* n.sp. — **e**, siphonal scales from above; **f**, base of siphonal spines. (Scales: 0.01 mm).

FIG. 164: *Pyura tasmanensis* n.sp. — a, aggregate of 2 individuals (QM GH1382); b, gut with endocarps and gonads (TM D189). (Scales: a, 5.0 mm; b, 2.0 mm).

REMARKS: The species resembles *Pyura obesa* and *P. isobella* n.sp. in its general body shape, its closely placed apertures and its endocarps on gut and gonads. The dorsal lamina of *P. obesa* is shorter than that of the present species, but *P. isobella* has a similar long dorsal lamina and protruberant dorsal tubercle. However, *Pyura tasmanensis* lacks the thick, sandy investment of both the former species, and is also readily distinguished by its needle-like spines, which are of even length and do not have the basal swelling of some of the spines of *P. isobella*.

Pyura viarecta n.sp.
(Figs 163e,f, 165)

DISTRIBUTION

TYPE LOCALITY: Queensland (Heron I., southern reef slope, 10 m, coll. P. Kott, March, 1975 holotype QM GH1388).

DESCRIPTION

EXTERNAL APPEARANCE: The holotype is 2 cm long, oval and slightly laterally flattened. It is fixed by the ventral surface. The test is cartilaginous and quite soft, and has sand embedded in it. Ventrally, there are irregular processes. The apertures are sessile, at opposite ends of the upper surface and directed away from one another. The sand investment covers the whole surface, almost to the apertures. Very small lobes around the rim of the aperture are covered with minute, overlapping curved scales that continue down into the outer, terminal part of the siphon lining.

INTERNAL STRUCTURE: The body wall has strong, longitudinal muscle bands that radiate from each siphon and cross one another over the sides of the body. These muscles fade out on the ventral surface. There are circular muscles around the siphons and around the base of the siphons, but none posterior to these siphonal muscles. At the base of each siphon is a strong, muscular sphincter. In the branchial siphon, it is just in front of the branchial tentacles and protrudes into the lumen. The branchial tentacles, which are long but not bushy, have primary and minute secondary branches. The dorsal tubercle is a moderate-sized, circular cushion at the top of the deep, V-shaped peritubercular area. The dorsal lamina is very long, the oesophageal opening being at the posterior end of the body.

There are 7 branchial folds on each side. They are wide and straight, running parallel to the longitudinal axis of the body. They do not curve up to the oesophageal rim, but join a retropharyngeal groove along the mid-line in the posterior end of the body. The internal longitudinal vessels are crowded on the folds. The branchial formula is: E4(9)3(14)2(16)4(20)3(20)3(16)2(9) 1DL. There are 4 to 6 oval stigmata per mesh.

The gut forms a wide, almost circular, loop. There is a large, arborescent liver diverticulum with quite large, paired accessory diverticula on the proximal part of the gut. The anal border is bilabiate. The rectum extends into the base of the atrial siphon.

Each gonad consists of about 12 lightly attached, rounded polycarp sacs on each side of central gonoducts. The left gonad is in the gut

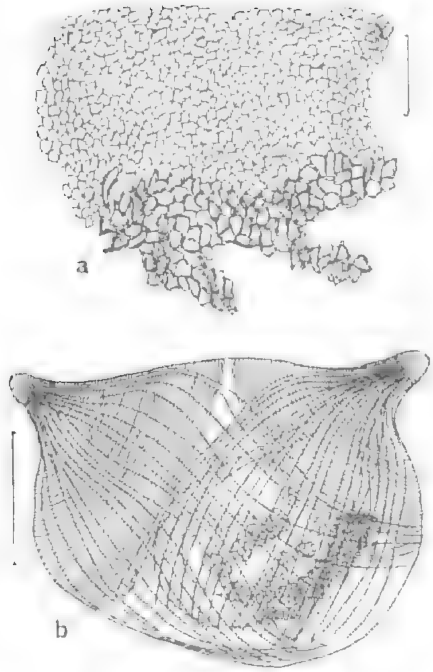


FIG. 165: *Pyura viarecta* n.sp. (QM GH1388) — a, external appearance; b, body removed from test. (Scales: 5.0 mm).

loop, lying along the inner curve of the ascending limb. There are no endocarps on the gut loop, although there are some on the gonads.

REMARKS: The species resembles *Pyura elongata* and *P. crassacapitata* n.sp. in its body shape, with siphons at opposite ends of the upper surface directed away from one another. It is distinguished from both these species by the complete investment of sand, which is also embedded in the test, and by its very straight branchial folds. It also lacks the thickened anterior ridge of test found in *P. crassacapitata*. The branchial folds of *P. molguloides* are more curved than those of the present species, although the species resemble one another in other respects.

Genus **Ctenyura** Van Name, 1918

Type species: *Ctenyura intermedia* Van Name, 1918

The genus has dorsal languets, branched liver diverticula and gonads divided into polycarp-like sacs, but is distinguished from *Pyura* by the presence of spiral stigmata and infundibula in the branchial folds.

The type species has no gonad on the left side of the body. However, this probably does not indicate a phylogenetic distinction from other species in the genus, particularly in view of the similarity in the form of the gonads, liver diverticula, dorsal languets and branchial sac. Siphonal spines, present in one of the two Australian species indicates a further close affinity with the genus *Pyura*, although these spines have not been reported in the accounts of the only two species previously described, viz. the type species from the Philippines and *C. comma* (Hartmeyer, 1906) from Japan. The largest known individuals of this genus are only 1.8 cm long (Van Name 1918).

The spiral stigmata also occur in other genera of the Pyuridae *viz., Heterostigma* Arnback, 1924, *Bolteniopsis* Harant, 1927, *Cratostigmata* Monniot and Monniot, 1961 and *Hartmeyeria* Ritter, 1913. Most species of these genera are small and simplified, and only the two last genera retain branchial folds that would justify their comparison with the present genus. Although they both resemble *Ctenyura* in their body size and branchial sac, they have a smooth dorsal lamina, undivided gonads, and pouches rather than branched diverticula from the pyloric part of the gut. They have closer affinities with *Microcosmus* and *Molgula* than has the present genus, which is most closely related to *Pyura*.

In Australian waters the genus *Ctenyura* is known only by 2 species, both from temperate waters and although several specimens are available for each, the records are only few. It is probable that the small size (which may be one of its characters) has resulted in specimens being overlooked by collectors.

Ctenyura tetraplexa n.sp.
(Fig. 166a–c)

DISTRIBUTION

TYPE LOCALITY: Victoria (off Cape Howe, 37°05′S 150°05′E, 60–100 m, Dr T. Mortensen's Pacific Expedition, 30.9.14, holotype ZMC, paratypes ZMC).

DESCRIPTION

EXTERNAL APPEARANCE: Spherical individuals, about 2.0 mm in diameter, are either sessile or have a short narrow stalk about 1.0 mm. The external surface is smooth, and white, due to large (0.08 mm diameter), stellate spicules with blunt-ended, cylindrical rays, that are evenly distributed in the rather thin but firm test. The apertures are sessile, 4 lobed, on the upper surface of the body.

INTERNAL STRUCTURE: The body wall is thin, with fine muscles radiating from each aperture and

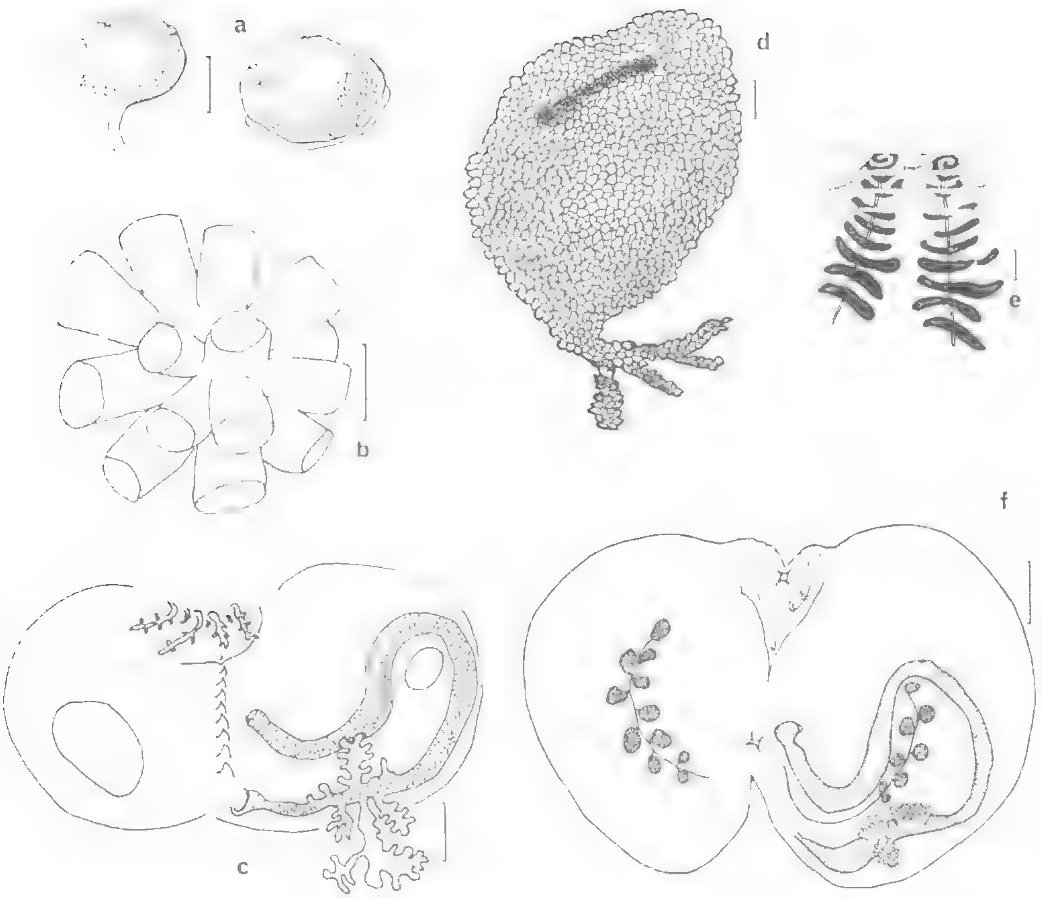


FIG. 166: *Ctenyura tetraplexa* n.sp. (ZMC holotype)—**a**, external appearance; **b**, spicule; **c**, internal structure. *Ctenyura tortuosa* n.sp.—**d**, external appearance (NMV H379); **e**, arrangement of stigmata in branchial fold (NMV H379), **f**, internal body wall (NMV H740). (Scales: **a,d,f**, 1.0mm; **b**, 0.02 mm; **c**, 0.5mm; **e**, 0.1mm).

it adheres closely to the test. There are 6 fairly long tentacles (with short, sparse branches) alternating with rudimentary tentacles. There are 8 rather long, triangular languets on the dorsal lamina.

The branchial sac has 4 folds, each with about 3 internal longitudinal vessels. There are no internal longitudinal vessels in the interspaces. There are 6 rows of stigmata forming infundibula in the folds. The stigmata are long and oval, crossed by parastigmatic vessels. The middle rows of stigmata are the longest.

The gut forms a rather long horizontal loop and the short rectum turns anteriorly to open at the base of the atrial opening. The most conspicuous feature of the gut is the long, flat, lobed liver diverticula that branch off both sides in the pyloric region. One of the diverticula is especially long, extending beneath the endostyle onto the right side of the body. There is a circular, upright endocarp in the gut loop and a larger one in a corresponding position on the right side of the body. No gonads were observed in any of the 4 specimens.

Remarks: Despite the absence of the gonads, the species is identified as a member of the genus *Ctenyura* by the stigmata arranged in infundibula in the branchial folds. The endocarps in the gut loop and on the right side of the body probably indicate the site where gonads would develop.

The blunt-rayed stellate spicules and their even distribution in the test are unique characters. Spicules reminiscent of those in the present species are present in certain *Pyura* spp. (*P. australis, P. gibbosa*). Other characters of the present species clearly distinguish it. The long, lobed liver diverticula, characteristic of *Pyura* and *Ctenyura* are conspicuous. The few branchial folds and small number of rows of stigmata are probably a result of a size reduction and simplification in this small species.

Ctenyura tortuosa n.sp.
(Figs 166d–f, 167a)

Distribution

Type Locality: Victoria (Bass Strait, 39°01.0'S 143°22.1'E, 84 m, Bass Strait Survey, 31.1.81, epibenthic sledge, holotype NMV H379, paratypes NMV H740 F51564).

Description

External Appearance: The individuals are very small, up to 7 mm high and about as wide across the upper surface of the rather top-shaped body, which narrows basally to a tuft of small, root-like test processes. Both sessile, 4-lobed apertures are in a slight median groove in the centre of the upper surface, about one-third of the length of the upper surface distant from one another. The test is thin, rigid and brittle with embedded sand.

There are long (0.08 mm), pointed, overlapping spines in the siphons.

Internal Structure: The body wall is very delicate and adheres closely to the test. Fine longitudinal bands radiate to halfway down the body from each aperture. Fine circular bands are present only around the apertures. There are only about 8 branchial tentacles, which alternate with rudimentary ones. They have very short primary branches and no secondary branches. The opening of the neural gland is a small J- or U-shaped slit in a wide peritubercular V. The neural ganglion is long and narrow. The dorsal lamina is moderately long, with numerous pointed languets.

The branchial sac has 6 narrow folds on each side of the body. The internal longitudinal folds are arranged according to the following formula: E0(2) 1(9) 1(9) 1(10) 1(4) 1(8) DL1(5) 1(3) 1(10) 1(9) 1(5) 1(3) 1E. The stigmata are curved to form infundibula; those in the top of the folds form a continuous spiral of about two complete, uninterrupted turns. There are 6 primary infundibula in each fold, alternating with the 6 primary transverse vessels. Each mesh is divided by secondary transverse vessels. The stigmata are crossed by parastigmatic vessels that extend up to the tip of each spiral in the edge of the fold. In the interspace, 4 stigmata lie on each side of the single internal longitudinal vessel.

The gut forms a wide, almost closed, loop. There are proximal paired and distal unpaired liver diverticula. The rectum curves anteriorly to the atrial aperture, forming a secondary loop. The anal border is bilabiate and smooth.

The gonads consist of almost spherical polycarp sacs on each side of the common duct. There are 5 pairs of sacs on the right side of the body and 4 pairs on the left. The left gonad is in the gut loop.

There are no endocarps on gut or gonads.

Remarks: *Ctenyura intermedia* Van Name, 1918 and *C. comma* (Hartmeyer, 1906) are the only species previously known in this genus. The former has 7 branchial folds on each side and has no gonad on the left side of the body. The latter has 8 branchial folds on the left and 9 on the right.

Genus **Herdmania** Lahille, 1888

Type species: *Cynthia momus* Savigny, 1816

The genus is monotypic, the only species being the pan-tropical *Herdmania momus*, characterised by remarkable barbed, calcareous needles

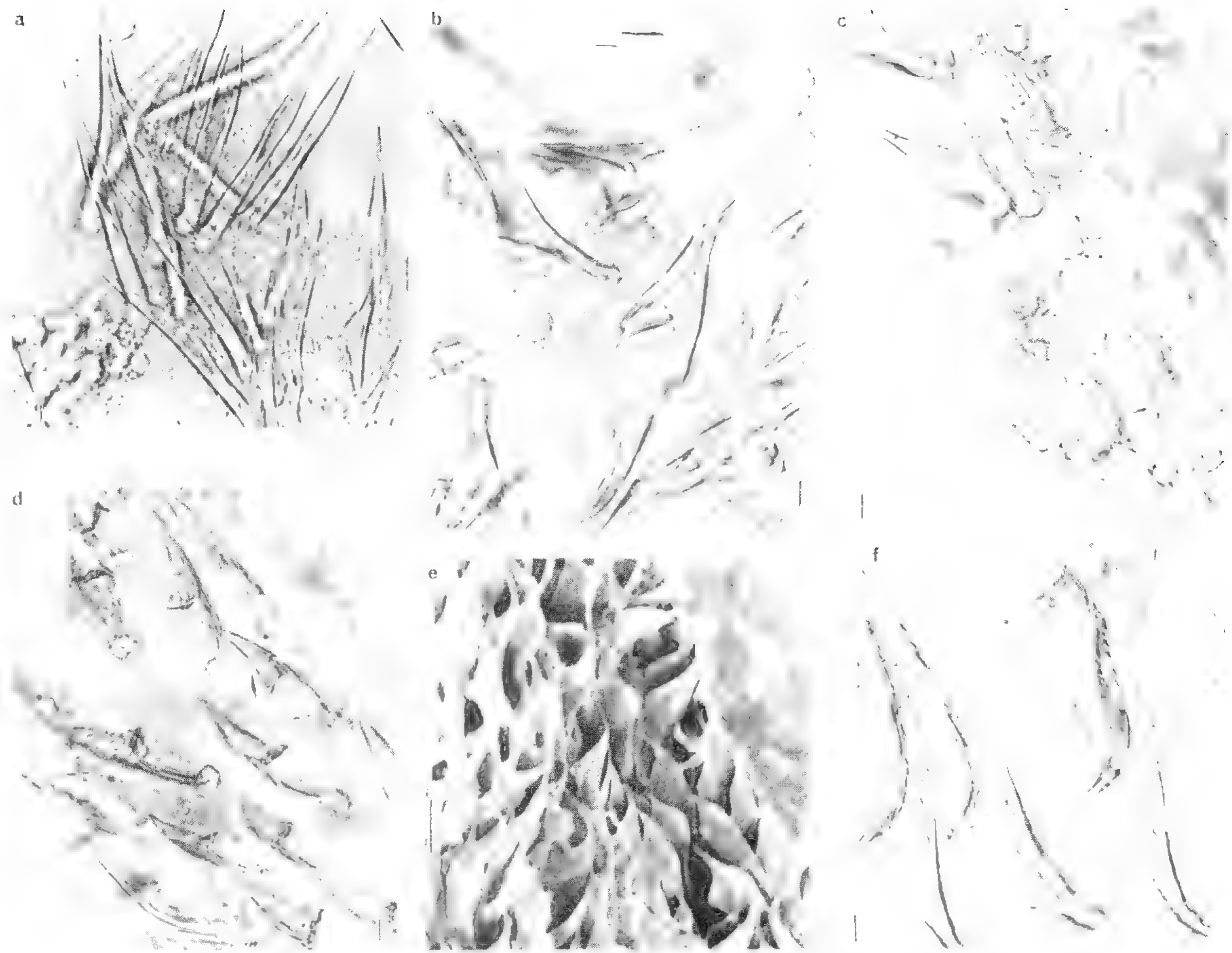


FIG. 167: *Ctenyura tortuosa* n.sp. (NMV H379) — **a**, siphonal spines. *Microcosmus australis* — **b**, siphonal spines. *Microcosmus exasperatus* — **c** - **e**, siphonal spines (**c**, basal view; **d**, profile; **e**, scanning electron micrograph). *Microcosmus madagascariensis* — **f**, siphonal spines. (Scales: 0.01 mm).

embedded in the body wall. *Herdmania momus* otherwise resembles *Pyura*, although its gonads remain entire and are not separated into polycarp-like sacs, and the small finger-like terminal lobules of the branching liver diverticula are grouped into compact clumps that are firmly embedded in the body wall around the pyloric part of the gut (rather than protruding into the atrial cavity as in *Pyura*). Individuals of this species are amongst the largest ascidians known, some reaching 20 cm in length. It is the only marine organism known to precipitate vaterite, rather than calcite or aragonite in its spicules (Lowenstam and Abbott 1975).

The genus is distinguished from *Ctenicella* by the position of the gonad (enclosed in the gut loop) and the presence of its long calcareous spicules.

Herdmania momus (Savigny, 1816)
(Pl. VIIe)

Cynthia momus Savigny, 1816, p.143.

Pyura momus: Michaelsen, 1918, f. typica p.9, f. pallida p.10; 1919, f. pallida p.30, f. kyamensis p.31, f. polana p.31, f. complanata p.54; 1921b, f. pallida p.1; 1934, f. pallida p.133. Van Name, 1921, f. pallida p.454; 1930, f. pallida p.498. Vasseur, 1967a, p.129. Michaelsen and Hartmeyer, 1927, f. galei p.194. Hartmeyer and Michaelsen, 1928, f. grandis p.441, f. galei p.443.

Herdmania momus: Michaelsen, 1919, p.30. Van Name, 1945, p.341. Tokioka, 1949b, f. grandis p.61; 1952, f. grandis p.137; 1953a, f. grandis p.277; 1961, f. galei p.132; 1967a, f. grandis p.206. Kott, 1952, f. galei p.281, f. curvata p.282, f. grandis p.279; 1964, f. grandis p.142, f. curvata p.143; 1966, f. grandis p.301; 1972a, p.41; 1972b, p. 189; 1976a, p.84; 1981, p.208. Millar, 1960b, p.126; 1963, p.740; 1966, p.374. Kott and Goodbody, 1982, p.548.

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

Halocynthia grandis: Michaelsen, 1905, p.85.

Cynthia pallida Heller, 1878, p.14. Herdman, 1881a, p.60; 1882, p.143; 1886, p.405. Traustedt, 1883a, pp.119, 133; 1885, p.35.

Rhabdocynthia pallida: Herdman, 1891, p.575; 1906, p.308. Sluiter, 1898a, p.25; 1904, p.54; 1905a, p.14; 1905c, p.102.

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

Pyura pallida: Michaelsen, 1908b, pp.269, 270. Hartmeyer, 1909, f. grandis p.1340.

Cynthia complanata Herdman, 1882, p.145.

Rhabdocynthia complanata: Herdman, 1891, p.577.

Microcosmus julinii Drasche, 1884, p.371. Herdman, 1891, p.575.

Microcosmus draschii Herdman, 1891, p.575.

DISTRIBUTION

NEW RECORDS: Western Australia (Rowley Shoals, WAM 1197-8.83; Exmouth Gulf, QM G9373; Broome, WAM 1187.83; Learmonth, WAM 1181.83 1184.83 1186.83; Carnarvon, WAM 1194.83; Port Hedland, WAM 1179.83, Houtman's Abrolhos, WAM 1199.83; Shark Bay, WAM 1180.83 1182.83 1185.83 1191-2.83 1196.83; Dirk Hartog I., WAM 1193.83 1195.83; Cockburn Sound, WAM 192.75 1183.83 1190.83). South Australia (St Vincent Gulf). Tasmania (Point Sorrell, TM D1852; Ninepin Pt., QM GH2017; Flinders I., TM D1190; Pardoe Beach, TM D1184). Victoria (Bass Strait, NMV H370 H414 H471 H791 F51578, QM GH933). New South Wales (Arrawarra, Iron Prince Reef, Lord Howe I.). Queensland (Moreton Bay, QM G10082 G12813 GH377; Mooloolaba, QM G10106; Hervey Bay, QM G9580; Heron I., QM G9514 G10030 G10165 GH351–2; Keppel I., QM G11999; NW of Bowen, QM GH658 GH673 GH751; Cleveland Bay, QM GH743; N of Innisfail, QM GH769–71; Lizard I., QM G9791).

PREVIOUSLY RECORDED: Western Australia (Geraldton to Albany — Hartmeyer and Michaelsen 1928, Kott 1952, Millar 1963). South Australia (Great Australian Bight, Investigator Strait, Spencer Gulf — Kott 1972b; West I., Wright I. — Kott 1972a). Victoria (Port Phillip Bay, Western Port — Kott 1952, Millar 1960 1963 1966). Tasmania (Kott 1952). New South Wales (Port Nelson, Port Stephens — Kott 1952; Port Jackson — Heller 1878; Herdman 1882, Drasche 1884, Millar 1963, Tokioka 1967a). Queensland (Capricorn Group, Bowen — Kott 1952). Arafura Sea (Tokioka 1952). Indonesia (Herdman 1886). Palau Is (Heller 1878). Fiji, Tahiti (Herdman 1882). Melanesia (Tokioka 1961). Marianas Is (Tokioka 1967a). Japan (Tokioka 1949b, 1967a). Sri Lanka (Herdman 1906). West Indian Ocean (Heller 1878, Michaelsen 1908b, Vasseur 1967a). Dar-es-Salaam (Michaelsen 1905). Red Sea (Savigny 1816, Michaelsen 1905). South Africa (Herdman 1882). Records are also from the Caribbean and West Indies and south to Rio de Janeiro (see Van Name 1945) but not from the eastern Pacific or from the eastern Atlantic or Mediterranean.

The species is pan-tropical, extending into temperate waters around South Africa and southern Australia in waters down to 100 m.

DESCRIPTION

EXTERNAL APPEARANCE: Small individuals (galei form) are almost spherical, slightly longer than their dorso-ventral height. The body is fixed by the posterior, postero-ventral or ventral surface. The apertures are either terminal and antero-dorsal respectively, or both on the upper surface and divergent. They are on short siphons, cylindrical to trumpet-shaped, and lined with red-pink and white bands in the living specimens. In smaller specimens (to 5 cm long), the test is translucent, smooth, a rosy-peach colour in life and whitish in preservative. The smaller specimens have spicules in the test as well as in the body wall.

In larger specimens (from 5 to 20 cm long), the test becomes opaque, leathery and covered with epiphytes, concealing the animals, except for the exposed red and white striped lining of their siphons. The siphons are turned away from one another, the branchial aperture often turned ventrally toward the substrate. In these larger specimens, the test is flaccid and has no spicules, and the outline of the body is irregular.

INTERNAL STRUCTURE: The body wall is muscular, with an external layer of circular muscles, and longitudinal bands from each siphon overlapping on the sides of the body. The most conspicuous aspect of the body wall are the long, white spicules embedded in it. The spicules have long shafts that taper to a point at each end. The shaft is encircled by regularly spaced rows of backward-projecting, short, pointed spines. There are long, branched, bushy tentacles. The dorsal tubercle is a large, flattened cushion with a V-shaped slit with spirally in-rolled horns. The slit becomes convoluted in larger specimens. The dorsal lamina has a single row of crowded languets.

The branchial sac also contains long, barbed spicules. There are 6 to 13 overlapping folds on each side of the body, the number apparently increasing with the age of the individual. There are from 10 to 30 internal longitudinal vessels on the folds and from 1 to 6 in the interspace, again depending on the age of the individual. Each mesh has up to 8 stigmata, though the largest individuals with more numerous longitudinal vessels often have only 3 to 5 stigmata per mesh.

The gut, an open D-shaped loop in the posterior end of the body, encloses the left gonad. In large specimens, the gut is deeply embedded in the thick, fleshy body wall. There are compact cauliflower-like patches of rounded to oval liver lobules embedded in the body wall and closely applied to the pyloric part of the gut loop. The anal border is lobed, the lobes becoming larger in larger specimens.

The single, long gonad on each side of the body consists primarily of a long ovary bordered by male follicles. The left gonad, enclosed in the gut loop, lies along the inside of the descending limb. The simple form of the gonads can be observed only in the smallest specimens. In larger specimens, the ovary appears to undulate and the male follicles appear to mix with the ovarian tissue.

REMARKS: Michaelsen (1919) reviewed the various forms of this species from several parts of the world. Kott (1972a) concluded that these probably represent different growth stages of a single species. The barbed, calcareous spicules are unique and readily distinguish the species.

Genus Ctenicella Lacaze Duthiers, 1877

(emend. Hartmeyer, 1911)

Type species: *Molgula appendiculata* Heller, 1877

Species of this genus have dorsal languets, as in the genus *Pyura*. The gonads are undivided and the male follicles are closely applied to the sides of the tubular ovary. The left gonad is outside the primary gut loop. The heart, a curved tube across the postero-ventral corner of the right side of the body ventral to the gonad, is hypertrophied and conspicuous. The liver is compact consisting of a number of tubular branching diverticula firmly embedded in the body wall. The stigmata are straight and do not form infundibula.

The position and form of the gonads and liver separate the genus from *Pyura*. It is most closely related to *Herdmania* from which it is distinguished by the position of its gonad and the absence of calcareous spicules.

Ctenicella undulata Tokioka, 1949 (from Japan) has an unusual liver, with proximal longitudinal liver folds in the pyloric region of the gut and a projecting clump of oval liver pouches distally. It does not resemble the stomach of any known pyurid genus. The species has been taken only once and its characters require confirmation.

The genus is not diverse. It is represented in Australia by a single, temperate, indigenous species. Apart from the unconfirmed record from Japan, the only other known species is the type, a common species from the Mediterranean (Harant 1933).

Ctenicella antipoda Kott, 1972
(Fig. 168)

Ctenicella antipoda Kott, 1972a, p.44.

DISTRIBUTION

NEW RECORDS: None

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — SAM I.E.4484–5 Kott 1972a).

The species has been recorded down to 20 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are up to 10 cm long, slightly dorso-ventrally flattened. They are very irregular externally and covered with rounded nodules that are especially common on the upper surface around the sessile apertures. In one specimen, the test around the apertures is elevated into a rounded ridge. Small, hard, brown papillae are present around the rim of the apertures. The test is up to 1.5 cm thick and entirely impregnated with sand, making it hard and rigid. There are no siphonal spines.

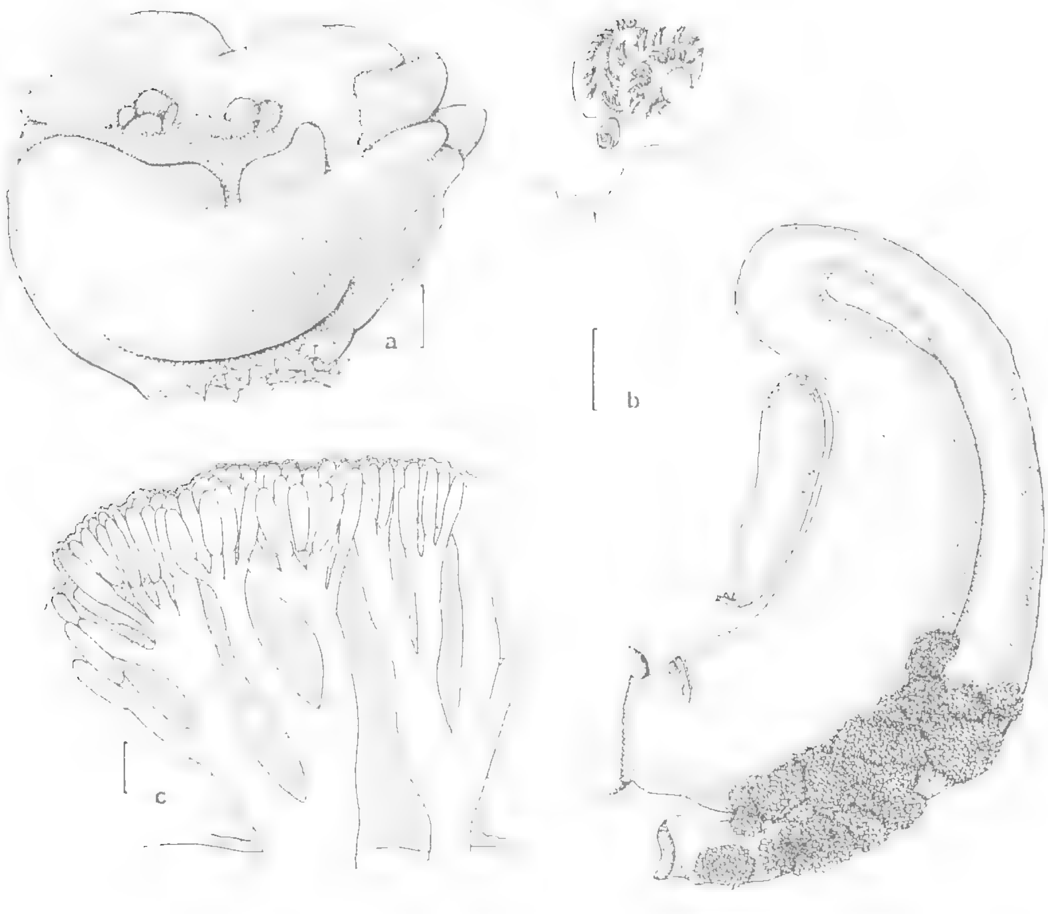


FIG. 168: *Ctenicella antipoda* (SAM I.E4485)—**a**, shape of body; **b**, left side of body showing some branchial tentacles, dorsal tubercle, prepharyngeal groove, gut loop and gonad; **c**, section through portion of liver perpendicular to surface of parietal body wall showing branched tubercles opening into gut and terminal lobules, all embedded in connective tissue of body wall. (Scales: **a**, 1.0 cm; **b**, 5.0 mm; **c**, 0.2 mm).

Internal Structure: The musculature is strong on the upper half of the body, with radiating longitudinal bands from each siphon and circular bands around each siphon and around the base of each siphon. On the ventral half of the body, two ventral strips of short parallel bands are the remnants of circular bands.

There are 15 large branchial tentacles with primary, secondary and minute tertiary branches. These alternate with rudimentary tentacles. The dorsal tubercle is at the base of the tentacles, in the anterior part of the wide V of the peritubercular area. It has a double-spiral slit, the open interval turned to the left. The dorsal lamina is short, with close-set, slender, pointed languets.

There are 6 wide, overlapping branchial folds on each side of the body. Internal longitudinal vessels are arranged according to the following formula: DL3(26)3(33)5(28)4(26)3(24)2(15)3E. There are about 12 straight, rectangular stigmata in each mesh, crossed by parastigmatic vessels.

The gut forms a narrow, only gently curved loop, slightly open at the pole. The descending limb is expanded and filled with mud. Numerous, branched liver diverticula open into the proximal half of the ascending limb of the gut loop. Their finger-like terminal lobules are crowded into clumps. Both the branching tubules and terminal lobules are embedded in connective tissue of the body wall and are thus held firmly in place, vertical to the gut wall. The anal border has about 30 or more rounded lobes.

On the right side of the body, the enlarged heart is a curved tube across the postero-ventral corner of the body, behind the right gonad.

There is a single gonad on each side. It is dorsal and parallel to the heart on the right, and to the gut loop on the left. Each gonad consists of a tubular ovary surrounded by groups of very small, pear-shaped male follicles, which sometimes extend over its mesial surface and project down into folds in its surface, where they appear to mingle with ovarian tissue. Vasa efferentia from each group of male follicles join a common vas deferens extending along the middle of the ovary to open with the oviduct. Both rectum and gonads curve dorsally and anteriorly to open at the base of the atrial siphon.

Remarks: In addition to the generic characters, this species is readily distinguished by its solid, sandy test, the large number of anal lobes, and the multiplicity of small branched liver diverticula.

Genus **Halocynthia** Verrill and Rathburn, 1879

Type species: *Ascidia papillosa* Linnaeus, 1767

The species of this genus form a closely related group in which the test is produced into stiff tubercles or spines that are especially long around the apertures. The stomach is bipartite. It is expanded into pronounced longitudinal glandular folds at the cardiac end. These taper in toward the pyloric end where there is a projecting collar of less regular and variably oriented lamellae with small rounded or finger shaped lobules along their edges. Between 2 and 6 large gonads on each side of the body extend parallel to one another across the descending limb of the gut loop. Each gonad has its own male and female apertures at the dorsal end. Male follicles are crowded along both sides of, and sometimes also beneath, the ovarian tubes.

The dorsal lamina has crowded languets, and there is usually a second row of lanquets on the right of the mid-line, as sometimes occurs in the genus *Pyura* (e.g., *Pyura abradata* n.sp. and *P. irregularis*). There is a tendency in the genus for the right gonad to be lost (Millar 1962a).

External test bristles similar to those characteristic of *Halocynthia* are known in *Hartmeyeria formosa* (see below) and in the genus *Boltenia* (see Van Name 1945); and a bipartite glandular stomach is known in some species of *Molgula* (e.g., *M. sabulosa*) and in *Hartmeyeria chinensis* Tokioka, 1967a and *Ctenicella undulata* Tokioka, 1949. However, it is unlikely that either the external bristles or stomach are indicative of phylogeny in these genera. Only in *Halocynthia* is the proximal part of the stomach so regular and symmetrical, with regular longitudinal folds that narrow distally. The multiplicity of gonads on each side of the body is also unusual in the *Pyuridae* and may be a primitive character indicating a relationship with the *Styelidae*. *Halocynthia* has several unique characters and is readily distinguished from other pyurid genera. Its affinities with those genera are obscure.

Species of the genus occur in the northern Pacific Ocean, southeast to California and southwest to Japan, and in the northern Atlantic, and the Mediterranean and Red Seas. Certain of these species have an extremely wide latitudinal range, e.g., *Halocynthia spinosa* Sluiter, 1905 from the Red Sea also occurs off South Africa (Millar 1962a). *Halocynthia hispida*, found on the southeastern and eastern coasts of Australia, appears to be conspecific with populations in Japan and Sri Lanka and, although unrecorded from Indonesia, the populations may be continuous. Kott (1968) suggested that this genus might be a relict of a Tethys Sea fauna, which would explain the distribution of species. Although arguments for this are highly speculative, the morphology of geographically distinct populations and species is so dramatically similar that it is unlikely to be the result of convergence, and an early origin from common ancestors is very probable.

KEY TO THE SPECIES OF *HALOCYNTHIA* RECORDED FROM AUSTRALIA

Test bristles branched and with secondary spines .... *H. papillosa*

Test bristles not branched and without secondary spines .... *H. hispida*

Halocynthia hispida (Herdman, 1881)
(Fig. 169; Pl.VIII)

Cynthia dumosa Stimpson, 1885b, p.388.
Cynthia hispida Herdman, 1881a, p.61; 1882, p.146.
Halocynthia hispida : Kott, 1952, var. typica p.283, var. crinitistellata p.284; 1954, var. crinitistellata p.129; 1968, p.77; 1972a, p.41; 1972b, p.189; 1975, p.15; 1976a, p.84. Millar, 1963, p.742.
Cynthia crinitistellata Herdman, 1899, p.34; 1906, p.313.

DISTRIBUTION

NEW RECORDS: South Australia (Kangaroo I., QM G11993; Knob I., QM G12002). Tasmania (off d'Entrecasteaux Channel; NW. coast, TM D986; Huon Channel, TM D1863; Bruny I., NMV F51586). Victoria (Bass Strait, NMV H412 H452 H466 H469 H733 H905 H925 F51538; Western Port QM GH2179; Flinders I., TM D1190). New South Wales (Port Hacking, QM GH39; Port Jackson). Queensland (Townsville, QM GH743 GH3034)

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf, Spencer Gulf — Kott 1968 1972a,b 1975). Tasmania (off d'Entrecasteaux Channel — Kott 1942; Maria I. — Kott 1954). Victoria (Bass Strait — Herdman 1882; Port Phillip — Millar 1963; Western Port — Kott 1976a). New South Wales (Port Jackson — Stimpson 1855b, Herdman 1899, Kott 1952). Sri Lanka (Herdman 1906).

DESCRIPTION

EXTERNAL APPEARANCE: The body is rounded and oval to spherical, with small, cylindrical or barrel-shaped siphons that are about one-third of the body length distant from one another. The siphons are often withdrawn, and each aperture is then surrounded by a roll of test. The apertures are made especially conspicuous by long, stiff, crowded bristles that project vertically from the test immediately around the opening. The surface of the remainder of the test is very variable, ranging from the *hispida* condition (smooth and even, without large projecting tubercles or bristles) to the *crinitistellata* condition (with tubercles and bristles). In the latter condition, tubercules are evenly distributed about 5 mm apart or sometimes irregularly scattered, usually with single, or groups of, long bristles (similar to those around the apertures) projecting from their surface or directly from the surface of the test. The tubercles and the bristles on them become progressively larger anteriorly. The bristles, which are sometimes branched, have a thick, straight stem up to 1 mm in diameter at the base and up to 4 mm long, narrowing terminally. There are circles of secondary spines at about 1 mm intervals up the stem with, between them, smaller, evenly spaced, pointed spinules.

Small papillae (about 1 mm high) are always crowded (almost confluent) on the surface of the test, interrupted only by tubercles and bristles when these are present. The papillae consist of a thick basal stalk and a crown of pointed processes. They give a downy appearance to the surface of the test, especially when it is otherwise smooth and even. Spinules, similar to those on the surface of the bristles, are also present on the tubercles, papillae and on the surface of the test between them. The test is moderately thick and is always tough and leathery externally.

The siphonal lining has scale-like swellings homologous with the papillae of the surface test and with the same surface spinules. Each scale has only a single point lower down the siphon.

INTERNAL STRUCTURE: The body wall has well-developed musculature with internal, radiating longitudinal bands and outer circular fibres. There are up to 16 branchial tentacles with well-developed primary branches and minute secondary branches. The dorsal tubercle is large, and its slit invariably forms a double spiral cone. There are crowded languets along the dorsal line, and a second row of less crowded processes on their right.

The branchial sac has 9 or 10 folds on each side of the body, but one of the folds about half way up each side is often rudimentary. There are up to 37 internal longitudinal vessels on each fold in large (5 cm or more) specimens and up to 18 in smaller (1.5 cm) specimens. There are 1 to 3 longitudinal vessels between the folds and 4 to 10 stigmata per mesh.

The gut loop is moderately narrow and deeply curved. The oesophagus is of moderate length. Its pyloric region is expanded, and has longitudinal glandular folds that narrow distally to a band of long folds projecting out from the narrow gut as

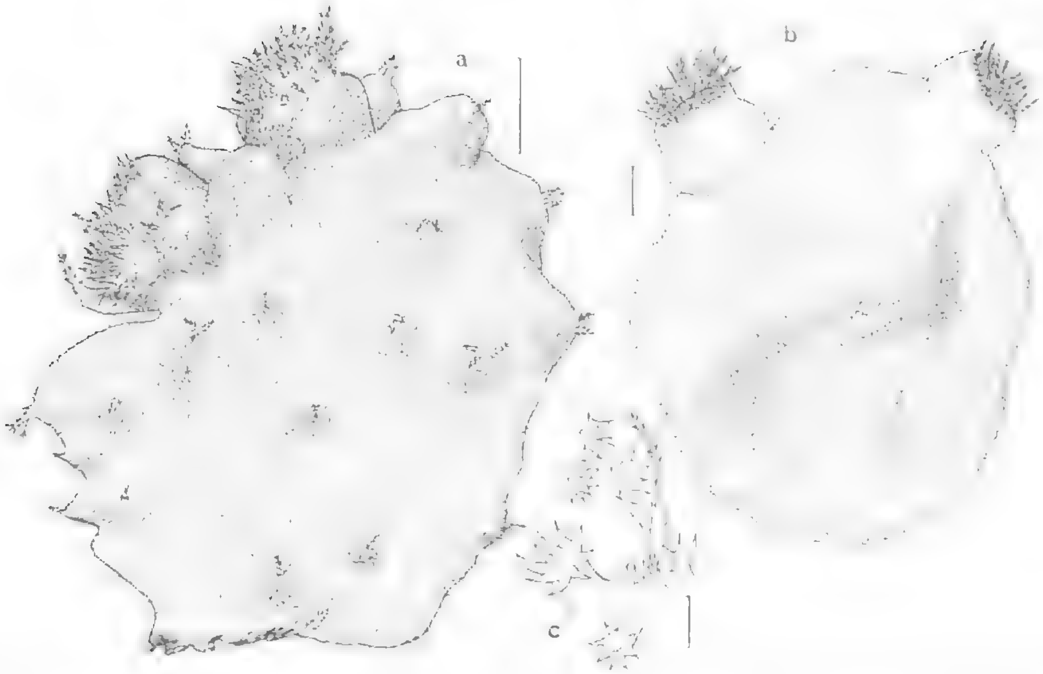


FIG. 169: *Halocynthia hispida* — a, b, external appearance (QM GH39, GH2179); c, test papillae and spines. (Scales: a, b, 5.0 mm; c, 0.25 mm).

a loose collar. These distal lamellae have numerous rounded or finger-shaped terminal lobules along their edge. The anal border is smooth and bilabiate.

The gonads consist of 2 to 10 parallel ovarian tubes, with male follicles along the sides, oriented at right angles to the antero-posterior axis of the body. On the left, the proximal ends of the gonads are in the gut loop, and they extend dorsally, across the descending limb of the gut loop, to terminate in short gonoducts near the atrial opening. The proximal part of the posterior gonad is bent up in the gut loop past the ends of those anterior to it, where the male follicles merge, causing the gonads to appear to be joined along their proximal ends. The male follicles along each side of the ovarian tubes fill the intervening spaces between the ovaries and sometimes extend beneath them, so that the whole gonad forms a compact mass covering an extensive part of the gut loop on the left and often occupying a large part of the body on the right. However, the right gonads are often missing or reduced.

REMARKS: Despite records from Sri Lanka (Herdman 1906) and Townsville, the majority of the Australian records are from temperate waters and there appears to be a discontinuity between the range of the Japanese and the temperate to tropical Australian species. Thus, species from the eastern Pacific and some Japanese species that were included in Kott's (1968) synonymy may be distinct from the present species. However, there are few morphological differences. The large test papillae of *H. cactus* Oka, 1932c (see Tokioka 1953a; Rho 1966a, 1966b) possibly represent a genetic difference from *H. hispida*. *Halocynthia okai* Ritter, 1907 from the eastern Pacific and its possible synonym, *H. igaboja* Oka, 1906 (see Huntsman 1912a, Van Name 1945) from the western side of the northern Pacific have long bristles randomly distributed over the surface of the test and do not have the supporting tubercles that are so often present in *H. hispida*. There is even less apparent difference between *H. hispida* and the northern temperate species *H. hilgendorfi* (Traustedt, 1885) from northern Japan (see Hartmeyer 1906; Oka 1935; Tokioka 1959a, 1962), which Tokioka (1959a) believed to be closely related to *H. igaboja* Oka. The species are obviously all closely related; their genetic status is far from resolved.

Halocynthia papillosa (Linnaeus, 1767)
(Fig. 170; Pl.VIIg)

Ascidia papillosa Linnaeus, 1767, p.1087.
Tethyum papillosum: Gunnerus, 1765, p.100.
Cynthia papillosa: Savigny, 1816, p.143. Heller, 1877, p.249. Lacaze-Duthiers and Délage, 1892, p.106. Roule, 1885, p.180. Herdman, 1891, p.576.
Ascidia rustica Risso, 1826, p.274.
Halocynthia papillosa: Hartmeyer, 1904, p.322. Michaelsen, 1918, p.10. Harant, 1929, p.66. Harant and Vernières, 1933, p.24. Pérès, 1958, p.161. Monniot, 1965, p.113. Kott, 1968, p.84.
Pyura papillosa: Hartmeyer, 1909, p.1340; 1912a, p.181.

DISTRIBUTION

NEW RECORDS: Queensland (Heron I., QM G7372).

PREVIOUSLY RECORDED: The species has previously been recorded from the Atlantic coast of France and in the Mediterranean, from amongst coralline algae, sand and shell and sand (Monniot 1965). The Queensland specimen from Heron I., was collected amongst coral debris at 13 m.

DESCRIPTION

EXTERNAL APPEARANCE: Upright, oval individual (3 cm high) with a terminal branchial aperture and an atrial aperture one-third of the distance down the dorsal surface. The apertures are on short, oval, slightly wrinkled siphons, constricted at their base. The root-like processes from a small area at the narrow posterior end of the body do not interrupt its even, oval outline. There are stiff, pointed spines (0.6 mm high) with wide conical bases (0.6 mm basal diameter) over the body, about 2 mm apart. There are longer (1.0 mm), narrow bristles at the ends of the siphons, immediately around the rim of the apertures, where they stand vertically in a crowded circle. The surfaces of both the bristles and the pointed spines are covered with minute spinules. There are also small scales with a papillated surface on the surface test between the bristles. The siphon lining, has conical, curved spines (about 0.1 mm long) with an oval, open base extending posteriorly and minute spinules on the outer surface, homologous with those on the surface of the bristles and surface spines.

The specimen is pink-red anteriorly in preservative. In life it was dark brown.

INTERNAL STRUCTURE: The branchial tentacles, which are not very bushy, have long primary branches, short secondary branches and minute tertiary branches. The dorsal ganglion is long. Near its anterior end is a minute rounded dorsal tubercle in the centre of the wide, open peritubercular area. The tubercle has a U-shaped slit directed anteriorly. The dorsal lamina is short,

FIG. 170: *Halocynthia papillosa* (QM G9372) — a, external appearance; b, gut and gonads; c, siphonal spines; d, spines and scales on test; e, spine from around apertures. (Scales: a, 5.0 mm; b, 2.0 mm; c, 0.05 mm; d, e, 0.1 mm).

and has a row of languets on each side of a wide, flat membrane.

There are 8 high, overlapping branchial folds on each side of the body, with up to 22 very evenly spaced internal longitudinal vessels on the folds, and 1 to 3 between.

The gut forms a wide, round loop in the postero-ventral part of the body. The loop is closed at its proximal end where the rectum makes a wide curve, its terminal part directed anteriorly to terminate in a smooth, bilabiate opening at the base of the atrial aperture. The oesophagus is moderately long and narrow. The stomach, which expands abruptly, has conspicuous longitudinal glandular folds that narrow toward the pyloric end. Here the folds curve and run obliquely and at right angles to those at the cardiac end of the stomach. Numerous upright, finger-like papillae or lobes project from the edge of each fold. There are also some upright lobules on the folds at the cardiac end of the stomach, but these are more sparse.

The two gonads on each side of the body meet ventrally to form a U. On the left, the base of the U runs antero-posteriorly, overlying the ascending limb of the gut loop. The parallel limbs of the U extend dorsally, in the secondary curve of the gut loop, converging to the atrial aperture. The gonads have the usual thick ovarian tube with branching male follicles around its border and beneath the ovary.

There are small endocarps scattered on the body wall anterior to the gut loop and the gonads.

REMARKS: The coincidence of habitat of this specimen and specimens of *H. papillosa* from the Mediterranean is surprising, in view of the great distance that separates the populations. No morphological differences have been detected. The oval body shape and oval siphons, constricted at the base are present in both and other characters are in complete agreement. Only a single specimen has been taken in Australian waters. Possibly, its cryptic habitat has resulted in its being overlooked by collectors. The species is distinguished from *H. hispida* by the absence of secondary spines on the bristles, and this, together with its U-shaped gonads and general body shape, establishes its identity.

Genus Microcosmus Heller, 1877

Type species: *Microcosmus vulgaris* Heller, 1877

A genus of the family Pyuridae with a plain, smooth-edged dorsal lamina. There are 6 or more wide branchial folds, usually with narrow interspaces with 1 or 2, and seldom more than 4, longitudinal vessels. A compact liver is formed by groups of parallel, relatively shallow elongate pouches that project out from the gut wall in the pyloric region. The single gonad on each side of the body has at least its distal part outside the primary gut loop, so that the gonoducts open anterior to the anal opening rather than between it and the oesophagus (as they do in *Pyura*). The gonads usually are long. They are sometimes undivided, but more often are divided into a single series of up to 4 lobes connected by the common ducts. The opening of the neural gland is usually symmetrical, both horns turning or spiralling inwards.

Species of this genus are robust, with a tough and often irregular or sandy test. The test appears to have strong adhesive qualities, and in most species has a remarkable capacity to develop irregular processes that help fix the individual firmly to hard substrates. Individuals are often found in aggregates, which results in some variability in the shape of the body and orientation of the siphons.

Minute, long, pointed, flattened spines; or short, rounded, and rather wide, scales; or hollow, conical or curved spines overlap one another in the siphonal lining, although there is less diversity in the form of the siphonal armature than in *Pyura*. Both flattened spines and rounded scales have a long, open base, with the upper border of the opening indented in the centre. Hollow, pointed, needle-like or curved spines occur less frequently in *Microcosmus* than they do in *Pyura*. The siphonal armature constitutes one of the very few reliable specific characters in this genus, which has a high degree of intraspecific variability but little interspecific morphological diversity.

Microcosmus stoloniferus and *M. planus* are the only species in the genus with short gonads, completely outside the gut loop, and short gonoducts opening a long way from the atrial aperture. In these two species, the male follicles are branched and spread out into the body wall some distance from the ovary. They do not form a compact mass with the ovary, as is more usual in the genus *Microcosmus*. These gonads are molgulid-like and similar to those in the genus *Hartmeyeria*. However, *Microcosmus stoloniferus* and *M. planus* do not have the long, thin stalk and branchial infundibula of *Hartmeyeria*.

More than half the species recorded in Australia are indigenous, usually from temperate waters, although some extend into the tropics. The remainder of the species collected in Australia have a wide range in the western Pacific and the Indian Ocean. The species that are most commonly recorded from most parts of the Australian continental shelf (*M. exasperatus* and *M. helleri*) are pan-tropical in their range. The genus is not represented in Antarctic waters; the affinities of the Australian species are more likely with the tropical fauna than with that of the Southern Ocean.

KEY TO THE SPECIES OF *MICROCOSMUS* RECORDED FROM AUSTRALIA

1. Left gonad entirely outside primary gut loop ....
   Left gonad partly enclosed in primary gut loop 3
2. Gonads rounded; body rounded .... *M. stoloniferus*
   Gonads elongate; body a laterally flattened one .... *M. planus*
3. Cartilaginous tongues at base of siphon; 6 branchial folds .... *M. helleri*
   No cartilaginous tongues at base of siphon; 6 or more branchial folds 4
4. Siphonal armature only rounded scales .... *M. squamiger*

TABLE XVII — SUMMARY OF CHARACTERS OF THE SPECIES OF *MICROCOSMUS* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australian waters	[2]Range in Australian waters	Dorsal tubercle	Siphonal armature: shape	Siphonal armature: size (mm)	Branchial folds	[3]Branchial sac	Gonads: shape; position	Additional features
M. helleri	Pan-tr	circum-Aust.	double spiral	—	—	6–6	3(20);8–10	divided; cross gut	cartilaginous tongues at base of branchial siphon papillated liver
M. tuberculatus n.sp.	—	Swain Reefs	horns turned in	conical spines	0.2	7–7	3–4(16);8	"	papillated liver
M. propinquus	—	SA - Moreton Bay	"	rounded scales & conical spines	0.02 0.06	6–7	1–3(20);10–15	"	"
M. squamiger	Red Sea	Broome - Bowen	double spiral	rounded scales	0.02	8–9	2–4(25);10–12	"	pocket values in siphon lining
M. exasperatus	Pan-tr	Western Port - Cockburn Sd	"	flattened spines	0.05	"	2–4(20);5–6	"	"
M. australis	WP	Bass St - Cockburn Sd	"	"	0.1	7–9	2–4(20);4–6	"	"
M. madagasca-riensis	Indian Ocean	Broome - Albany	horns turned in	flattened spines	0.14	7–7	1–3(18);6–8	entire branched; sometimes cross gut	deeply curved gut loop; papillated liver
M. stoloniferus	—	SA - Lizard I.	"	"	0.1	6–8	0(24);8–9	entire; outside gut loop	stalked; endocarps present
M. planus	—	SA	"	"	0.03	7–7	0(6);8	entire; outside gut	laterally flattened body; brittle sandy test
M. pupa	Indian Ocean	Princess Charlotte Bay	"	needle-like spines	0.15	7–7	3–4(24);4	entire; cross gut	♂ follicles spread out in body wall

[1]Pan-tr, pantropical; WP, western Pacific. [2]Range given anti-clockwise around the continent. [3]Internal longitudinal vessels; between folds (on folds); stigmata/mesh.

Siphonal armature not only rounded scales 5
5. Stigmata 10–15 per mesh; siphonal spines and scales .... *M. propinquus*
Stigmata fewer than 10 per mesh; siphonal spines only present 6
6. Siphon lining with conical, pointed spines .... *M. tuberculatus*
Siphon lining with flat, pointed spines 7
7. Siphonal spines with completely open base 8
Siphonal spines with partially closed base .... *M. pupa*
8. Siphonal spines less than 0.07 mm .... *M. exasperatus*
Siphonal spines greater than 0.08 mm........ 9
9. Sand embedded in test; deeply curved gut loop...................... *M. madagascariensis*
Sand not embedded in test; gently curved gut loop................................ *M. australis*

The following species have been recorded from the Indo-West Pacific, but not from Australia:

Microcosmus arenaceus Sluiter, 1904, a sandy species that resembles *M. helleri*, is distinguished by its complex and interrupted dorsal tubercle and papillae on the parastigmatic vessels at their junctions with the interstigmatic bars.

Microcosmus curvus Tokioka, 1954a; 1967a, from the Palau Is and western Pacific, has very much lobed (but not divided) gonads, 7 or 8 branchial folds with up to 17 internal longitudinal vessels on the folds, 1 or 2 (rarely 3) vessels in the interspace, 3 to 5 stigmata per mesh and very small siphonal spines. The species is distinguished from *M. madagascariensis* by the two last characters.

Microcosmus miniaceus Sluiter, 1900a, a stalked species from Hawaii, also has papillae between the stigmata and on the longitudinal vessels.

Microcosmus multiplicatus Tokioka, 1952, from the Arafura Sea, has 10 to 12 branchial folds and siphonal spines up to 0.35 mm long.

Microcosmus australis Herdman, 1899
(Figs 167b, 171)

Microcosmus australis Herdman, 1899, p.23. Kott, 1972e, p.53. Kott and Goodbody, 1982, p.546. (Not: Millar, 1963, p.741, < *M. exasperatus*. Kott, 1966, p.302; 1972c, p.245; 1976a, p.85, < *M. exasperatus*).
Microcosmus ramsayi Herdman, 1899, p.25.
Microcosmus claudicans : Hartmeyer and Michaelsen, 1928, var. exasperatus p.403.
Microcosmus exasperatus : ?Van Name, 1918, p.82. Tokioka, 1967a, p.207 (part, specimen from Hsia-men).

Distribution

New Records: Western Australia (Shark Bay, QM G9364; Cockburn Sound, WAM 5.75 146.95). Victoria (Bass Strait, NMV H374). New South Wales (Port Jackson, BM 1881.10.6.47). Queensland (Moreton Bay, QM G5140 G5142 G6085 G10067 G10080 G11981 G12715 GH342 GH346; Hervey Bay, QM GH2177; Bundaberg, QM GH2176; Gladstone, QM G9783 G10061; Wistari Reef, QM G11918; Heron I., QM G10065; NW of Bowen, GH667; Lizard I., QM GH2341).

Previously Recorded: Western Australia (Hartmeyer and Michaelsen 1928). New South Wales (Port Jackson — Herdman 1899). Northern Territory (Gulf of Carpentaria — Kott 1972e). ? Philippines (Van Name 1918). China (Hsia-men — Tokioka 1967a). Hong Kong (Kott and Goodbody 1982).

The species appears to have a range in the tropical latitudes of the western Pacific, extending into temperate waters off China and down the eastern and western coasts of Australia.

Description

External Appearance: Individuals are either upright, up to 5 cm high, the body narrowing anteriorly and the atrial aperture about two-thirds of the body length distant from the terminal branchial aperture; or they are fixed ventrally, with both apertures on the upper surface and turned away from each other. The test is moderately thin and very tough, usually naked, but sometimes with some epibionts. Living specimens are purple, but in preservative become peach coloured to white. The test is sometimes rough and wrinkled, but often smooth and shiny. Some individuals appear to have their posterior end embedded in soft substrates. The outer surface is covered with minute, pointed spines, which may confer a downy appearance. They continue into the terminal part of the siphon lining, where they become crowded and overlapping. They are relatively long (0.08 to 0.10 mm), hollow and flattened for most of their length. The base of the spines is almost at right angles to the surface of the siphon lining and the antero-posterior axis of the open base. The distal part of the spine is long and curves forwards. The posterior rim of the oval, open base is expanded into a knob that bends forwards to form a small hook. The hook is not present in the spines towards the base of the siphon, in which the posterior end of the long outer surface is flat and scale-like.

Internal Structure: Four pockets in the siphon lining form a cuspid valve at the base of the siphon. In fresh material, the siphons are lined with red stripes. The tentacles are rather long and bushy. The dorsal tubercle is large, and both horns of the slit spiral inwards. The dorsal lamina is long.

FIG. 171: *Microcosmus australis* — a, b, external appearance (QM G10067, G9364); c, gonads from right side of body (QM G10080, specimen with two gonads on right). (Scales: a, b, 1.0 cm; c, 2.0 mm).

The branchial sac is tough, with 7 to 9 moderately high branchial folds on each side. There are up to 20 internal longitudinal vessels crowded on a fold, although in many specimens the maximum number is 10. The interspace has 2 to 4. There are 4 to 6 stigmata per mesh.

The gut forms a narrow, deeply curved loop. The expanded pyloric region has numerous, crowded clusters of parallel glandular lamellae. The anal border is bilabiate.

The gonads are divided into 3 or 4 separate blocks, with common ducts extending between them. The proximal part of the left gonad crosses the descending limb of the gut loop. One specimen (QM G10080) has two gonads on the left.

REMARKS: The species is very closely related to *M. exasperatus*, but can be distinguished by its longer and more upright siphonal spines. In the Scanning Electron Microscope, these are seen to have rolled in around their longitudinal axis, appearing long and needle-like (see Kott and Goodbody 1982). In *M. exasperatus* the horns of the dorsal tubercle slit coil inwards to a greater extent than in the present species, and the branchial folds tend to have fewer longitudinal vessels; however, these characters are variable and by themselves are unreliable for species determination.

Molgula madagascariensis Michaelsen has similar siphonal armature to the present species, but its, gonads, although lobed, are not divided into separate blocks.

Microcosmus exasperatus Heller, 1878
(Figs 167c-e, 172)

Microcosmus exasperatus Heller, 1878, p.17. Michaelsen, 1908b, f. typica p.272. Van Name, 1945, p.346 (and synonyms from Atlantic locations). Tokioka, 1952, p.130. Vasseur, 1967a, p.120; 1967b, p.142. Kott, 1981, p.206.

Microcosmus variegatus Heller, 1878, p.17. Traustedt, 1883a, p.122; 1885, p.42.

Microcosmus distans Heller, 1878, p.18.

Microcosmus haemisphaerium Sluiter, 1904, p.52.

Microcosmus claudicans: Hartmeyer and Michaelsen, 1928, var. australis p.402. Kott, 1952, var. australis p.286.

Microcosmus australis: Millar, 1963, p.741. Kott, 1966, p.302; 1972c, p.245; 1976a, p.85.

Microcosmus hirsutus: Sluiter, 1913, p.70; (not: 1900a, p.30)

DISTRIBUTION

NEW RECORDS: Western Australia (Montebello I., WAM 1164.83 1173.83 1175.83; Dampier Archipelago, WAM 1165.83 1171.83; Cape Preston, WAM 1163.83; Carnarvon, WAM 1168-70.83; Shark Bay, WAM 1167.83 1172.83 1174.83; Cockburn Sound, WAM 68.72 106.72 117.72 125.72 221.73). Queensland (Tallebudgera Creek, QM GH2170; Moreton Bay, QM G9569 G9957 GH346 GH2171 GH2175; Fraser I., QM GH3103; Mary River Heads, QM GH2174; Hervey Bay, QM G9365-6 GH1450 GH2172; Gladstone, QM G9783; Heron I., QM GH2173 GH2677 GH2970 GH3106; Wistari Reef, QM G11918 GH3018; Abbot Point, QM GH752; Townsville, QM GH753; Cooktown, QM GH786).

PREVIOUSLY RECORDED: Northern Australia (Arafura Sea, Geraldton, Darwin, Thursday I. — Tokioka 1952, Kott 1952 1966). Victoria (Western Port — Kott 1976a; Port Phillip Bay — Millar 1963). New South Wales (Heller 1878). Queensland (Moreton Bay, Hervey Bay — Kott 1952 1966 1972c). Indonesia (Sluiter 1904 1913). New Caledonia (Vasseur 1967b). Fiji (Kott 1981). Formosa (Michaelsen 1908b). West Indian Ocean (Michaelsen 1908b, Vasseur 1967a). West Indies (Heller 1878, Traustedt 1882, Michaelsen 1908b, Van Name 1902).

The species appears to be pan-tropical, but extends into the temperate waters of southern Australia and Formosa. On the Australian coast, it extends around the southeastern corner of the continent, but has not been recorded across the southern coast.

DESCRIPTION

EXTERNAL APPEARANCE: The external appearance of this species is extremely variable. The body is often upright, narrowing anteriorly to a terminal branchial aperture. The atrial aperture is about two-thirds of the body length distant and is either sessile or is on a siphon of variable length, diverging from the branchial aperture or directed parallel to it. Sometimes both apertures are on short siphons on the upper surface, directed away from one another. The test is moderately thick. It is translucent and cartilaginous internally, but externally is opaque and very tough. Sometimes it is produced into a short ventral stalk. It is usually (though not always) rough and wrinkled on the surface. Individuals often occur in very tight aggregates. In preservative they are white, pinkish or reddish brown. Living specimens are reddish-brown.

Short, flattened, but pointed branchial spines line the outer part of the siphons and extend onto the external surface around the apertures. The spines are 0.04 to 0.05 mm long, curved around their long axis. Their open base (where it is embedded in the body wall) is half the total length. The widest part of the spine is at the level of the anterior border of the open base. Anteriorly, the spine tapers abruptly to the terminal point. It also narrows posteriorly, but swells to a small, knob at the proximal tip. This knob bends anteriorly to form a small hook. It is absent from the spines toward the base of the siphons, which flatten out posteriorly. The spines lie almost flat along the wall of the siphon.

INTERNAL STRUCTURE: There are 4 pockets in the siphon lining, which form a cuspid valve at the base of the branchial siphon. The branchial tentacles are long but not bushy. They have slender primary branches of moderate length, but only a few, very small secondary branches; tertiary branches are minute or absent altogether. The dorsal tubercle is moderately large. The slit is a large, deep, U-shape, with both horns turned in. These do not spiral more than once. The dorsal lamina is long.

There are 8 or 9 branchial folds on each side of the body, with up to 20 internal longitudinal vessels on the folds and, in larger specimens, up to 4 in the interspace. Each mesh has 5 or 6 stigmata, crossed by parastigmatic vessels.

The gut forms a narrow, deeply curved loop, and the liver consists of many clusters of crowded, parallel lamellae. The anal border is smooth and bilabiate. Each gonad is divided into 3 blocks, the proximal one on the left crossing the descending limb of, and becoming enclosed in, the gut loop.

REMARKS: The species is distinguished from *M. squamiger* by its short, wide, pointed, spines (rather than rounded scales). Also, the dorsal

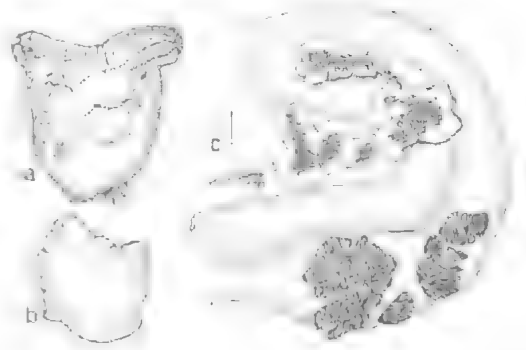


FIG. 172: *Microcosmus exasperatus* — **a**, **b**, external appearance (QM GH346); **c**, gut and gonad (QM G9957). (Scales: **a**, 1.0 cm; **b**, 5.0 mm; **c**, 1.0 mm).

tubercle slit coils only very few times, in contrast to the double spiral cone in *M. squamiger* and *M. australis*.

The relationship between the present species and *M. australis* is very close indeed, and the fact that the two species are sympatric for at least part of their range has resulted in considerable confusion. The distinction between the two species is based primarily on the overall length of the siphonal spines and on their curvature, the present species having shorter spines that extend in a more or less straight line from their posterior end, while in *M. australis* the basal part of the curved point stands almost perpendicular to the base of the spine and the surface of the siphon lining.

Microcosmus helleri Herdman, 1882
(Fig. 173)

Microcosmus helleri Herdman, 1882, p.131. Sluiter, 1895, p.184. Hartmeyer, 1919, p.19. Hartmeyer and Michaelsen, 1928, p.397. Hastings, 1931, p.72. Van Name, 1945, p.349. Kott, 1952, p.292; 1972a, p.43; 1972e, p.54; 1976a, p.85. Millar, 1963, p.742.

Microcosmus goanus Michaelsen, 1918, p.12.

Microcosmus manaarensis Herdman, 1906, p.311. Millar, 1975, p.309.

DISTRIBUTION

NEW RECORDS: Western Australia (Port Hedland, WAM 1178.83; Cockburn Sound, BM 1861.9.20.19, WAM 168.75 1177.83). Victoria (Western Port, NMV). Queensland (Point Vernon, QM G9365 G9366; Gladstone Harbour, QM G9683 G9715 G9718 G9803; NW of Bowen, QM GH662 GH667 GH672 GH747 GH2326 GH2329 GH2330; Townsville, QM GH754 GH2337 GH2338 GH2339; Mission Beach, QM G4983; Lizard I., QM GH2169 GH2679; Nymph I., QM GH2334; Princess Charlotte Bay, QM GH2168 GH2333; Thursday I., QM G9812 G9815; Murray I., QM G9813-5; off Cairns, QM GH782-3 GH2320 GH2324; off

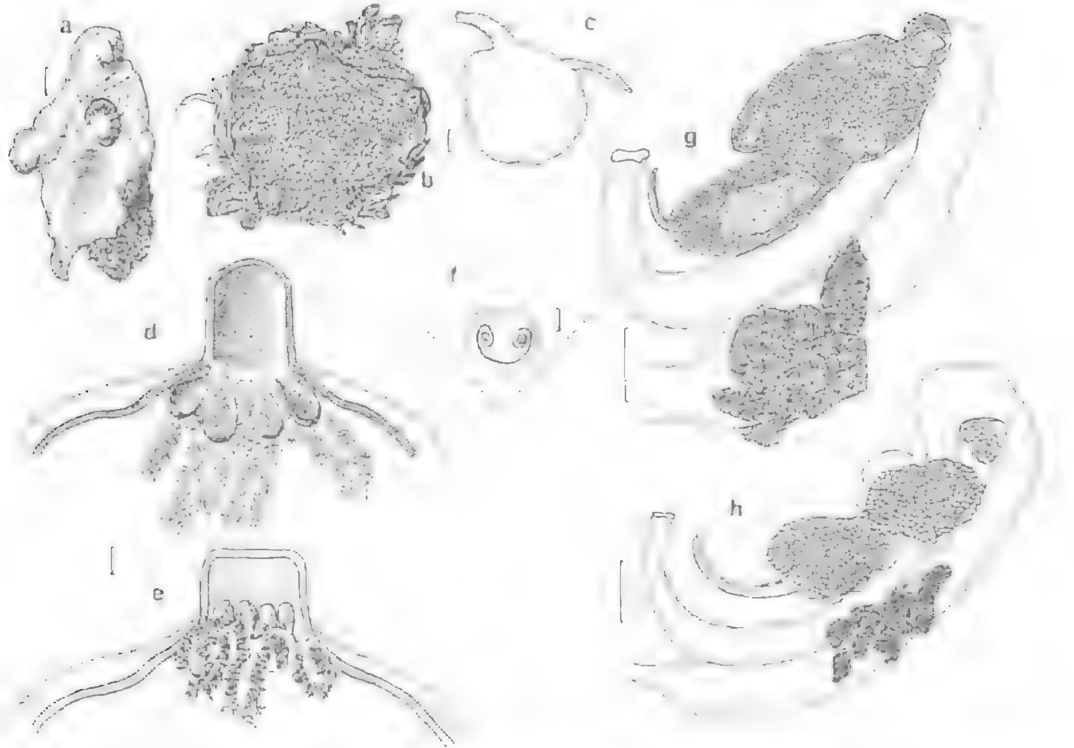


FIG. 173: *Microcosmus helleri* — a, b, external appearance (QM G9815, G4983); c, body removed from test (QM G4983); d, e, branchial siphon, showing cartilaginous tongues open and closed, respectively (QM G4983); f, dorsal tubercle (QM G4983); g, h, gut and gonad (QM GH662, GH782). (Scales: a, 1.0 cm; b, c, 2.0 mm; d, e, 1.0 mm; f, 0.5 mm; g, h, 5.0 mm).

Mossman, QM GH2325; off Cooktown, QM GH784 GH2332; off Murdoch Pt., QM GH2331; Weymouth Bay, QM GH2336; Barrow Point, QM GH2335).

PREVIOUSLY RECORDED: Western Australia (Cape Jaubert to Fremantle — Hartmeyer 1919, Hartmeyer and Michaelsen 1928, Millar 1963; Trigg I. — Kott 1952). South Australia (St Vincent Gulf — Kott 1972a). Victoria (Western Port — Kott 1976a). Queensland (Great Barrier Reef — BM 1930.12.17.4 Hastings 1931, Kott 1952). Northern Australia (Torres Strait — Herdman 1882; Gulf of Carpentaria — Kott 1972e). Singapore, Java Sea (Millar 1975). Sri Lanka (BM 1907.8.30.11 Herdman 1906). Indonesia (Sluiter 1895). East Africa (Michaelsen 1918). West Indies (holotype BM 1887.2.4.44 Herdman 1882, Van Name 1945).

The species has a range in tropical waters of the western Atlantic and Indo-West Pacific, but has not been recorded from the eastern Atlantic. In Australia, it extends around the continent and into temperate waters.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are more or less rounded, up to 6 cm in diameter. They often occur in aggregates. In some specimens, the tough, cartilaginous and opaque white test is largely naked and irregular, with creases and wrinkles and some projecting tubercles or processes, especially on the ventral or posterior surface, where they adhere to, or form roots in, the substrate. In other specimens, the test is thin, translucent and thickly coated with sand, which adheres to irregular branching and anastoming processes and strands of test. The siphons are invariably naked and project from this protective casing, which is often irregular, and up to 1 cm thick. Sometimes sand is embedded in the test, making it very brittle. The condition of the surface test, with or without its coat of sand, appears to be a response to the habitat of the individual. Specimens with both conditions occur at the same location, and some individuals even have thick sand adhering to parts of the test, while elsewhere they are naked. The test is pinkish and translucent in juvenile specimens. It is white and glistening internally.

The apertures are on siphons of variable length at opposite ends of the upper surface and turned away from one another. There are often pointed or rounded tuberosities on the test that shield the apertures, and often a thickened ridge of test between the apertures.

There are neither spines nor scales in the siphon lining.

INTERNAL STRUCTURE: The body wall has strong musculature on its upper half, but is delicate ventrally. The most distinctive feature of this species is the group of 4 tongue-like, rather hard, cartilaginous processes just anterior to the branchial tentacles. They are associated with the sphincter muscle at the base of the tentacles. The processes sometimes project forwards; sometimes they are at right angles to the siphonal wall, occluding the lumen; and sometimes they project backwards into the lumen of the pharynx, covering the tentacles (which lie against the branchial sac) and form a canal into the pharynx. The last appears to be the feeding position. In this position, only the tips of the tentacles project beyond the end of the lobes, and they curve inwards over the end of the canal leading into the pharynx.

The body wall is purple and closely adherent to the test. The muscles radiate from each of the siphons to form a mesh over the sides of the body. The internal siphons are sometimes very long and thin and are always directed away from one another. The dorsal tubercle is large, its slit forming a double spiral. The dorsal lamina is a very long, plain-edged membrane, the oesophageal opening being at the posterior end of the branchial sac. The atrial velum is wide and membranous and divided into 3 wide lobes. These are not thickened and cartilaginous like the branchial tongues.

The 6 high, overlapping branchial folds on each side of the body are quite straight, not curving up to terminate around the oesophageal opening, but joining a retropharyngeal groove along the posterior end of the branchial sac. The internal longitudinal vessels are well spaced, both on the folds and in the interspace. There are about 3 internal longitudinal vessels in the interspace and 15 to 20 on the folds, with 8 to 10 stigmata per mesh.

The gut loop is long, narrow and gently curved. It is open only at the pole and occupies most of the ventral curve of the body. There are tight clusters of parallel liver lamellae in the pyloric region, with upright papillae on their surface. The anal border is smooth. The oesophagus is short, but the rectum is moderately long, curving forwards to the atrial aperture.

On the left, the gonad is divided into 3 or 4 separate blocks, the proximal block of the left gonad crossing over into the gut loop. An endocarp is present on each block of the gonad and on the pole of the gut loop. The right gonad is sometimes entire and not subdivided.

REMARKS: The species is characterised principally by the remarkable cartilaginous tongues that protect the branchial aperture and create a passage down into the lumen of the pharynx when in the open position, and also by the conspicuously diverging siphons, and 6 broad, straight, branchial folds.

The Australian specimens are identical with West Indies material (holotype BM 1887.2.4.44 and BM 1931.5.4.3 from St Vincent). The holotype is naked, but the latter specimen has thin test with sand-entangled test processes that form a capsule around the specimen. The Atlantic populations therefore show the same variation in the condition of the test as is found in the Indo-Pacific material.

The cartilaginous tongues appear to develop from pocket valves at the base of the siphons, similar to those in *M. squamiger*, *M. exasperatus* and *M. australis*. In *M. helleri* the valve becomes considerably extended and projects back into the pharynx, and its membranous wall is thickened.

Microcosmus madagascariensis Michaelsen, 1918
(Figs 167F, 174)

Microcosmus sulcatus Michaelsen, 1915, p.378 (part, specimen from Madagascar).

Microscosmus madagascariensis Michaelsen, 1918, p.20. Hartmeyer and Michaelsen, 1928, p.398. Vasseur, 1969, p.929.

Microcosmus agglutinans Hartmeyer, 1919, p.26.

DISTRIBUTION

NEW RECORDS: Western Australia (Broome, BM 1903.9.23.2).

PREVIOUSLY RECORDED: Northwestern Australia (Cape Jaubert — Hartmeyer 1919; Port Hedland, Shark Bay, Cockburn Sound, Albany — Hartmeyer and Michaelsen 1928). Malagasy (Michaelsen 1918, Vasseur 1969).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens up to 9 cm are known. The body is an upright, irregular oval shape, slightly laterally flattened, with a terminal branchial aperture and an antero-dorsal atrial aperture. The apertures are on siphons of variable length with the atrial siphon sometimes the longer of the two and produced anteriorly parallel to the branchial siphon so that the apertures open at more or less the same level. The atrial aperture is directed upwards; the branchial aperture is turned away from it. The siphons originate very close together. The lobes around each aperture are free of sand. There are some irregular furrows and creases on the outer surface, and 4 longitudinal furrows on each siphon. Surface irregularities are obscured by a layer of embedded sand. The test is often rather thin, tough and rigid with sand. The internal test is pearly. The test has occasional irregular processes, to which sand adheres. They are especially common at the posterior end of the body, where they fix the animal to the substrate.

Overlapping, pointed spines line the siphons. They are 0.075 to 0.14 mm long and have a long, open base as in *M. exasperatus*, *M. australis* and other species of the genus. These spines continue almost to the base of the siphons and extend anteriorly out onto the external surface of the test, where they can be seen on the sand-free lobes around the apertures.

INTERNAL STRUCTURE: The body is semitransparent, but the musculature is well-developed, although the longitudinal radiating bands do not extend onto the ventral half of the body. There is a layer of circular muscle posterior to the circular siphonal muscles. In the base of the siphonal lining, is a papillated zone with longer, thread-like projections scattered amongst the smaller papillae. The 12 branchial tentacles are bushy, with up to 4 orders of branching. Rudimentary tentacles alternate with the larger ones. The dorsal tubercle is a conspicuous, oval cushion. The U-shaped tubercular slit has both horns turned in and its open interval directed anteriorly. The peritubercular area is very shallow, the prepharyngeal groove extending in an almost straight line across the anterior end of the dorsal lamina. The prepharyngeal area is narrow. The dorsal lamina is narrow and long, the oesophageal opening being at the posterior end of the body.

The 7 branchial folds on each side of the body are high and overlapping. Up to 18 wide and strong internal longitudinal vessels are crowded on the folds, with usually fewer than 3 in the interspaces. The branchial formula for a specimen of about 3 cm is: E0(9)1(12)1(18)1(15)1(15)1(14)1(16)3DL3. The stigmata (6 to 8 per mesh) are crossed by parastigmatic vessels. The branchial folds, which are relatively straight, extend from the prepharyngeal to the retropharyngeal groove.

The gut forms a narrow, deeply curved loop, open at the pole and extending forwards almost to the prepharyngeal groove. The oesophagus is short and broad. It expands abruptly into a pear-shaped stomach. The stomach wall expands into circular clumps of crowded, glandular liver lamellae,

FIG. 174: *Microcosmus madagascariensis* (BM 1930.9.23.2)—a, external appearance; b, body removed from test; c, dorsal tubercle; d, gut with endocarps and gonad; e, gonad and endocarps on right. (Scales: a, b, 5.0 mm; c, 1.0 mm; d, e, 2.5 mm).

which are covered with long tapering, sometimes curved, papillae that line the peribranchial cavity. The stomach gradually reduces in diameter to the intestine. The long rectum turns anteriorly, terminating in a smooth, bilabiate anal opening near the atrial aperture at a point level with the pole of the gut loop.

There is a single oval gonad on each side of the body. These organs are branched, but not divided, and are embedded in endocarp-like thickenings of the body wall. The gonad on the left sometimes, though not always, crosses the ascending limb of the gut loop so that its proximal part is enclosed in the pole of the primary gut loop. In specimens from NW Australia (Hartmeyer 1919 and BM 1930.9.23.2), the left gonad does not cross into the gut loop.

Irregularly lobed endocarps, additional to the thickenings in which the gonads are embedded, project from the surfaces of the gonad and gut, and in the gut loop. These are conspicuous in larger specimens, being present also on the anterior third of the body wall.

REMARKS: The large siphonal spines extending deep into the siphons; the closely placed siphons; the undivided, branched gonads; the crowded internal longitudinal vessels on the folds; the crowded, rounded clumps of liver lobules; the deeply curved gut loop; the body wall with papillae and endocarps; the very long rectum; and the endocarps on the gut and in the gut loop distinguish this species from others in the genus.

Microcosmus planus Kott, 1975
(Fig. 175a)

Microcosmus planus Kott, 1975, p.15.

DISTRIBUTION

NEW RECORDS: None

PREVIOUSLY RECORDED: South Australia (Great Australian Bight — paratype QM G7510 Kott 1975).

The species was taken at 31 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are laterally flattened, circular in outline, with body apertures sessile and close together on the upper surface. The test is thin, but crowded sand particles adhere to hair-like processes to form a hard capsule around each specimen, giving it the appearance of a hardened disc of sand. The hair-like processes are longer posteriorly where, with their enmeshed sand, they form a sandy keel around the ventral surface. These individuals appear to stand upright, the lower part of the body being stabilised in a sandy substrate by this keel-like structure.

The flattened spines, about 0.04 mm long, in the siphon lining are similar to those of *M. madagascariensis*, the posterior end curving out, rather than being bent under in a hook (as in *M. exasperatus*).

INTERNAL STRUCTURE: Longitudinal muscle bands radiate from each siphon and cross one another over the sides of the body. There are also horizontal bands crossing the dorsal and ventral borders of the body; possibly they are associated with its lateral flattening. About 30 branchial tentacles, with primary and very short secondary branches, alternate with rudimentary tentacles. The dorsal tubercle is long and narrow, protruding into the pharynx. It has a long slit that is turned up at its posterior end to form a pronounced J-shape. There is a long dorsal ganglion between the two apertures. The dorsal lamina is long and wide.

Seven narrow branchial folds on each side of the body have up to 10 internal longitudinal vessels on the folds and never more than one in the interspace. Often vessels are absent from the interspace. Stigmata curve in at each end to form incipient infundibula. There are 8 per mesh, crossed by parastigmatic vessels.

The gut forms a long, narrow loop to the left of the ventral curve of the body. The liver consists of clusters of parallel lamellae in the pyloric wall. The anal border is bilabiate. The rectum extends forward almost parallel to the descending limb of the primary loop.

Gonads are present on each side of the body. The left gonad lies in the secondary gut loop, parallel to the descending limb of the intestine and the anteriorly directed rectum. Each gonad consists of a sinuous ovarian tube with male follicles both beneath it and along its posterior border. Owing to the curves of the gonad, male follicles sometimes appear to be mixed with the ovarian material.

REMARKS: This is an unusual species, highly specialised for its upright habit and sandy habitat. It is distinguished from other species by its shape, by the small number of internal longitudinal branchial vessels, and by the unusual, undivided gonads, entirely outside the primary gut loop.

Microcosmus propinquus Herdman, 1882
(Figs 175b, 176)

Microcosmus propinquus Herdman, 1882, p.132. (Not: Traustedt, 1885, p.42, Sluiter, 1904, p.51. Tokioka, 1952, p.128).

Microcosmus polymorphus : Herdman, 1882, p.133. (Not: Heller, 1877, p.246)

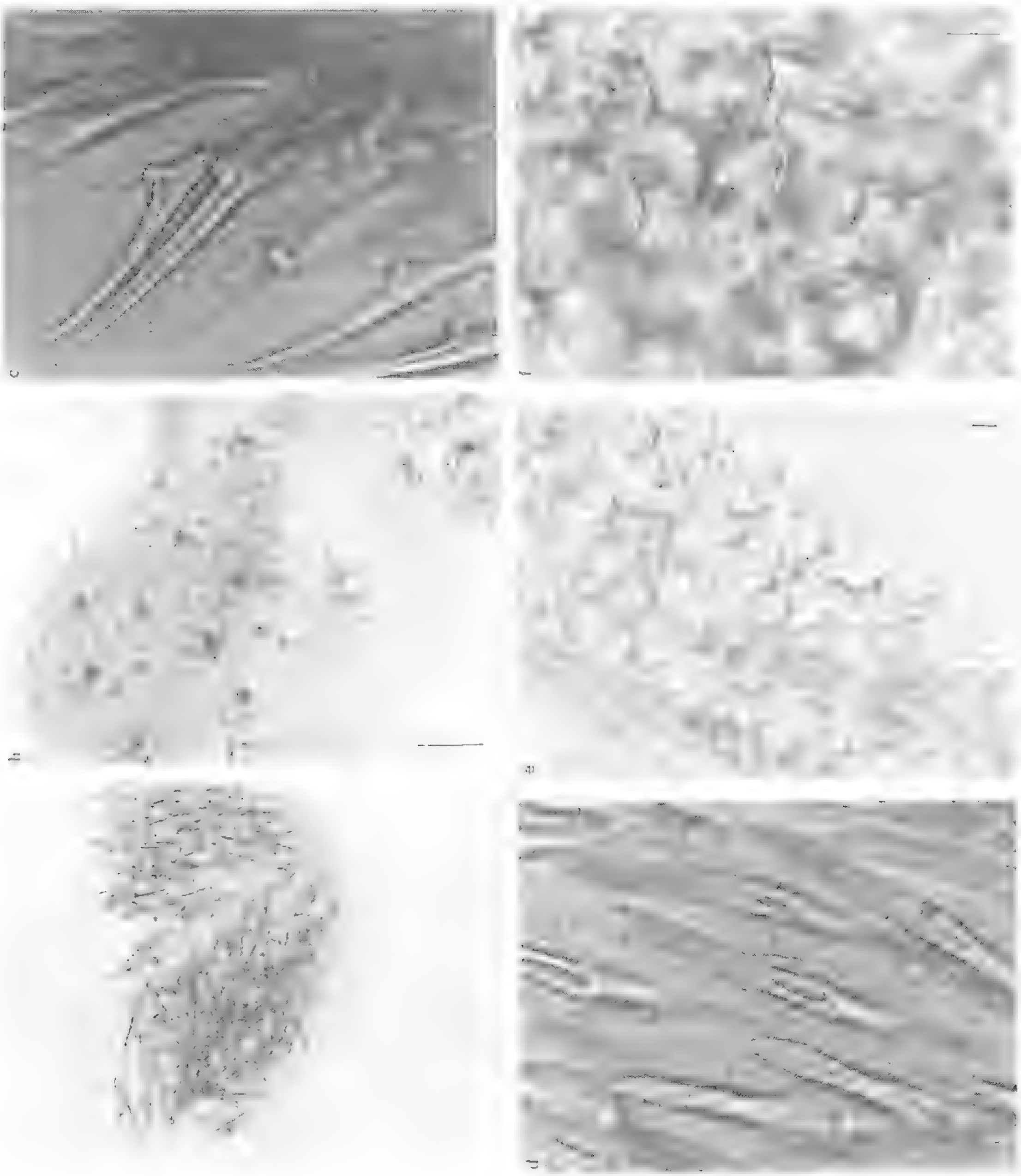


FIG. 175: *Microcosmus planus* — **a**, siphonal spines. *Microcosmus propinquus* — **b**, siphonal spines and scales. *Microcosmus pupa* — **c**, **d**, siphonal spines (**c**, profile; **d**, from below). *Microcosmus squamiger* — **e**, **f**, siphonal scales. (Scales: **a**, **c** – **f**, 0.01 mm; **b**, 0.1 mm).

Microcosmus nichollsi Kott, 1952, p.290; 1972a, p.43; 1972c, p.245; 1976a, p.85.

DISTRIBUTION

NEW RECORDS: South Australia (St Vincent Gulf, QM G9302). Victoria (Bass Strait, NMV H913 F51537).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1972a). Victoria (Bass Strait — BM 1887.2.4.45-46 Herdman 1882; Western Port — Kott 1952 1976a). Queensland (Moreton Bay — Kott 1972c).

The species has been taken from 8 to 80 m depth. It appears to be a temperate indigenous species.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals, which are more or less spherical or oval, are up to about 12 cm long. The surface is rough and irregular, ridged and creased or, when sand is embedded in the test, hard and rigid. Root-like projections of the test are present on the posterior surface. The apertures are varying distances apart, the atrial aperture often near the posterior end of the body. The branchial aperture is often terminal, but can also be on the upper surface. Both apertures are on short, ridged siphons, often surrounded by rounded projections of the test. In preserved specimens, the test is white with some pink pigmentation.

Large, conical spines, up to 0.1 mm high, crowd on the test around the apertures. They have a wide (0.15 mm diameter), hemispherical base and a narrow, sharp terminal point. They continue into the siphonal lining, where they become smaller (0.03 to 0.06 mm high) and slightly curved. They are sparsely but evenly distributed, the space between the spines being occupied by minute, flattened scales with rounded borders (0.02 mm long).

INTERNAL STRUCTURE: The body wall is very muscular, especially around the siphons, which are long and directed away from one another. Longitudinal muscle bands radiate from both siphons across the sides of the body to form rectangular meshes. However, on the left side, they fade over the gut region. Circular muscles are present around the base of each siphon. There are 4 cuspid valves formed in the siphonal lining at the base of the branchial siphon, just anterior to the branchial tentacles. A branchial sphincter muscle is associated with the base of the branchial tentacles. These tentacles are moderately bushy, with primary and secondary branches and minute tertiary branches. About 12 tentacles alternate with rudimentary ones. The large dorsal tubercle has a U-shaped slit with horns turned or spiralling in. The dorsal ganglion is elongate, half the length of the plain-edged dorsal lamina.

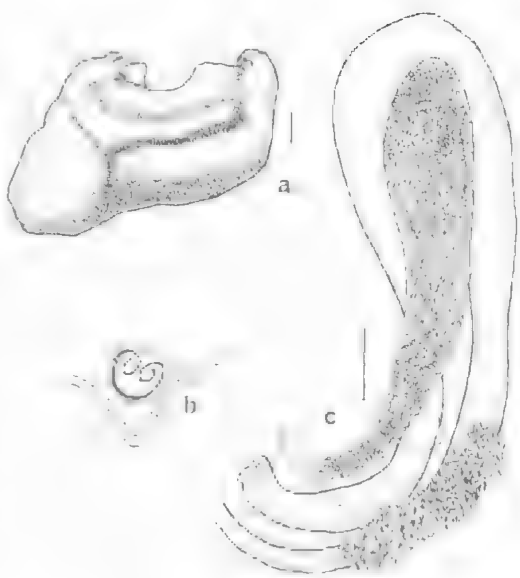


FIG. 176: *Microcosmus propinquus* (QM G9329) — a, external appearance; b, dorsal tubercle; c, gut and gonad with some overlying endocarp. (Scales: a, c, 1.0 cm).

There are usually 7 high, overlapping branchial folds on each side of the body, with up to 20 internal longitudinal vessels on the folds and 1 to 3 in the interspace. The 10 to 15 stigmata in each mesh are crossed by parastigmatic vessels. The internal longitudinal vessels are as well spaced on the folds as between them, forming wide meshes, especially at the base of the folds.

The gut forms a long, narrow, curved loop that occupies most of the ventral curve of the left side. It terminates in a smooth or irregularly lobed anus. There are compact clusters of parallel liver lamellae in the wall of the pyloric region of the gut. Minute, upright papillae often occur on the lamellae. The gut is embedded in the body wall.

The gonads are divided into 3 successive blocks, joined by common gonoducts. On the left, the proximal section of the gonad is enclosed in the gut loop. The gonad crosses the descending limb of the gut loop, and the two distal sections of the gonad extend parallel and close to the anterior border of the loop. Gonads are deeply embedded in the body wall of the larger specimens. Sometimes there is a fur of fine papillae projecting into the peribranchial cavity from most of the inner body wall. These are especially conspicuous over the liver. Block-shaped endocarps, which develop over the gonads, project into the atrial cavity.

REMARKS: This species is one of the largest known from Australian waters. Reliable characters for identification are the siphonal spines and scales and the large number of stigmata in each branchial mesh. The number of branchial folds provides confirmatory evidence of identity, for *M. exasperatus* and *M. australis* (which have gonads resembling those of the present species) usually have more than 7 branchial folds (the number most often found in the present species). The siphonal spines of *M. propinquus*: Tokioka, 1952 are those of *M. exasperatus* rather than of the present species.

The type species of *M. propinquus* and *M. polymorphus* have been examined and are found to be conspecific with one another and *M. nichollsi*.

Microcosmus pupa (Savigny, 1816)
(Figs 175c,d, 177)

Cynthia pupa Savigny, 1816, p.151.
Microcosmus pupa: Hartmeyer, 1909, p.1345. Michaelsen, 1919, p.58.

DISTRIBUTION

NEW RECORDS: Queensland (Princess Charlotte Bay, QM GH2178).

PREVIOUSLY RECORDED: Red Sea (Savigny 1816, Michaelsen 1919).

DESCRIPTION

EXTERNAL APPEARANCE: The single Australian specimen is upright, 5 cm high and 3 cm wide. It has a short, terminal branchial siphon and an atrial siphon halfway down the dorsal surface, which is directed laterally. The animal is fixed by the rounded posterior end. The test is very hard, with superficial ridges and wrinkles, and very thin but tough. It is off-white to beige in preservative.

Long (0.15 mm), pointed spines line the siphons. They have a long base, which is closed posteriorly but remains open anteriorly where the scale expands in a rather narrow basal flange. The base is approximately half the length of the spine. The point is narrow, sharp and only slightly curved.

INTERNAL STRUCTURE: The body wall adheres very closely to the test. There are 12 moderate-sized branchial tentacles alternating with rudimentary ones. None of the tentacles is bushy, the primary branches being small and the secondary branches minute. The dorsal tubercle is a large cushion with a deep slit that has both horns coiled in once only. The peritubercular area is a narrow V, almost completely filled by the tubercle. There is a long dorsal lamina with a smooth margin.

There are 7 wide, overlapping branchial folds on each side of the body. The internal longitudinal vessels are arranged according to the following formula: E2(12)4(18)4(18)4(22)3(24)3(22)3(21) 4DL. There are 4 stigmata per mesh.

The gut loop is narrow and deeply curved into a pronounced J, the rectum being curved anteriorly. The liver is represented by compact, parallel folds in the gut wall. Small pointed papillae project into the peribranchial cavity from the mesial surface of the liver. The anal border is smooth.

The gonad is massive and diffuse. The ovarian sac is large and irregular, but is not subdivided. On the left, its proximal end is enclosed in the gut loop and crosses the descending limb of the loop. Testis follicles, which are present in the centre of the mesial surface of the ovary, penetrate down into the ovarian tissue between folds of the ovarian sac. Testis follicles also form an almost continuous layer over both limbs of the gut loop. On the right, male follicles form a similar layer over the body wall outside the ovary, and project down into the ovarian tissue as they do on the left side of the body.

REMARKS: Both the siphonal spines, with their almost completely closed bases and narrow flanges, and the very numerous male follicles that form an extensive sheet over the body wall and gut loop, are distinctive characters described by Michaelsen (1919) for specimens from the Red Sea.

Microcosmus squamiger Hartmeyer and Michaelsen, 1928
(Figs 175e,f, 178)

Microcosmus claudicans: Hartmeyer and Michaelsen, 1928, s.sp. *squamiger* p.405.
Microcosmus squamiger: Kott, 1972a, p.43; 1976a, p.86.
Microcosmus exasperatus: Michaelsen, 1908b, s.sp. *australis* p.272; 1918, p.11 (part, not *M. australis* Herdman and *M. ramsayi* Herdman).

DISTRIBUTION

NEW RECORDS: Western Australia (Cape Boileau, BM 1930.10.8.5; Broome, WAM 1161.83; Cockburn Sound, WAM 25.100.72 112.72 216.73 205.82 1162.83; Bunbury, WAM 18.75; Albany, WAM 51147). South Australia (St Vincent Gulf, QM G9309 G9322 G9330). Tasmania (Bruny I.; Kingston, QM G10142; Swan Bay, QM G10128). New South Wales (Arrawarra, QM GH2167 GH2251). Queensland (Moreton Bay, QM G5978 G9569 G9973-5 G9993 GH349 GH2009 GH2163 GH2165 GH2681-2 GH2684 GH3078; Mooloolaba, QM GH2009; Tannum Sands, nr. Gladstone, QM GH2166; Hervey Bay, QM G9375 GH3210; Heron I., QM GH2982 GH3100; Yeppoon, QM GH2164; Abbot Pt, QM GH659 GH660 GH671).

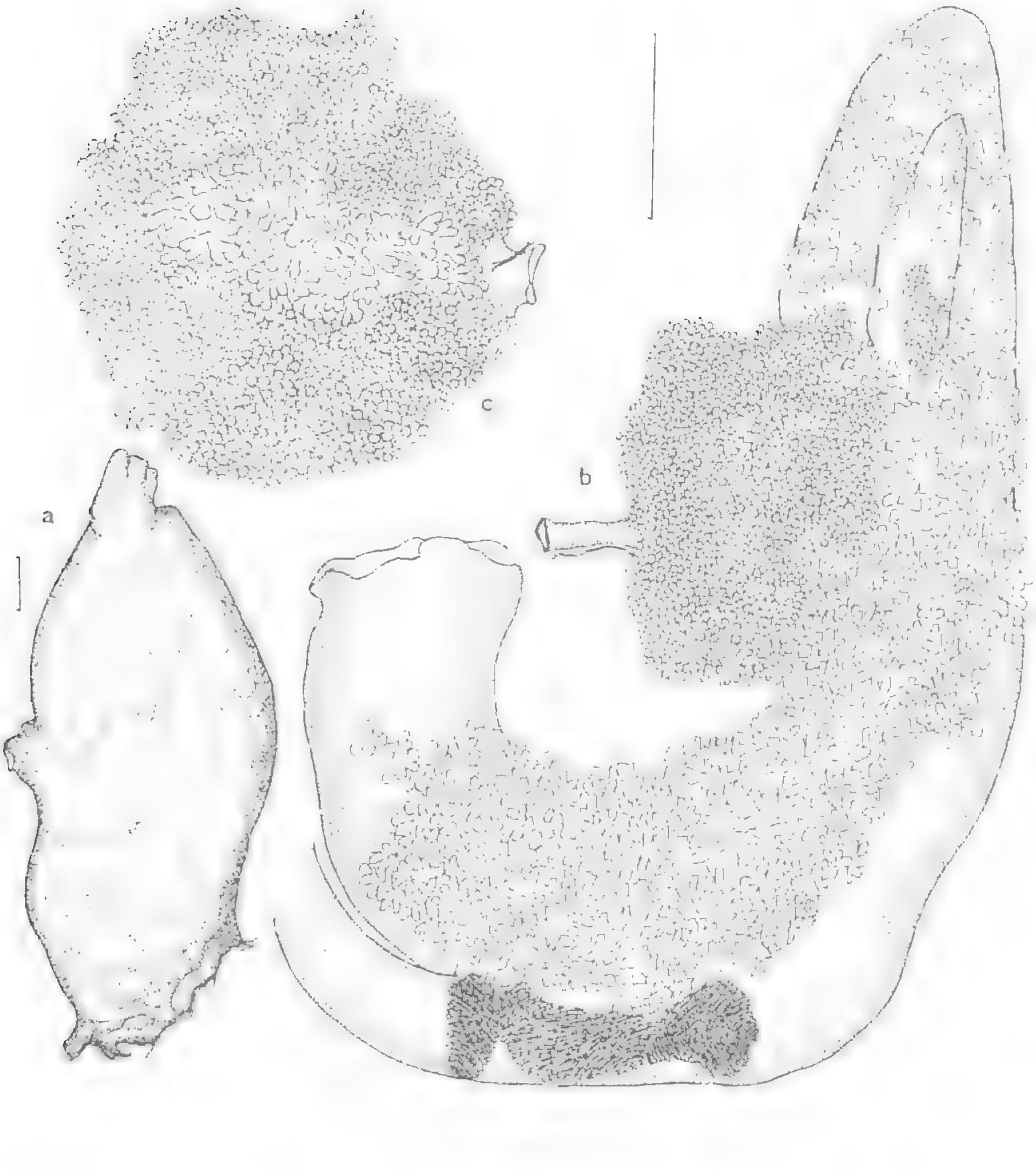


FIG. 177: *Microcosmus pupa* (QM GH2178) — a, external appearance; b, gonad and gut on left side of body; c, gonad from right side. (Scales: 5.0 mm).

FIG. 178: *Microcosmus squamiger*—a, external appearance (QM G9309); b, gut and gonad on left (QM G9375); c, dorsal tubercle and ganglion (QM G9375). (Scales: a, 1.0 cm; b,c, 2.0 mm).

PREVIOUSLY RECORDED: Western Australia (Shark Bay to Albany — Hartmeyer and Michaelsen 1928). South Australia (St Vincent Gulf — Kott 1972a). Victoria (Port Phillip Bay, Western Port — Kott 1976a). New South Wales (Port Jackson — Michaelsen 1908b). Queensland (Bowen, Rockhampton — Michaelsen 1908b). Red Sea (Michaelsen 1918).

The species is found on rocky substrate, on concrete, on cave walls and in both sheltered and exposed locations. It is common in large aggregates at Cleveland Pt (Moreton Bay). At Princess Harbour (Albany) and Bruny I. (Tasmania), it has been found amongst oysters (and has been noted as very destructive to these at the former location). It has been recorded down to 35 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are relatively small (up to 3 cm in diameter), rounded, or irregular. They usually occur in large aggregates. The surface of the test is raised into ridges and swellings and is produced into irregular projections that help the individual adhere very firmly to the substrate and to other individuals in the aggregate. The test is beige to pinkish brown or purple.

The test is very leathery and tough, not very thick, but sometimes hard and occasionally quite brittle. It is purple internally. Large (0.2 mm), spherical bladders cells are present in the test of juvenile specimens. The apertures are on short, sometimes wart-like, siphons, about one-third of the body length apart and directed away from one another; or the branchial aperture, on a long straight siphon, is terminal and well removed from the atrial aperture which is about halfway along the club-shaped body on a short siphon (QM GH3078, GH3100).

The terminal part of the siphonal lining has small, overlapping, curved scales with rounded borders, 0.01 to 0.02 mm long.

INTERNAL STRUCTURE: The body wall is a reddish purple and very muscular, the siphons linings have red stripes in fresh material. In the base of the branchial siphon lining are 4 pockets which form a cuspid valve. The branchial tentacles are strong and muscular, and there is a a strong sphincter muscle at their base. The dorsal tubercle is a large cushion that completely fills the peritubercular area. Its slit forms a double spiral cone, with the open interval directed forwards. The dorsal ganglion is quite long, lying behind the dorsal tubercle over the anterior half of the long dorsal lamina.

The branchial sac is tough. There are 8 or 9 broad, overlapping branchial folds. Up to 25 internal longitudinal vessels are crowded on the folds, but in the interspaces there are only 1 or 2. Each mesh has 10 to 12 stigmata.

The gut forms a fairly narrow, curved loop, but the pole is open, enclosing the proximal part of the left gonad. The liver is compact, consisting of a proximal part with shorter lobules and a distal part with longer, parallel lamellae. The liver is often orange, the distal part darker than the proximal part.

The gonads are divided into 3 blocks, joined by median common ducts. The left gonad crosses over the descending limb of the gut loop, from the pole of the loop, to extend toward the atrial aperture.

REMARKS: With the exception of the siphonal armature and the more numerous stigmata in each mesh, there is little in the external or internal structure of this irregularly-shaped species with its tough, leathery, purple-red pigmented test, that distinguishes it from *M. australis* and *M. exasperatus*. The pockets of the cuspid valve are sometimes pulled back into the pharynx, when they resemble the cartilaginous tongues of *M. helleri* and indicate the homology of those structures.

Microcosmus stoloniferus Kott, 1952
(Figs 179a, 180)

Microcosmus stolonifera Kott, 1952, p.291; 1972a, p.43; 1972c, p.245; 1975, p.16; 1976a, p.85.

DISTRIBUTION

NEW RECORDS: Tasmania (Port Davey, QM GH2019 GH2020). Victoria (Bass Strait, NMV H397 H916). Queensland (Gladstone, QM GH9684; NW of Bowen, QM GH676 GH749 GH1482 GH1483; Townsville, QM GH756; Innisfail, QM GH1805; Nymph I., QM GH1785).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1972a; Spencer Gulf — Kott 1975). Tasmania (East Coast — Kott 1952). Victoria (Western Port — Kott 1976a). Queensland (Moreton Bay — Kott 1972c).

The species apparently extends along the whole eastern coast of Australia, but westwards only to South Australia.

DESCRIPTION

EXTERNAL APPEARANCE: The body is spherical to top-shaped, usually with a posterior stalk or short, root-like processes. Individuals may adhere to one another to form aggregates. The apertures, which are on short siphons, are varying distances apart. Sometimes they are quite close together in the centre of the upper surface, but in one specimen they open at opposite ends of a long depression. There is usually a rounded swelling of test around the upper surface enclosing the apertures. The border of each aperture is divided into 4 thickened, triangular lobes, which close together around the opening. Some specimens have 4 additional short, finger-like processes of the test around each aperture. The test itself varies in thickness. It is often brittle with sand, and sand often obscures the shape of the body; or the test is hard and leathery.

The test around the apertures is covered with large, pointed overlapping scales that extend down into the siphons and line their whole length. They are 0.06 to 0.1 mm long, with an open base. The scales are slightly striated.

INTERNAL STRUCTURE: The body wall is thin and adheres closely to the test. Muscle bands radiate from each siphon and cross one another to form regular meshes over the whole length of the body. About 12 branchial tentacles alternate with rudimentary ones. The larger tentacles branch 3 times, but are not very bushy. The dorsal tubercle is a round, delicate cushion, with a U-shaped slit, the horns sometimes turned out. The dorsal lamina is broad, smooth and long, the oesophagus opening at the posterior end of the branchial sac.

There are 6 to 8 branchial folds on each side of the body. Up to 24 crowded internal longitudinal vessels are present on the folds. The interspaces, with about 9 stigmata per mesh, never have more than a single vessel. The stigmata, which are long, are crossed by a parastigmatic vessel. The branchial formula of a specimen 2 cm long is: E0(10)0(12)0(14)1(15)1(13)1(7)1(12)1DL.

The gut forms a narrow loop to the left of the ventral curve of the body. The liver consists of crowded groups of parallel, elongate, glandular pouches, which protrude slightly from the gut wall in the pyloric region.

Gonads consist of a tubular ovary with branching male follicles around its ventral border. The male follicles are primarily pyriform, but they branch prolifically, and become long and finger-like. Well-developed testis follicles form a mass at least the same size as the ovary, and spread beneath it and onto its mesial surface. The vas deferens extends along the postero-ventral border of the ovary and crosses beneath its distal end to open with the short oviduct, which is terminal or slightly displaced onto the dorsal border of the ovary. Proliferating male follicles, together with the ovary, sometimes create an almost circular gonad. The left gonad is in the posterior part of the curve of the gut loop outside the primary loop. The right gonad is in a corresponding position toward the postero-ventral corner of the right side. Kott (1972a) reports that the right gonad is sometimes divided into two lobes.

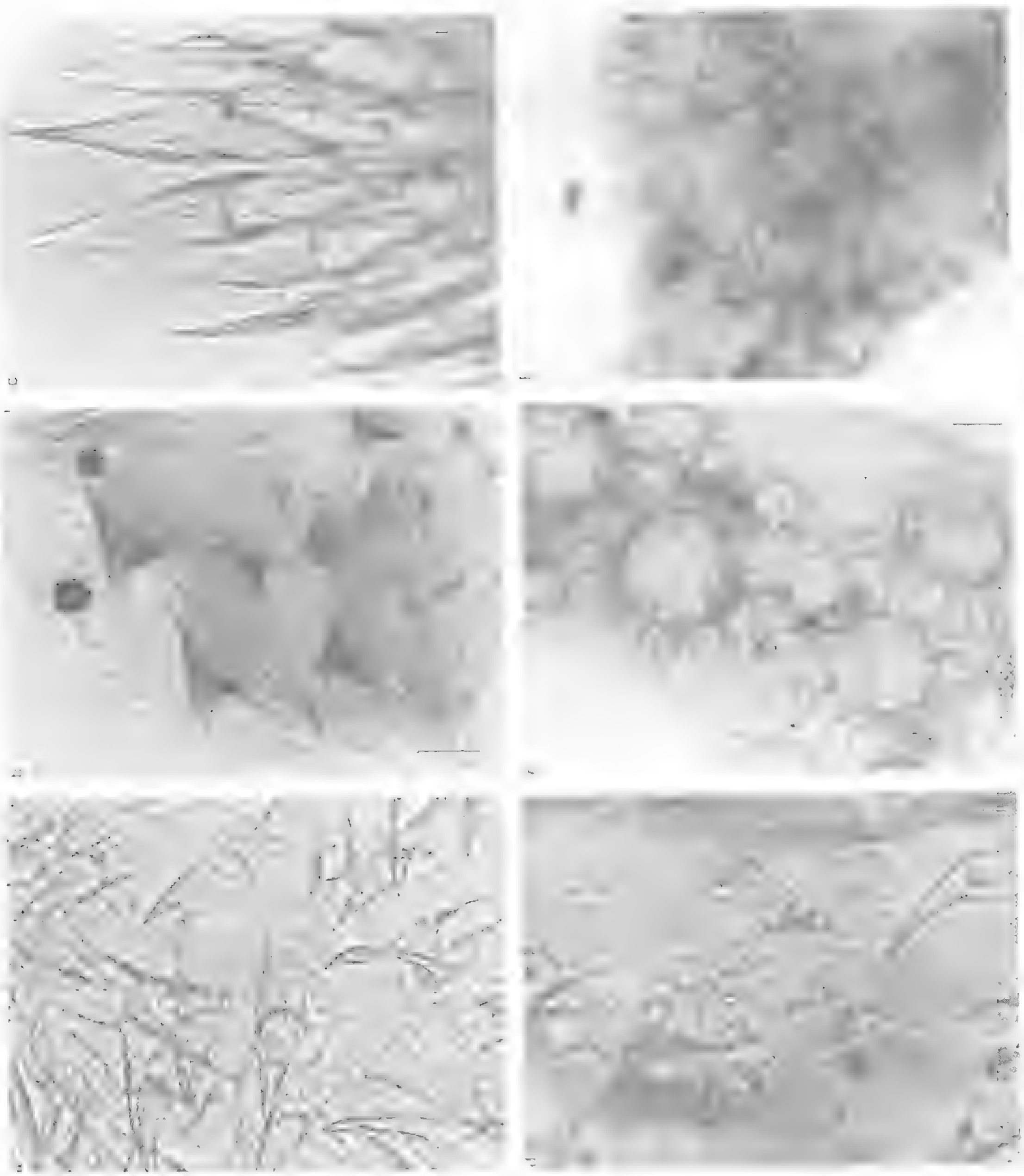


FIG. 179: *Microcosmus stoloniferus* — **a**, siphonal spines. *Microcosmus tuberculatus* n.sp. — **b**, siphonal spines. *Hartmeyeria formosa* — **c**, spines near base of siphon; **d**, spines near top of siphon; **e**, spines and papillae near apertures; **f**, papillae on test. (Scales: a, c, d, 0.01 mm; b, e, f, 0.1 mm).

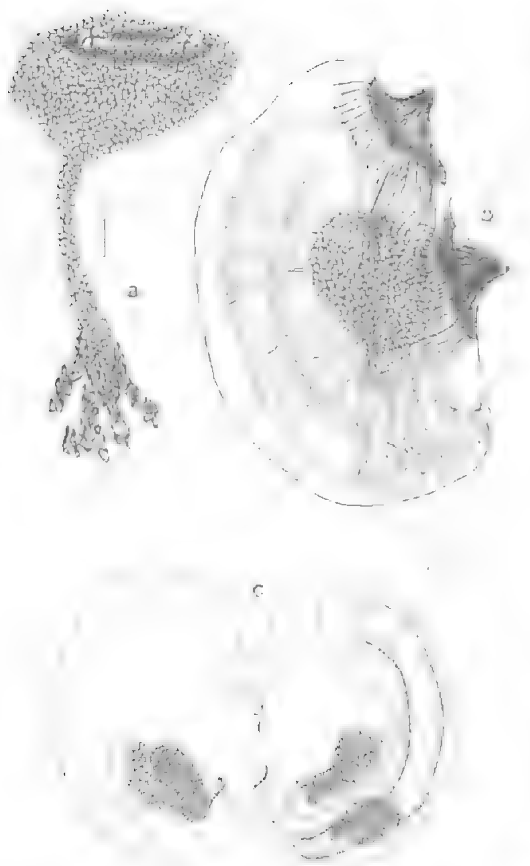


FIG. 180: *Microcosmus stoloniferus* — a, external appearance (NMV H397); b, left side of body removed from the test (QM GH674); c, inner body wall (QM GH1805). (Scales: a, 5.0 mm; b, c, 2.0 mm).

REMARKS: The top-shaped to spherical body with the siphons on the upper surface is distinctive, although variations can sometimes be confusing. The siphonal spines resemble those of *M. exasperatus*. However, in the present species, the position of the left gonad entirely outside the primary gut loop, the shape of the gonads and the small number of internal longitudinal vessels between the folds, are, together, characteristic.

Microcosmus pedunculatus Pérès (see Millar 1962a) from western and southern Africa is a similar shape to the present species. It also has long, branched male follicles spreading out into the body wall around the ovary but its long gonads cross into the pole of the gut loop, unlike the gonads of *M. stoloniferus*.

Microcosmus tuberculatus n.sp.
(Figs 179b, 181)

DISTRIBUTION

TYPE LOCALITY: Queensland (Swain Reefs, 21°52.4'S, 142°12.6'E, Queensland Fisheries Survey, 27.6.80, holotype QM GH1405, paratype QM GH1406).

DESCRIPTION

EXTERNAL APPEARANCE: The largest specimen is 3 cm long. It is more or less spherical, with conspicuous apertures at opposite ends of the horizontal upper surface. Each aperture is on the end of a short, thick siphon that protrudes from the surface and is surrounded by test swollen into large, rounded lobes. The test is tough, leathery, and brownish white in preservative. The surface has some widely spaced creases, especially around the base of each siphon.

Broad-based, conical spines extend in a rather irregular row across the top and are scattered over the surface of each of the lobes that surround the apertures. These spines are about as wide across their base as they are high (from 0.06 to 0.25 mm). They become more crowded toward the apertures and overlap one another on the terminal half of the siphon lining.

INTERNAL STRUCTURE: The body musculature consists of longitudinal bands from each siphon crossing one another over the sides of the body to form an open mesh. There is a narrow velum at the base of the branchial siphon just in front of the branchial tentacles. The 12 branchial tentacles alternate with minute ones. The larger tentacles have long primary branches, but only very small secondary branches. An elongate dorsal tubercle, fills the upper part but does not reach to the base of the narrow, V-shaped peritubercular area. The slit is a long U, with both horns turned in. The dorsal lamina is a long, plain-edged membrane.

There are 7 folds on each side of the branchial sac, with up to 16 internal longitudinal vessels on each fold and 2 to 4 in the interspace, arranged according to the following formula: DL2(15)2 (14)3(16)4(14)4(12)3(10)3(3)OE. The ventral fold on each side is small and rudimentary. The 8 stigmata in each mesh are crossed by a parastigmatic vessel.

The gut forms a long, narrow loop, curving around more or less parallel to the endostyle. It is open at the pole. Irregularly arranged groups of short, parallel lamellae are crowded in the pyloric region. Small, narrow and almost pointed papillae project from the liver lamellae. The anal border has about 8 broad lobes, sometimes irregularly subdivided along their borders.

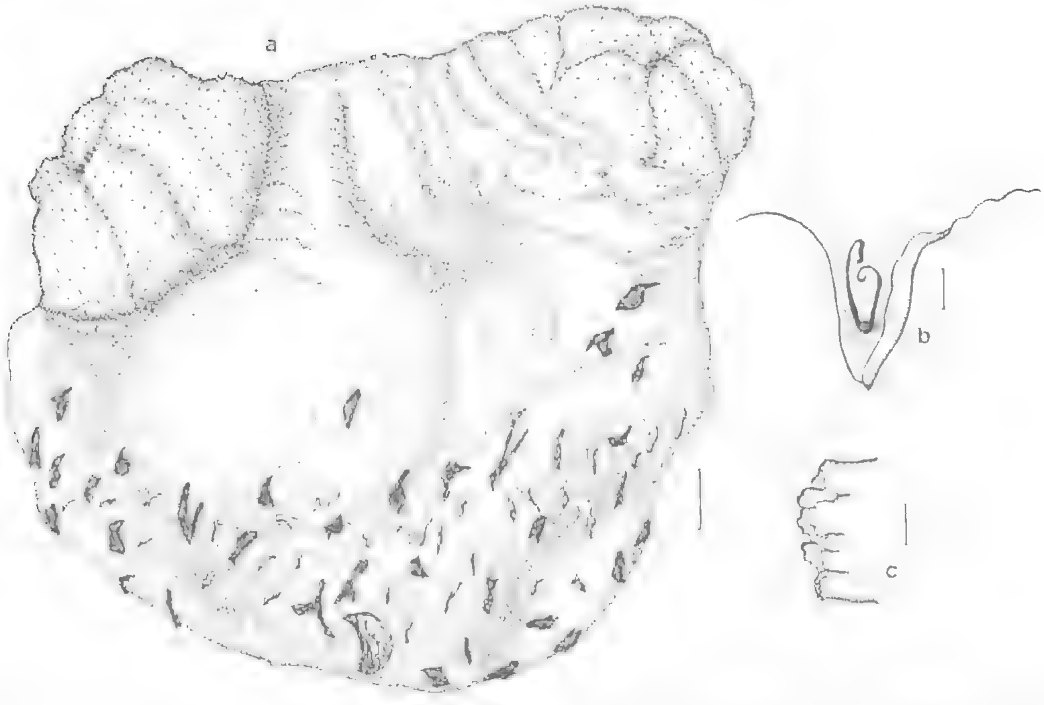


FIG. 181: *Microcosmus tuberculatus* n.sp. (QM GH1405) — a, external appearance; b, dorsal tubercle; c, anal border. (Scales: a, 2.0 mm; b, c, 0.5 mm).

The long gonads are of the usual type, each divided into a single series of 3. The proximal part of the left gonad is enclosed in the open pole of the gut loop.

REMARKS: The gonads, gut, branchial sac and dorsal tubercle of this species are similar to those found in many others in the genus. The papillae on the liver lamellae are also quite commonly encountered (e.g., *Microcosmus madagascariensis* and *M. propinquus*).

The species is distinguished from others by its wide conical spines, which resemble those of *Polycarpa olitoria*. In the family *Pyuridae*, similar spines occur only around the apertures in *Hartmeyeria formosa* and *M. propinquus*. However, the small scales between the large conical spines in the siphon lining that characterise the latter species are not present in *M. tuberculatus*.

Genus **Hartmeyeria** Ritter, 1913

Type species: *Hartmeyeria triangularis* Ritter, 1913

The genus is characterised by its almost sessile apertures, smooth oval to top-shaped body, posterior stalk and coiling of the stigmata in the edge of each fold.

The genus is not diverse and only 7 species are known. In addition to *H. formosa* (reported on below) these are *Hartmeyeria triangularis* Ritter, 1913 from the northern Pacific (Van Name 1945); *H. monarchica* Hartmeyer, 1922 from the Gulf of Aden; *H. hupferi* (Michaelsen, 1908a) from the western coast of Africa; *H. bouilloni* Monniot and Monniot, 1976c from Mozambique; *H. orientalis* Oka, 1929 from Japan; and *H. chinensis* Tokioka, 1967a from China. The last 2 species differ from the others in having more internal longitudinal branchial vessels, better developed gonads and multiple openings of the vas deferens. Only *H. monarchica* has apertures on short, diverging siphons. Generally, however, all the known species of *Hartmeyeria* resemble one another. They always have 6 branchial folds on each side of the body, with the second fold on each side very much smaller than the others and often represented only by a single longitudinal vessel. Except in the Australian *H. formosa*, internal longitudinal branchial vessels are absent from the interspaces, where the oval to elongate stigmata lie in rectangular meshes crossed by parastigmatic vessels. The dorsal lamina is either smooth or has a toothed margin. The liver, which is sometimes bipartite, consists of longitudinal and rounded glandular pouches in the gut wall (as in the Molgulidae) rather than groups of short, parallel lamella (as in *Microcosmus*). The molgulid-type gonads have relatively short oviducts, loose (rather than compact), long branched male follicles around the whole or part of the border of the ovary; and short gonoducts opening some distance from the atrial aperture. The thin-walled heart is sometimes mistaken for a kidney, which it does not have. The musculature varies from the pyurid condition with numerous longitudinal bands from each siphon crossing those from the opposite siphon on the side of the body, to modified musculature with bands of short, parallel muscles. The siphonal spines resemble those of *Microcosmus* spp., but are less curved.

Cratostigmata Monniot and Monniot, 1961 appears to be very closely related to *Hartmeyeria*, differing from it only in those characters that might be the result of size-reduction and simplification, *viz*., simple branchial tentacles and a gonad present only on the right side of the body.

The close similarity in structure between species of the genus *Hartmeyeria*, especially their external appearance and the tendency to loss of the second branchial fold, suggests that they represent a natural group of phylogenetically related species. Other characters suggest that they can be appropriately regarded as the genus of the family Pyuridae most closely related to *Microcosmus*. However, they do have some molgulid-like characters reflected in the glandular stomach folds and pouches, the form of the gonads and a tendency for stigmata to form infundibula. These may be characters convergent with those in the Molgulidae, or they may indicate a relationship with some earlier *Microcosmus*-like ancestor of the Molgulidae.

Only a single species of this genus is known from Australian waters.

Hartmeyeria formosa (Herdman, 1899)
(Figs 179c–f, 182)

Cynthia formosa Herdman, 1882, p.139.
Cynthia spinifera Herdman, 1899, p.32.
Microcosmus spinifera: Kott, 1952, p.286; 1972c, p.244.
Microcosmus spiniferus: Millar, 1966, p.373.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H389 H740 H900 F51572 F51576–7 F51580 F51587, QM G12751). Queensland (Moreton Bay, QM G5981–6 G10072; Gladstone, QM G9802; Calliope River, QM GH2761; Abbot Point, QM GH775; Townsville, QM GH3031; Mossman, QM GH787).

PREVIOUSLY RECORDED: Victoria (Port Phillip Bay — Millar 1966). New South Wales (Port Jackson — Herdman 1899). Queensland (Moreton Bay — Kott 1952, 1972c). Northern Australia (Torres Strait — holotype BM 1887.2.4.51 Herdman 1882).

The species has a range along the eastern Australia coast from Victoria to Torres Strait. It has been taken down to 95 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are always top-shaped, with a flat, wide upper surface up to 2.5 cm in diameter, narrowing abruptly to a thin stalk of varying length. The stalk is divided basally into root-like branches. The apertures are on the flat, upper surface, separated by about one-third of its diameter. Each aperture protrudes very slightly. Its rim is divided into 4 lobes, surrounded by a ring of crowded, fine bristles. Outside these, there are upright, pointed, and sometimes branched, test bristles about twice the length of those immediately around the apertures. These processes are reduced in height the further they are from the apertures. Between the test bristles, the whole surface is covered with short, rounded elevations or papillae with numerous pointed spines on their surface, which give a granular consistency to the surface of the thin, but tough, test.

The siphonal lining has petal-shaped, slightly pointed, hollow, overlapping scales of about 0.06 mm. In the terminal part of the siphon lining and around the apertures are small, conical spines, tapering to a very sharp point from a wide, rounded base.

INTERNAL STRUCTURE: The body wall is closely adherent to the test. The siphons are turned away from one another. Longitudinal muscle bands radiating from each siphon extend the whole length of the body and converge around the top of the stalk. They do not cross one another. There is also an outer layer of circular muscle fibres. A circular sphincter muscle lies at the base of each siphon. The dorsal tubercle is a rounded cushion with a U-shaped slit and both horns spiralling inwards. The dorsal lamina is a broad membrane of moderate length. It is fringed with small flat, rounded, transparent tongue-shaped lobes. There are 24 very bushy branchial tentacles.

The branchial sac has 6 high, overlapping folds on each side of the body, each with up to 30 wide and ribbon-like internal longitudinal vessels. There are up to 3 longitudinal vessels in the interspace, and 8 to 10 stigmata per mesh. The branchial formula for a specimen from Port Jackson, 1 cm

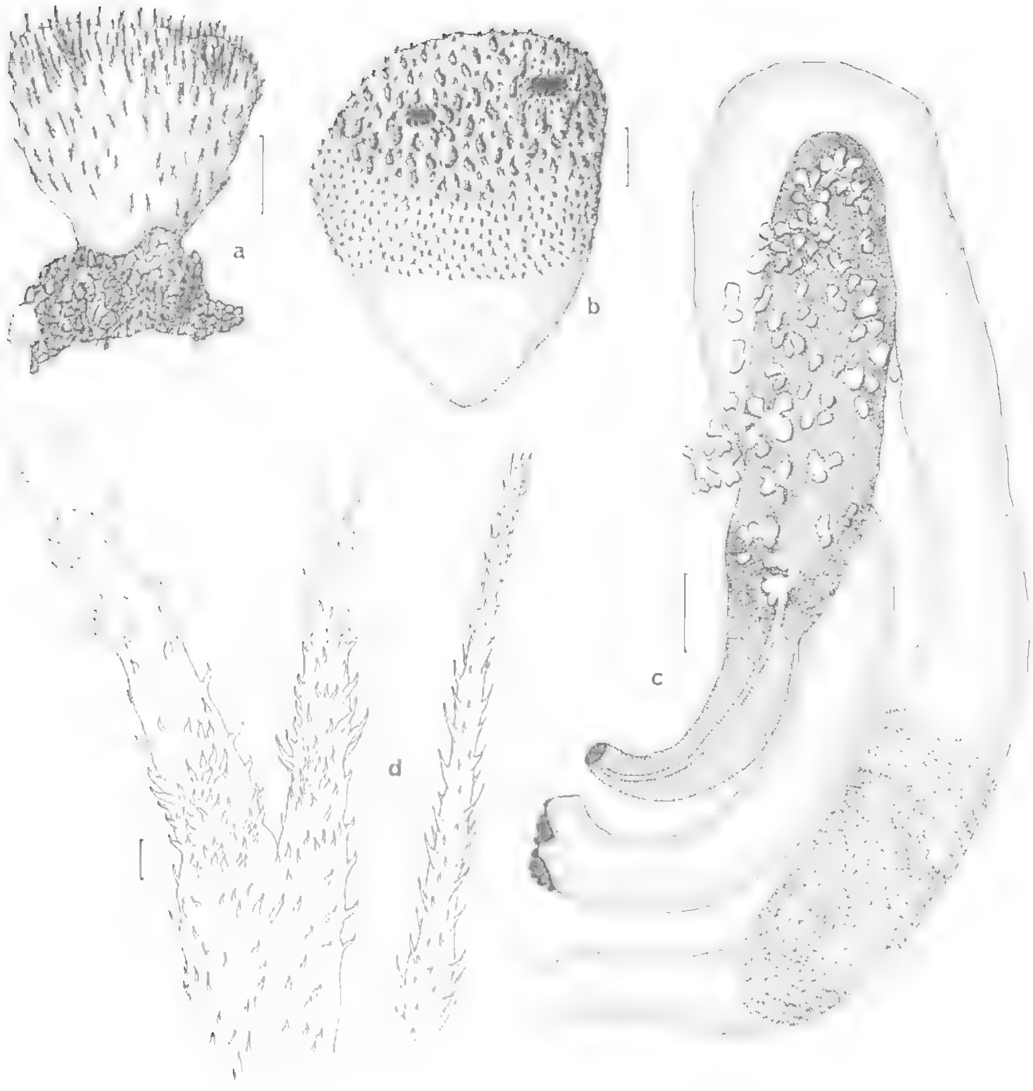


FIG. 182: *Hartmeyeria formosa* — **a**, **b**, external appearance (QM G9571, GH775); **c**, gut and gonad (QM G5985); **d**, spines from around the apertures (QM GH775). (Scales: **a**, **b**, 5.0 mm; **c**, 1.0 mm; **d**, 0.1 mm).

in diameter, is DL1(25)1(19)2(26)2(29)2(30)3(19)1E. A specimen of 2 cm diameter has the formula: E1(15)3(20)3(23)3(23)3(13)1(21)1DL. The second fold on the right is always only about half the size of the other folds. The second fold on the left is also the smallest on that side of the body. In the edge of the folds, under the marginal internal longitudinal vessel, the stigmata coil up to 3 times.

The gut forms a long and extremely narrow, slightly curved loop around the ventral curve of the body just to the left of the mid-line. The pyloric region is enlarged, with internal longitudinal folds that extend the full length of the stomach. There are no external liver lamellae or lobules. The anal border has about 4 shallow indentations.

The gonads are long and undivided. They have a large ovarian tube with branched male follicles in a double row beneath it, along the sides, on the mesial surface or (occasionally) a little removed from the side of the ovary. The male ducts curve around the ovary and join a common vas deferens along the middle of its mesial surface. The proximal end of the left gonad is enclosed in the narrow pole of the gut loop. It crosses the descending limb of the gut loop halfway down, and the distal half of the gonad extends close and parallel to the anterior border of the rectum. The gonoducts open together (near the anus) at the base of the atrial siphon.

REMARKS: The body shape and external bristles are constant, and characteristic of this species. Other characteristic features are the very narrow gut loop and the undivided styelid-type gonads crossing the gut, the coiled stigmata and the internal longitudinal glandular folds in the stomach (all of which are typical of *Hartmeyeria* spp.). The regular, tongue-shaped lobes along the edge of the dorsal lamina appear to be homologous with similar structures on the dorsal lamina of *Boltenia echinata* (see Berrill 1950) from the Arctic. It is a coincidence that the latter species also has test bristles that resemble those of the present species.

Specimens of the other species of *Hartmeyeria* are about 1 cm in diameter, with the exception of *H. orientalis* (up to 2.0 cm). They are all distinguished from the present species by their lesser number of internal longitudinal vessels on the folds and the complete absence of bristles on their external tests.

Family MOLGULIDAE Lacaze-Duthiers, 1877

The stigmata have a tendency to coil and usually spiral around infundibula (conical invaginations of the pharyngeal wall) that protrude into the pharynx. A closed kidney is present in the body wall postero-ventral to the right gonad. There is a single, relatively short and undivided gonad on each side of the body. Each gonad consists of a large, sometimes elongate but often rounded, ovarian sac. Testis follicles are in the body wall around all or part of the perimeter of the ovary. The gonoducts often open some distance from the atrial aperture. Gonads are sometimes outside the primary gut loop (e.g. *Molgula* and *Pareugyrioides*), but in other genera are partly or entirely contained in it (e.g. *Eugyra* and *Molguloides*).

The test is usually relatively thin, but often is strengthened with embedded or adherent sand. Many species also have test hairs to which sand and other foreign particles adhere. Usually the body wall is also thin and transparent, with fine muscle bands that do not form continuous layers. The musculature is often specialised, forming groups of short parallel bands, that are adapted to a firm and often brittle test which does not allow for a high degree of flexibility. The musculature around the apertures is often modified to provide for their withdrawal into the surface of the test, an adaptation that may be associated with the free-living habit of so many species on the open sea floor. In most species, wide, fibrous vela occur at the base of both atrial and branchial siphons, which may also be an adaptation for a sandy habitat. Similar vela are present in the sand-adapted *Pyura molguloides*. Longitudinal muscle bands radiating from each siphon do not usually cross one another as they do in Pyuridae. Most of the species of this family have a wide, unperforated membrane in the dorsal mid-line surrounding the oesophageal opening. The posterior end of the dorsal lamina divides to extend along each side of this membrane (which is widest at a level with the oesophageal opening, narrowing posteriorly to a retro-pharyngeal groove).

The branchial sac comprises the most conspicuous character separating the family from the Pyuridae (see also Annotated Glossary, infundibula; Fig. 3). Species in which the branchial sac is least changed from the pyurid condition (of true folds with mainly straight stigmata crossed by parastigmatic vessels) occur in the genus *Molgula*. In these species, the stigmata, especially those on the edge of the fold and on the flat part of the branchial sac between the folds, curve inwards at each end and only sometimes spiral. They usually increase in length as they do so (e.g., *Molgula ficus, M. sabulosa, M. incidata* n.sp.). There are also species of *Molgula* in which either the edge or a greater part of the width of the fold is divided into conical projections that form some part of the infundibula (from just the apex to the whole). In these species, long stigmata curve around the sides of the cone from one side of the fold to the other (e.g., *Molgula mortenseni, M. mollis, M. diversa*). The transverse vessels that hold the folds in place are always present between the infundibula. A membrane often connects these vessels to the cone. However, apart from some delicate connecting vessels the cones often are isolated from both the internal longitudinal and transverse vessels and stand more or less free in the lumen of the pharynx.

The branchial sac is most changed from the pyurid condition in *Molgula rima, M. sphaera* and *M. calvata* and in the genera *Eugyra, Pareugyrioides* and *Eugyrioides*, in all of which 2 long stigmata spiral together in each mesh. In the first three species, vestiges of the folded branchial sac can be seen in the 2 or more internal longitudinal vessels along the top and sides of each row of infundibula. These longitudinal vessels are supported by the transverse vessels, which project into the pharynx between the infundibula. In *Eugyra* and related genera, all trace of branchial folds is lost; and only one or two longitudinal vessels extend along the centre of each row of the very regular coils of stigmata.

The stigmata coils of genera in which the branchial sac is flattened also differ from those with folds, or vestigial folds: these stigmata form a circle or square at the base of the infundibulum. They are not laterally flattened into an ellipse by branchial folds as they are in *Molgula* (where the stigmata are drawn in to the upright transverse vessel at each end of the infundibula). In *Molguloides*, the base of the infundibulum is rounded but the projecting cones have numerous internal longitudinal vessels, distinguishing this genus from *Eugyra* and related genera which have only 1 or 2.

The molgulid glandular liver pouches in the pyloric region of the gut are folds in the gut wall, as in *Microcosmus*, and are not stemmed, arborescent diverticula as in *Pyura*. However, their form varies. In *Molgula* the pouches are usually long and irregular or oblique, and often subdivided into rounded pouches. In *Eugyra* and *Pareugyrioides*, they are short, regular and longitudinal and lack the complexity of those of *Molgula* spp.

In all genera of the Molgulidae, the male follicles are long and branched. They are either at the proximal end of the ovary, or along all or part of its border. The long follicles spread out in the body wall and may be separated from the ovary to some extent. The testis and ovary do not form the compact hermaphrodite organs that *Pyura* always, and *Microcosmus* usually, have. The left gonad is outside the gut loop in *Molgula, Paramolgula* and *Pareugyrioides*, but is partially or completely enclosed by the gut loop in *Molguloides* and *Eugyra*.

Berrill (1950) suggested that the spiral arrangement of stigmata in this family is an adaptation for maximum filtering efficiency in small individuals occupying unstable habitats that impose a necessity for early maturity. The large number of small, free living species, reaching early maturity, that have been recorded from Moreton Bay (Queensland), tends to support Berrill's hypothesis: Moreton Bay is an essentially estuarine habitat influenced especially by heavy tropical rainfall and reduced salinity during the summer months. However, the small and sand-covered species of this family generally occur on sandy, and sometimes in interstitial, habitats. Their filtering efficiency and small size at maturity may well be primarily an adaptation for this habitat, rather than an adaptive response imposed by instability in the environment.

Molgulid larvae also appear to be adaptated for open sea-floor habitats. Although they resemble those of other solitary stolidobranch (and phlebobranch) families, in that most adult and larval organs are not well differentiated, they differ in the absence of the adhesive organs and the ocellus. Further, many species are known to be viviparous and in some, the otolith is also lost and development is direct (Berrill 1931, 1955). In the Australian fauna, specimens of *Molgula rima, M. incidata* n.sp. *M. calvata* and *Eugyra pellucida* have larvae and *M. ellistoni* has anural embryos in the peribranchial cavity. The latter is probably a direct developing species. Similar adaptations occur in certain viviparous *Polycarpa* spp. (see also Annotated Glossary, larvae).

The Molgulidae are relatively diverse in waters south of the Subantarctic convergence (Kott 1969a), and several of these species are recorded from Australian waters. Some of the temperate indigenous species are related to the subantarctic species. These are also species from the tropical Indo-West Pacific and indigenous species that may be related. The Australian molgulid fauna appears to have affinities with both southern and tropical fauna.

The abyssal family Hexacrobylidae Seeliger, 1906, related to the Molgulidae (Kott 1969a), is not represented in Australian waters, although its type genus *Hexacrobylus* (a junior synonym of the carnivorous *Oligotrema* Bourne, 1903) is known from deeper waters of the seas to the north of Australia (see Kott 1969a).

The abyssal genera *Namiella* Monniot and Monniot, 1968 (monotypic) and *Minipera* Monniot and Monniot, 1974a (polytypic) from the North Atlantic; *Fungulus* Herdman, 1882 (polytypic) from Antarctica; and *Protomolgula* Monniot, 1971 (polytypic) from the tropical Atlantic have not been recorded from Australia. The monotypic *Anomopera* Hartmeyer, 1923 (known from only a single specimen) and *Xenomolgula* Arnback, 1931 are known only from Arctic and northwestern European waters. *Rhizomolgula* Ritter, 1901 (polytypic) has only been recorded from the Arctic. *Paramolgula*, Traustedt, 1885 (monotypic) is known only from the sub-Antarctic waters of the Scotia Ridge. *Molguloides* Huntsman, 1922 (polytypic), recorded from Japan, the Antarctic and the tropical western Pacific at a range of depths from abyssal to shelf waters, is not yet reported from Australia but most likely will be found to occur here.

KEY TO THE GENERA OF MOLGULIDAE
(* not yet recorded from Australia)

1. Excretory vesicles numerous ....*Namiella* *
   Excretory vesicle one only 2
2. Branchial folds present...........................3
   Branchial folds absent.............................8
3. Gonad absent from left side of body ....*Anomopera* *
   Gonad present on left side of body 4
4. Gut loop encloses left gonad.....................5
   Gut loop does not enclose left gonad........7
5. Gut loop completely encloses gonad..........6
   Gut loop partially encloses gonad .... *Molguloides* *
6. Gonads present on both sides of the body ....*Xenomolgula* *
   Gonad absent from right side of body ....*Rhizomolgula* *
7. Stigmata present ....*Molgula*
   Stigmata absent .... *Fungulus* *
8. Protostigmata present; no true stigmata......9
   Protostigmata not present; with true stigmata..10
9. Internal longitudinal branchial vessels present .... *Protomolgula* *
   Internal longitudinal branchial vessels not present .... *Minipera* *
10. Primary coils of stigmata in rows beneath and between internal longitudinal vessels; left gonad always outside primary gut loop ....*Paramolgula* *
    Primary coils of stigmata in rows beneath internal longitudinal vessels; left gonad not always outside primary gut loop 11
11. Left gonad absent or partially enclosed in primary gut loop; stigmata coiled, not much interrupted, project on conical infundibula *Eugyra*
    Left gonad outside primary gut loop; stigmata coiled, very interrupted, form wide, flat spirals .... *Pareugyrioides*

Genus **Molgula** Forbes, 1848

Type species: *Molgula oculata* Forbes, 1848

Species of this genus have a gonad on each side of the body, entirely outside and dorsal to the gut loop on the left and antero-dorsal to the kidney on the right. The branchial sac is always gathered into folds, usually 7, but occasionally 6 or 8, on each side. A wide velum with delicate circular muscles, is usually present at the base of each siphon.

The genus is represented in Australia by 6 indigenous species, 3 of which are temperate, and 3 recorded only from Moreton Bay; 3 tropical species that have a range extending into the western Pacific; 2 species recorded from Bass Strait that apparently have a sub-Antarctic range: one (*M. mortenseni*) being recorded from New Zealand and one (*M. malvinensis*) being recorded from both New Zealand and the Scotia Ridge; and one introduced species *M. manhattensis* from the northern Atlantic. The last has also been recorded from Japan where its populations have become established. It has been recorded twice from Australia, but it is possible that the Australian populations are ephemeral.

Most of the species recorded have sand embedded in the test and attached to test hairs. They appear to be adapted for the open sea floor lying on, or rooted in, sand.

KEY TO THE SPECIES OF *MOLGULA* RECORDED FROM AUSTRALIA

1. Testis follicles grouped at proximal end of elongate ovary.................................2
   Testis follicles not grouped at proximal end of elongate ovary..................................4
2. Male duct short opening on proximal end of ovary ....*M. sabulosa*
   Male duct long, opening with oviducal opening 3
3. Branchial infundibula exceed 12 per row; body not laterally flattened*M. ficus*

TABLE XVIII — SUMMARY OF CHARACTERS OF SPECIES OF *MOLGULA* RECORDED FROM AUSTRALIA

Species	Range outside Australia[1]	[2]Range in Australian waters	Apertures	Shape of dorsal tubercle	Dorsal lamina	Curve of gut loop	Liver folds	Branchial sac [3]infundibula	Branchial sac [4]internal longitudinal vessels	Gonad shape	Testis position	Testis ducts	Additional features
M. mollis	—	SA - Mackay	sessile	longitudinal or S	long	shallow	rounded pouches	6×2	(6)0	flask	proximal end of	long	apertures depressed; laterally flattened
M. ficus	WP	Broome - Bowen	siphons divergent	reverse S or C	very short	very deep	bipartite	12×2×2	(8–10)3–5	″	″	″	no oesophagus
M. sabulosa	—	Cockburn Sd - Western Port	sessile close	U	long	shallow	″	″	(3)0	elongate	″	short	hollow lobes around apertures; no internal vessels on dorsal side of branchial folds
M. ellistoni	—	SA	siphons divergent	longitudinal	″	deep	transverse	6×2	″	spherical	around	″	development direct; oviparous
M. sphaera	WP	Albany, Moreton Bay	sessile	circular	″	shallow	irregular clumps of parallel folds	6×2+	(3–4)0	″	″	long	irregularly subdived infundibula; sandy brittle test
M. incidata n.sp.	—	Norfolk I., Innisfail	sessile apart	longitudinal	″	deep	longitudinal	6×1	(5)0	″	posterior border of	″	
M. mortenseni	Sub-Antarctic	Bass St	siphons divergent	longitudinal or prostrate S	″	shallow	longitudinal and subdivided	6×2(×2)	(5–6)0	broad	″	″	no oesophagus
M. diversa	WP	Moreton Bay Gladstone	″	longitudinal		very deep	rounded pouches	7×2×2	(3–5)0	elongate			tall, narrow infundibula
M. manhattensis	W Atlantic	Vict., S. Qld	long siphons divergent	U	very short	″	longitudinal	12×2×2	(4)0	″	around	short multiple	naked test
M. calvata	WP	NSW - Albany	siphons divergent	reverse C	short	″	oblique	6×2	(2)0	″	″	″	viviparous; sandy brittle test
M. malvinensis	Sub-Antarctic	Bass St	sessile	longitudinal C or Z	long	shallow	longitudinal	8×2	(7–14)0–1	sinuous	″	long	gonads curve over anterior end of gut and kidney
M. rima	—	Moreton Bay	long siphons divergent	reverse C	″	deep	longitudinal and subdivided	″	(10)0	″	″	″	long test hairs, sandy test

[1]WP, western Pacific. [2]Range is given anti-clockwise around continent. [3]Number per row × subdivisions. [4](on folds) interspace.

Branchial infundibula fewer than 12 per row; body laterally flattened .... *M. mollis*
4. Male duct short, opening on surface of ovary ... 5
Male duct not short, opening with oviducal opening ... 7
5. Ovary spherical ... *M. ellistoni*
Ovary elongate ... 6
6. Internal longitudinal branchial vessels 2 per fold ... *M. calvata*
Internal longitudinal branchial vessels more than 2 per fold ... *M. manhattensis*
7. Ovary spherical or broader than long ... 8
Ovary not spherical and longer than broad ... 10
8. Testis follicles in an almost closed circle around ovary ... *M. sphaera*
Testis follicles confined to proximal border of ovary ... 9
9. Stigmata long and coiled ... *M. mortenseni*
Stigmata neither long nor coiled ... *M. incidata* n.sp.
10. Gonads long and sinuous ... 11
Gonads not long and sinuous ... *M. diversa*
11. Gonad curves close around anterior end of kidney ... *M. malvinensis*
Gonad does not curve close around anterior end of kidney ... *M. rima*

Only a few species of *Molgula* have been recorded from the Indo-West Pacific. In addition to those discussed below, the following species have been recorded from the area, but have not been taken in Australian waters:

Molgula celebensis Millar, 1975, from the Celebes and the Java Sea, is similar to *M. calvata*, but has a greater number of internal longitudinal vessels.

Molgula crinita Sluiter, 1904, is an unusual species with a coiled oviduct.

Molgula longipedata Sluiter, 1904 and *M. flagrifera* Sluiter, 1904, both from Indonesia, are species of *Pareugyrioides*.

Molgula ridgewayi (Herdman, 1906), also from Sri Lanka, does not appear to resemble any species occuring in Australia.

Molgula taprobane Herdman, 1906, from Sri Lanka, resembles *M. mollis* in the number of longitudinal vessels and the gut loop, gonads and body-shape. However, its projecting siphons and short, straight stigmata are distinguishing features.

Molgula calvata Sluiter, 1904
(Figs 183a, 184)

Molgula calvata Sluiter, 1904, p.116. Kott, 1964, p.144. Millar, 1975, p.322.
Molgula reducta Hartmeyer, 1922, p.306. Hartmeyer and Michaelsen, 1928, p.447.
Molgula medusa Kott, 1952, p.297.
Molgula minuta Kott, 1952, p.295.

DISTRIBUTION

NEW RECORDS: New South Wales (Arrawarra, QM GH2213 GH2249). Queensland (Gladstone, QM GH1841).

PREVIOUSLY RECORDED: Western Australia (Triggs I. — AM Y793 Kott 1952; Albany — Hartmeyer 1922, Hartmeyer and Michaelsen 1928, AM Y794 Y1900 Kott 1952). Queensland (Noosa — QM G4956 Kott 1964; Innisfail — AM Y1883 Kott 1964). Indonesia (Sluiter 1904). Philippines (Millar 1975).

The species was taken off the test of specimens of *Ascidia sydneiensis* from fouling plates in Red Rover Creek (Gladstone), and in Oyster Harbour (Albany) at depths between 5.5 and 0.75 m. Other Australian specimens were taken at low tide level.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are rounded or laterally flattened, up to 3 cm in height. Mature gonads are present in specimens from about 0.8 cm. Apertures are either sessile or on short siphons close together on the upper surface of the narrow but deep body; they are directed away from one another. The test is very thin and transparent and has long, fine, hair-like extensions to which sand adheres. The borders of the apertures are produced into small, pointed processes.

INTERNAL STRUCTURE: The body wall is delicate and transparent. Radiating longitudinal muscles extend from the siphons, but are absent from the ventral half of the body. There is a very fine layer of circular fibres. A band of short, parallel muscles extends along the dorsal surface on each side of the mid-line and continues along the upper surface of each siphon. There are broad vela in the base of the siphons. The larger branchial tentacles (about 8) have a few quite long, primary and secondary branches. They alternate with rudimentary tentacles. The dorsal tubercle is large, with a C-shaped slit turned to the left or right, sometimes with inrolled horns. The neural gland is very large. The dorsal lamina is short, the oesophageal opening being halfway down the branchial sac.

There are 7 very reduced branchial folds. Each of the 6 most dorsal folds has a row of 6 shallow infundibula; the most ventral fold in larger specimens has twice that number. Only 2 internal

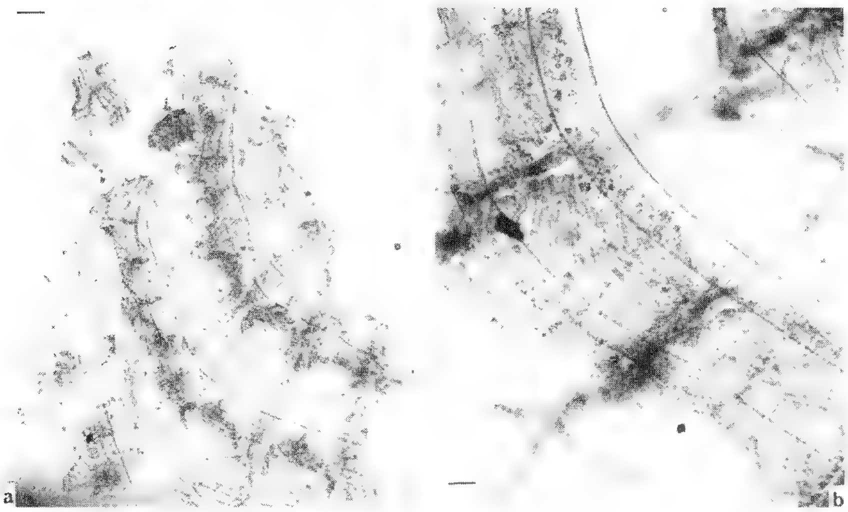


FIG. 183: portion of branchial sacs — **a**, *Molgula calvata* showing 2 stigmata coiling together in each infundibulum; **b**, *Molgula mollis* showing a single stigmat coiling in each infundibulum. (Scales: 0.1 mm).

FIG. 184: *Molgula calvata* — a, right side of body removed from test (QM GH1841); b, gut and gonad on left showing numerous male ducts (AM Y1900); c, liver pouches in pyloric region of gut (AM Y1900); d, kidney and gonad from small specimen with single vas deferens (QM GH1841). (Scales: 1.0 mm).

longitudinal vessels extend over each row of infundibula, one across the apex of each cone and one slightly ventral. There are no internal longitudinal vessels between the folds. The infundibula are moderately tall and wide. They are usually simple, but sometimes divide into 2 at the tip of a cone. The stigmata are long, separate in the interspaces, but curving in pairs around the infundibula. With growth, the separate, initially straight, stigmata in the interspaces curve in to meet the corresponding perforations on the opposite side of the fold at each side of the base of each infundibulum.

The gut loop is long, very narrow and deeply curved. In mature specimens, the pole of the loop is turned over to almost form a circle with its oesophageal end, although this does not occur in specimens less than 6 mm in length. Elongate but broad and loosely arranged glandular pouches are set in oblique rows on the wide pyloric part of the gut. The oesophagus is moderately long.

The gonads consist of a long, cylindrical ovary with a terminal oviduct and long, branched testis follicles, which form a sometimes discontinuous fringed border along the sides of the ovary, sometimes encroaching onto its the upper surface, and sometimes extending beneath it. Vasa efferentia join on the mesial surface of the ovary and open by a variable number of short common ducts along the middle of the upper surface of the ovary. The oviduct is long and wide, with a wide opening at the base of the atrial siphon inside the velum. The left gonad fits into the deep curve of the gut loop, its oviducal opening near the anal opening. The right gonad is parallel to the long, relatively narrow, kidney. The specimen from Albany (AM Y1900, *M. medusa* Kott, 1952) is the largest known specimen (3 cm). It has about 25 crowded male ducts on each ovary. Intermediate-sized specimens from Noosa (1.5 cm) have about 7 male ducts on each side. Smaller specimens have only 1 to 3 male openings on the surface of the ovary.

There are tailed embryos present in the peribranchial cavity of specimens collected from Gladstone in December, 1975 (QM GH1841). They are small and spherical, with an otolith but no ocellus. Eggs are present in the atrial cavity of specimens collected from Triggs I. in December 1948.

REMARKS: The deeply curved gut loop resembles that of *M. manhattensis, M. ficus, M. diversa*, and other species. The present species also resembles *M. manhattensis* in its gonads, deep body, short, diverging siphons and the variable number of short vas deferens openings along the surface of the ovary, distant from the opening of the oviduct. However, the species is distinguished from *M. manhattensis* by its long, coiled stigmata; simple infundibula that are only occasionally subdivided in the top of the cone; no more than 2 internal longitudinal vessels on the folds; short, broad liver pouches and viviparous habit. The sand-embedded test of the larger specimens also distinguishes the present species from *M. manhattensis*.

The most closely related species is *Molgula brieni* Monniot and Monniot, 1976c from Mozambique, differing from the present species in the orientation of its gonads.

Molgula celebensis Millar, 1975 from the Celebes and the Java Sea resembles the present species in its body musculature; the C-shaped opening of its neural duct; the form of its gonads, with a long oviduct opening near the atrial opening; its long, branched male follicles surrounding the ovary; the multiple male ducts on the surface of itsovary; and its loose, radiating liver pouches. The species is distinguished from *M. calvata* only by the large number of internal longitudinal vessels on each fold.

Millar's (1975) specimen from the Philippines differs from the Australian ones in the orientation of its C-shaped slit on the dorsal tubercle. Further, the gut loop resembles that of juvenile Australian specimens and is not as deeply curved as that of the larger Australian specimens. The testis follicles appear to cover the ovary and probably obscure the multiple vasa deferentia. The branchial sac and the large neural gland are identical, however, and possibly the lesser curve of the gut loop is a characteristic of the Philippine populations.

The absence of a light-sensitive ocellus in the larva of *M. calvata*, together with its viviparous habit, suggests that the species is well-adapted for living on the open sea floor.

This species resembles *Euygra* in its small number of longitudinal branchial vessels. However, the stigmata form, tall, wide cones, with curved basal stigmata that meet those of the opposite side at each end of the cone; rather than the square, continuous and relatively flat spirals of *Eugyra* and related species.

FIG. 185: *Molgula diversa* — **a, b**, internal body wall, right and left sides of the body (QM G5991, G9559). (Scale: 2.0 mm).

Molgula diversa Kott, 1972
(Fig. 185)

Molgula diversa Kott, 1972c, p.252. Kott and Goodbody, 1982, p.549.

DISTRIBUTION

NEW RECORDS: Queensland (Gladstone Harbour, QM G9687; Calliope River, QM GH2160; Tannum Sands, QM G9559).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1972c). Hong Kong (Kott and Goodbody 1982).

The species is taken from sand, shell grit and sandy mud substrates down to 10 m. It was taken in Moreton Bay less frequently than were other *Molgula* species that occur there (Kott 1972c).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are either dome-shaped and fixed to a hard substrate (or to other ascidians) by a wide, flat base; or they are almost spherical or oval, lying free on the substrate. They have some test hairs, usually confined to the posterior part of the body. Sand and mud adhere to the hairs and to the test to form a coating of variable thickness. The apertures are on very short siphons, fairly close together on the upper surface and directed away from one another.

INTERNAL STRUCTURE: The body wall is very delicate. Longitudinal muscle bands are confined to the anterior part of the body, radiating from the siphons. Siphonal vela limiting the diameter of the lumen are present in the base of each siphon. The 8 branchial tentacles have long primary branches, but short, secondary branches and minute tertiary branches. These alternate with rudimentary tentacles. There is a wide prebranchial area. The dorsal tubercle, in a fairly shallow peritubercular area, is small, with a simple, oblique slit. The dorsal lamina is a wide, flat membrane, passing to the left of the oesophageal opening at the posterior end of the branchial sac.

Seven tall folds, each with 7 deep infundibula, are present on each side of the branchial sac. The infundibula are subdivided for the greater part of their depth in the fold; the primary meshes are evident only between the folds. The infundibula are subdivided again at the tip of each cone in the edge of the fold. There are 3 to 5 internal longitudinal vessels on each fold. However, those on the dorsal side are delicate, while those on the ventral side are sturdy. There are no longitudinal vessels in the interspace.

The gut forms a long, narrow and deeply curved loop, the pole curving dorsally and reaching the prepharyngeal groove or sometimes curving back into the secondary loop. The oesophagus is short. Small, rounded, glandular pouches are crowded on the expanded pyloric part of the gut. The kidney is relatively small and slightly curved, in the postero-ventral curve of the right side of the body.

The right gonad is dorsal to the kidney; the left gonad lies along the inner curve of the proximal part of the gut loop. The gonads are asymmetrical: the crowded, small terminal branches of very much branched male follicles form a sometimes large and irregular mass along the posterior side of the rather elongate but broad ovarian sac. The terminal oviduct is very short. The vas deferens extends onto the mesial surface of the distal end of the ovary to open near the oviduct.

REMARKS: Characteristic of the species are the divergent apertures; broad siphonal vela; relatively long dorsal lamina; tall subdivided infundibula; deeply curved gut loop; and the arrangement of male follicles along the posterior side of the ovary.

Molgula ellistoni Kott, 1972
(Fig. 186)

Molgula ellistoni Kott, 1972b, p.190.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: South Australia (Elliston Bay — SAM E907 Kott 1972b).

The single record of the species has been from caves where it is subjected to strong swell.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are spherical, small (0.5 cm diameter) and sandy, sometimes forming aggregates and sometimes adhering to individuals of *Euherdmania australis*. The apertures are at opposite ends of the upper surface, directed away from one another.

INTERNAL STRUCTURE: The longitudinal muscles radiating from the short siphons terminate a short distance down the body. There is a very fine external layer of circular muscles around the base of the siphons. The strong circular muscles around both siphons continue into the siphons inside the longitudinal bands. A moderately wide branchial velum is present. The branchial tentacles have short, sometimes rounded and stumpy, primary branches, but no secondary branches. The opening of the neural gland is oval, longitudinally oriented and present on a small tubercle in the centre of a deep, V-shaped peritubercular area. The dorsal lamina passes to the left of a very narrow, unperforated area along the mid-dorsal line of the branchial sac. The oesophageal opening is at the posterior end of this narrow, unperforated area. The dorsal lamina is narrow, with a rather irregular edge.

The dorsal border of the branchial sac is relatively short and the branchial sac is deep, the folds being deeply curved. There are 7 branchial folds on each side of the body, each having a row of 6 primary infundibula, with 3 internal longitudinal vessels: 1 on each side and 1 along the top of each row. Each infundibulum divides into 2 halfway up the fold and the stigmata in the base of each cone are bisected.

FIG. 186: *Molgula ellistoni* (SAM E907) — a, inner body wall; b, gut and gonad. (Scales: 0.5 mm).

The gut forms a narrow, deeply curved, open U-shaped loop around the deep ventral curve of the body. There are broad glandular pyloric folds at right angles to the length of the gut.

The left gonad is in the curve of the gut loop; the right gonad is slightly antero-dorsal to the short, rather broad, bean-shaped kidney, but well separated from it. Each gonad consists of a spherical ovary produced into a long, wide oviduct, its aperture directed posteriorly. The long, branched male follicles radiate around the ovary. The short male duct curves over onto the mesial surface of the ovary and immediately opens to the peribranchial cavity.

REMARKS: Other species (e.g., *M. sphaera*, *M. incidata* n.sp.) have an almost spherical ovary. However, the present species is the only one in which the male duct does not extend along the mesial surface of the ovary to open near the oviduct.

Anural embryos were present in the peribranchial cavity in May, 1971. Direct development has not previously been reported in an Australian species of *Molgula*.

Molgula ficus (Macdonald, 1859)
(Fig. 187)

Caesira ficus Macdonald, 1859a, p.368.
Molgula forbesi Herdman, 1881a, p.236; 1882, p.78; 1891, p.568. Traustedt, 1885, p.19. Sluiter, 1885, p.180; 1890, p.330. Whitelegge, 1889, p.294. Hartmeyer, 1909, p.1323.
Molgula martensii Traustedt, 1885, p.19. Millar, 1975, p.320. Kott and Goodbody, 1982, p.548.
Ctenicella martensii: Hartmeyer, 1914, p.13.
Molgula godeffroyi Michaelsen, 1908a, p.142.
Molgula mortoni Kesteven, 1909, p.289.
Molgula sabulosa: Kott, 1952, p.298; 1964, p.144; 1972c, p.248. Millar 1960b, p.136; 1966, p.374. ? Hartmeyer and Michaelsen, 1928, p.449.
Molgula mollis: Kott, 1975, p.16.
Molgula batemani Kott, 1952, p.296 (part, not specimens from Garden I. < *Eugyra pellucida*).

Distribution

New Records: Western Australia (Broome, WAM 1203.83, BM 1931.2.1.8a; Port Hedland, WAM 1205.83; Barrow I., WAM 198.75; North West Cape, WAM 1202.83; Shark Bay, WAM 1204.83; Cockburn Sound, AM Y2011; Albany, WAM 1200.83 1301.83). South Australia (Spencer Gulf, QM G12799; St Vincent Gulf, QM G10133 GH2000; Kangaroo I., QM G10004). Tasmania (Swan Bay, QM G10127; Hobart, TM D1701). Victoria (Bass Strait, NMV H408 H416 H751 H794 H908, QM G11872; Port Phillip Bay, QM G11868). New South Wales (Solitary I., QM GH9563; Arrawarra, QM GH2250). Queensland (Tallebudgera, QM G10069; Moreton Bay, QM G9492 G9494–7 G9962–72 G9991–2 GH348 GH1376 GH2685 GH3079; Hervey Bay, QM G9369 GH2220; Bundaberg, QM GH2212; Gladstone Harbour, QM G1180 G9798 G10059–60,GH2435; Calliope River, QM G11880 G11885–6 GH2157; Yeppoon, QM GH2235; Heron I., QM G9570).

Previously Recorded: Western Australia (Dampier Archipelago — Traustedt 1885; Shark Bay — Macdonald 1859a; Cockburn Sound, Albany — AM Y789–90 Y1884 Kott 1952). South Australia (Upper Spencer Gulf, Investigator Strait — Kott 1975). Tasmania (Kott 1952; Hobart — Kesteven 1909). Victoria (Port Phillip Bay — Millar 1960b 1966). New South Wales (Port Jackson — Herdman 1881a 1882, Kott 1952). Queensland (Moreton Bay, Gladstone — Kott 1952, QM G6045–6054 G6061–4 G6072–5 Kott 1964 1972c; Bowen — Michaelsen 1908a). Gulf of Siam, Singapore (Millar 1975). Hong Kong (Kott and Goodbody 1982).

This is the widest-ranging *Molgula* species in the Indo-West Pacific. It is especially common in Moreton Bay and Gladstone Harbour.

Description

External Appearance: Individuals are spherical to hemispherical or slightly laterally flattened. Specimens up to 8 cm in diameter have been recorded from Tasmania, but they are seldom more than 4 cm at other locations. The apertures are both on the upper surface, directed away from one another and usually with a thickened ridge of test in the median line between them. The test around the apertures is thickened into conspicuous, wedge-shaped lobes, 6 around the branchial aperture and 4 around the atrial aperture. The apertures and ridge of thickened test are often depressed slightly into the surface, with a raised rim of test surrounding the depressed area. In the larger specimens, the ridge between the apertures is lost and the siphons are longer and divergent. They have external longitudinal furrows between the lobes around the apertures. The apertures themselves are fringed with 2 circles of small, inconspicuous, pointed papillae. The outer circle (on the rim of the branchial aperture) has 18 minute points; the inner circle (just inside the siphon) has 6 groups of 3 pointed papillae, the central projections in each group being the longest. Similar projections are present around the atrial aperture.

In the smaller specimens, the test is white, translucent and relatively tough, but thin and papery in appearance. It has some irregular processes externally and usually has sand or mud, or both, adhering to it (and sometimes embedded in it), causing the test to be rigid. In larger specimens the test is firmer, often almost leathery. Aggregates of this species are often found.

Internal Structure: The musculature consists of radiating longitudinal bands terminating around the upper surface and an external layer of circular fibres that continue down into the siphons inside the longitudinal muscles. Circular muscles are present in the wide velum at the base of each siphon. The opening in the centre of these muscular vela is very small. The branchial tentacles are very bushy. There is a wide prebranchial area with a large, circular, dorsal tubercle just behind the ring of tentacles. The slit of the dorsal tubercle is nearly always reverse S-shaped, although it becomes slightly irregular and convoluted in larger specimens, and the horns are rolled inwards in all but the smallest specimens (0.6 mm, QM G6067). In a single specimen from Western Australia (AM Y1884), the slit is U-shaped, the opening directed forwards with both horns rolled inwards. There is a V-shaped peritubercular area behind the dorsal tubercle. The dorsal lamina is very short indeed, dividing just posterior to the peritubercular area to extend along each side of a wide, unperforated, elliptical, membranous area containing the mid-dorsal opening of the oesophagus toward its posterior end. The pointed posterior end of this

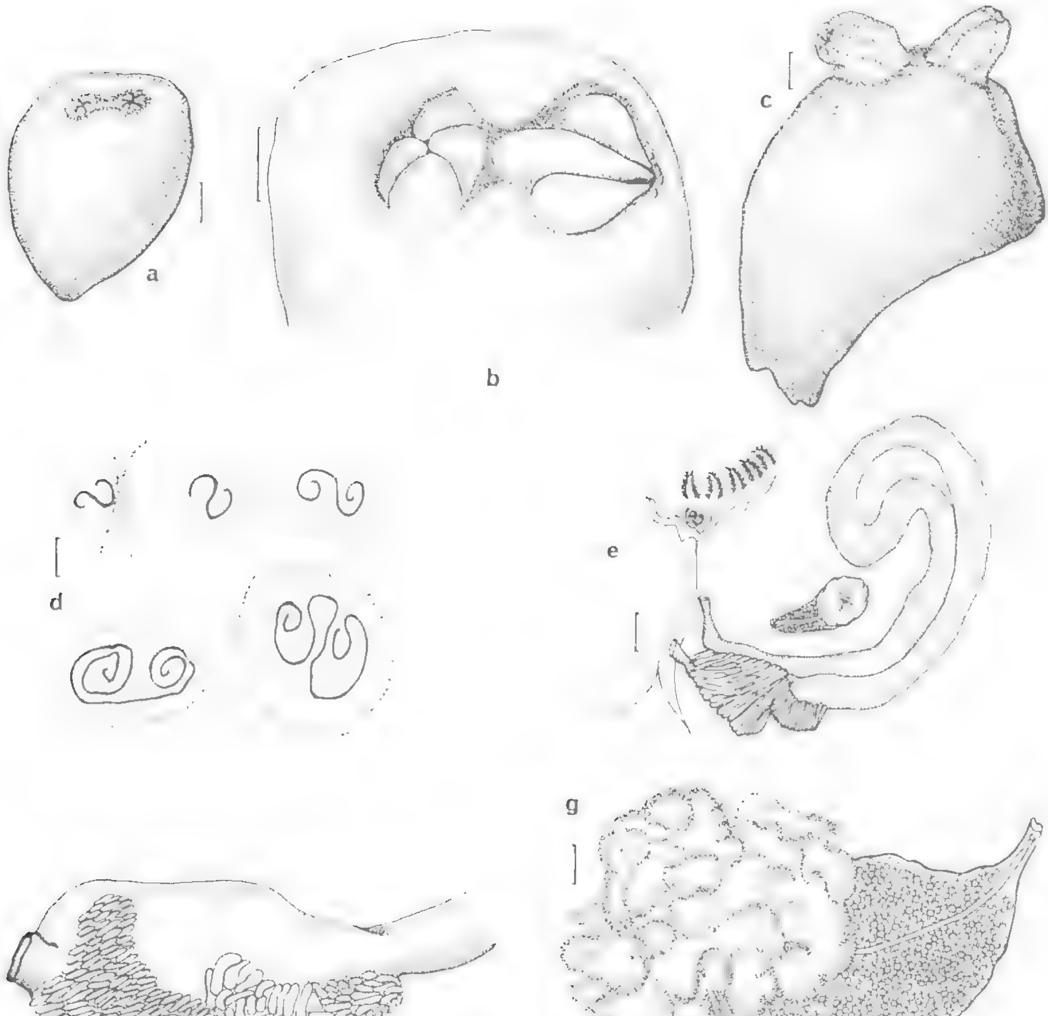


FIG. 187: *Molgula ficus* — **a** – **c**, variations in external appearance (NMV H794, QM G6061, NMV H416); **d**, variations in dorsal tubercle; **e**, left inner body wall (QM GH1376); **f**, well developed liver pouches (QM GH348); **g**, gonad showing exceptional development of male follicles (QM GH348). (Scales: **a** – **c**, 5.0 mm; **d**, 0.5 mm; **e** – **g**, 1.0 mm).

membranous area is continuous with a retropharyngeal groove.

The branchial folds are deeply curved, their posterior ends terminating around the posterior half of the mid-dorsal membranous area. There are usually 7 folds on each side of the body, although one large specimen from Hobart (TM D1701) has an eighth fold on the left. A minimum of 7 internal longitudinal vessels are distributed on both sides of the folds, although the vessels on the dorsal side of the fold are thin, while those on the ventral side are robust and protuberant. Internal longitudinal vessels are usually present between the folds. In large specimens, these vessels are often very irregular and, together with the transverse vessels, break up the area between the folds into extremely irregular meshes. Specimens of less than 2 cm have a single fine vessel between the folds. Branchial formulae are: DL7(8)3(10)3(12)3(12) 2(10)1(6)1(6)OE (4 cm specimen, QM GH348); EO(7) 3(9) 4(10) 5(8) 4(8) 5(7) 4(6) 6DL (8 cm specimen, TM D1701). The 12 primary meshes in each fold are each subdivided by intermediate transverse vessels. The stigmata in the folds are divided once or twice, so that up to 8 tall, narrow infundibula are in each primary mesh. However, the stigmata never coil, although in smaller specimens where the stigmata in the interspaces are still long and regularly arranged, they do curve up toward the fold at each end of the primary mesh. The specimen from Swan Bay, Tasmania (QM G10127), has small punch hole stigmata; it is possibility senescent.

The gut forms a very long, narrow loop, the open terminal part being sharply bent dorsally and posteriorly toward the oesophageal opening to form a C. There is no oesophagus, the opening from the branchial cavity expands immediately into the short, wide pyloric part of the gut. The liver pouches are in two distinct sections. The proximal section consists of relatively long, parallel, oblique folds, which are sometimes broken up into rounded caecae. Distally there is an arc of short, parallel pouches that become more complex in large specimens. The possibly senescent specimen from Tasmania (QM G10127) has both gut and gonads deeply embedded in the body wall.

The left gonad is in the curve of the gut loop, lying parallel to the proximal part of the loop. The right gonad forms an angle with the anterior end of the rather long, curved kidney, or it lies parallel to the kidney. Each gonad consists of a flask-shaped to elongate ovarian sac narrowing to a short terminal oviduct. The long, branched male follicles form a semicircle round the proximal end of the ovary. From outside the body wall, the long, straight edges of these fan shaped lamellae are seen radiating in toward the end of the ovary. However, from inside the peribranchial cavity, the curved and lobed outer arcs of the fan shaped follicles are crowded together and form a hemisphere that obscures the proximal end of the ovary. There is a depression in the centre of this hemisphere over the pointed distal end of the follicles where they meet the vas deferens. The vas deferens extends up over the end of the ovary and along the entire length of its mesial surface to open at the base of the oviduct. When filled with sperm, the vas deferens is wide, narrowing towards its opening.

REMARKS: Millar (1975) accurately distinguished the present species (as *M. martensii*) from *M. mollis* (as *M. sabulosa*) by its long and recurved gut loop, but overlooked distinctions between *M. mollis* and *M. sabulosa*. Kott and Goodbody (1982) separated *M. sabulosa* from *M. martensii* on the basis of valid differences in the branchial sac, length of vas deferens and body shape, but overlooked the characteristic gut loop of *M. martensii* (< *M. ficus*) that distinguishes it from both *M. sabulosa* and *M. mollis*. *Molgula ficus* is distinguished from both *M. mollis* and *M. sabulosa* by its deeply curved gut loop and by the male follicles, which form a close semicircle around the end of the ovary (in the two last species, the male follicles do not actually surround the proximal end of the ovary). It is further distinguished from *M. mollis* by its more numerous branchial infundibula and internal longitudinal vessels and its longer siphons; and is further distinguished from *M. sabulosa* by its longer vas deferens and by the arrangement of the more numerous internal longitudinal branchial vessels on both sides of the folds. The tall, narrow infundibula of the branchial sac resemble those of *M. sabulosa*; however, in the present species, the stigmata are shorter and more often straight (not coiled and irregular as in *M. sabulosa*).

A similar deeply curved gut loop also occurs in *Molgula calvata, M. diversa* and *M. manhattensis*. However, other characters, particularly the gonads, distinguish these species.

Molgula conchata Sluiter, 1898a, from South Africa, has a similar branchial sac, gut and gonads to those of the present species, but its apertures are sessile and can be withdrawn into the body (as in *M. mollis*).

The broad siphonal vela; S-shaped slit on the dorsal tubercle; very short dorsal lamina; tall, narrow infundibula and short stigmata; the presence of longitudinal vessels on both sides of each fold and in the interspaces; long, deeply curved gut loop; the virtual absence of an oesophagus; and the arrangement of liver pouches all distinguish the species.

Molgula incidata n.sp.
(Fig. 188)

DISTRIBUTION

TYPE LOCALITY: Queensland (Mission Beach, epibiont on *Ascidia* sp. intertidal on rubble, coll. P. Kott, August 1961, holotype QM GH1806, paratype QM GH1807).

FURTHER RECORDS: Norfolk I. (QM GH2057). Queensland (Heron I., QM GH2474, paratype GH2559, GH3076).

In addition to the type specimens which were found adhering to the test of an unidentified *Ascidia* sp., individuals were found on *Ascidia liberata* (QM GH3076) at low tide level under boulders. Only a single specimen from Heron I. was found attached directly to the substrate. This does not necessarily indicate a habitat preference. The small sandy specimens are likely to be overlooked unless they are taken as epibionts.

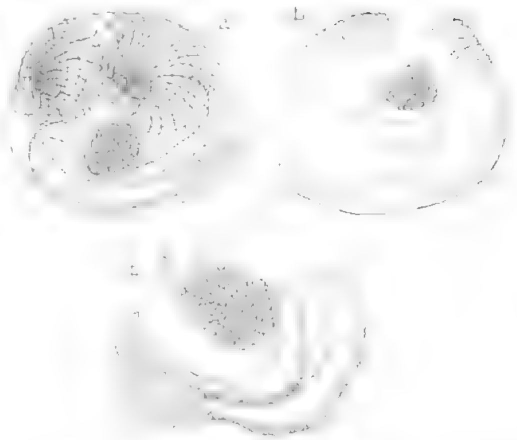


FIG. 188: *Molgula incidata* n.sp. (QM GH1806) — a, body removed from test, from left side; b, body removed from test, from right side; c, gut and gonads. (Scale: 0.5 mm).

DESCRIPTION

EXTERNAL APPEARANCE: The specimens are very small (up to 0.5 cm in diameter), laterally flattened and circular. The apertures are at least half the length of the body distant from one another. The test is very thin and delicate, impregnated with sand.

INTERNAL STRUCTURE: The body wall is very delicate. Radiating longitudinal muscle bands extend from the siphons halfway down the body. There is an external layer of very fine circular bands around the siphons and around the remainder of the body. Wide siphonal vela are present at the base of each siphon. The branchial tentacles have the usual sickle-shaped axis, but only very short, stumpy primary branches and no secondary branches. The dorsal tubercle is an elliptical cushion with a simple longitudinal slit.

There are 6 branchial folds on each side of the body. Each fold has 6 primary meshes and 5 internal longitudinal vessels: 2 on the ventral side of the fold, 2 on the dorsal side and 1 on the rim of the fold. In the paratypes, the stigmata are very short and elliptical, arranged in 2 rows in each mesh, and oriented obliquely from the centre of each mesh toward the outer edge of the fold. However, in the larger holotype, the stigmata are longer and curved in at each end toward those on the opposite side of the fold.

The terminal half to one-third of the gut loop is slightly open and curves toward the dorsal surface to form an approximate right angle with the remainder of the loop. In smaller specimens, the liver pouches in the wall of the expanded pyloric part of the gut are small and rounded, giving a mulberry-like appearance to that part of the gut. In larger specimens, they become elongate and oblique.

The left gonad is in the curve of the gut loop, its proximal border lying parallel to the terminal part of the loop. The right gonad is parallel to the relatively long, curved kidney. The gonads are broad, consisting of a round ovarian sac with male follicles closely applied to its proximal (ventral) border. The short, broad oviduct, from the middle of the dorsal side of the ovarian sac is curved around to open postero-ventrally. The vas deferens extends dorsally across the surface of the ovary from the ventral border. Its distal half, which is slightly sinuous, projects into the atrial cavity, surrounded by a layer of the body wall. Eggs (QM GH1086-7, GH2559) and tailed embryos (QM GH2057, GH3076) 0.2 mm long with an otolith but no ocellus were present in the peribranchial cavity. Their retention in that cavity, rather than being released through the atrial aperture, is probably a result of the ventral orientation of the oviducts.

REMARKS: The gonads of this species resemble those of *M. millari* Kott, 1971 from the sub-Antarctic. However, it is unlikely that the latter species has a range from tropical to sub-Antarctic waters. Morphologically, the Subantarctic species can be distinguished by its longer gonoducts, smaller liver pouches and fewer internal longitudinal vessels, confined to the ventral sides of the folds.

Molgula malvinensis Arnback, 1938
(Fig. 189)

Molgula malvinensis Arnback, 1938, p.5. Van Name, 1945, p.407. Kott, 1954, p.135; 1969a, p.149. Millar, 1960b, p.132.
Molgula spiralis Kott, 1954, p.134.
Molgula herdmani Brewin, 1958, p.451. Millar 1982a, p.91.
Molgula bathamae Millar, 1982a, p.91.
Molgula longivascula Millar, 1982a, p.93.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H391 H397 H788).

PREVIOUSLY RECORDED: New Zealand (Stewart I. — Brewin 1958; Otago — Millar 1982a). Sub-Antarctic (Macquarie I. — Kott 1969a, Millar 1982a; Falkland Is — Arnback 1938; South Georgia — Millar 1960b). Antarctic (Weddell Sea — Kott 1969a).

DESCRIPTION

EXTERNAL APPEARANCE: The Bass Strait records each represent only a single specimen. They are all small, the maximum external dimension (length) being approximately 1.5 cm. This measurement includes the very thick coat of mud and sand attached to, and enmeshed in, the fine test hairs that are present all over the surface. The hairs are longest posteriorly. The test itself is very thin and delicate. The apertures are sessile, the branchial aperture terminal and the atrial aperture about one-third of the body length distant from it. The body is rounded in section and only slightly laterally flattened.

INTERNAL STRUCTURE: The bodies of the newly recorded specimens, when removed from the test, are only about 5 mm long (antero-posterior) and 3 mm wide (dorso-ventral). The body wall is firm, with rather strong longitudinal musculature along its whole length. Transverse bands extend across the dorsal and ventral mid-line posterior to the apertures. The branchial tentacles have long primary and secondary branches, but the tertiary branches are minute. The peritubercular area is a wide V. The small, circular dorsal tubercle has a simple, vertical slit. The dorsal lamina is long and wide.

There are 6 rounded branchial folds on each side of the body. The 2 ventral folds on each side have 5 internal longitudinal vessels; the 4 most dorsal folds have 7. The vessels are on both sides of the folds, but are absent between the folds. There are 8 simple infundibula with long, coiled stigmata projecting up into each fold.

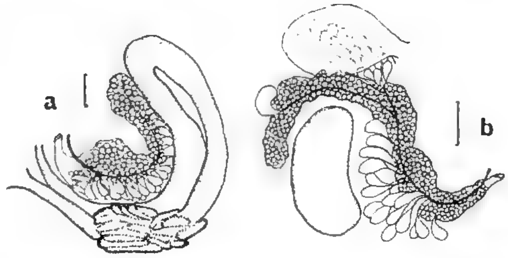


FIG. 189: *Molgula malvinensis* (NMV H397) — **a**, gut and gonad; **b**, kidney and gonad with anterior male follicles embedded in an endocarp-like thickening of the body wall. (Scales: 0.5 mm).

The gut forms a narrow loop, only slightly open at the pole. It is curved into a wide, shallow U. The oesophagus is quite long. The long, oblique and slightly irregular liver pouches are green.

The ovaries are long and narrow. The large, branched male follicles are scattered in irregular groups around the sides of the ovary and out into the body wall some distance from the ovary. The left gonad follows the inner curve of the gut loop. Sometimes (NMV H397), it almost reaches to the pole of the loop, but does not extend anterior to it. On the right, the sinuous gonad curves dorsally and posteriorly over the anterior end of the broad, oval kidney from about halfway down its ventral border. The distal half of the long gonad diverges from the dorsal border of the kidney and curves dorsally and anteriorly to terminate in long, separated male and female ducts, both of which open near the atrial opening. Vasa efferentia join the vas deferens, which runs along the middle of the mesial surface of the ovary.

There is a large, circular, endocarp-like thickening of the body wall over the pole of the gut loop and the proximal end of the left gonad. On the left, a similar thickening occurs in a corresponding position over the outer part of the anterior curve of the gonad.

REMARKS: Millar (1982a) believes many of the synonyms listed above to be distinct from one another on the basis of the relative length of the oviduct and vas deferens. Both ducts open together and are quite long in *M. malvinensis* Arnback (from Kerguelen, the Scotia Ridge, Weddell Sea, and the Antarctic continent); the vas deferens is exceptionally long and the oviducts very short in *M. longivasculosa* Millar (from Macquarie I.) and *M. herdmani* Brewin (from Stewart I.); and *M. bathamae* Millar (from the Otago Peninsula) has a long oviduct and long vas deferens, although the latter extends dorsally from halfway along the ovary. *M. malvinensis* and *M. longivasculosa* are known from numerous specimens; *M. bathamae* and *M. herdmani* from only a few.

There is some evidence from the pattern of occurrence of these characters that the Macquarie I. population may be genetically isolated, although a relationship with populations sampled at Stewart I. appears to persist. However, specimens from Portobello have long oviducts resembling those of specimens from the Scotia Ridge and Falkland Is. The male and female gonoducts of the present specimens from Bass Strait are identical to those of the type material.

The variations in characters so far recorded are not inconsistent with the intraspecific variability that could be expected in such a wide-ranging species. On the available data, separation of the species appears not to be justified.

Molgula malvinensis closely resembles *M. rima*. It is distinguished primarily by the left gonad which, in the present species, curves anteriorly in its proximal half, parallel to the gut loop, while in *M. rima* it bends posteriorly.

Molgula manhattensis (De Kay, 1843)
(Fig. 190)

Ascidea manhattensis De Kay, 1843, p.259.

Molgula manhattensis: Van Name, 1945, p.385 and synonymy. Tokioka and Kado, 1972, p.21. Kott, 1976b, p.450. Nakauchi and Kajihara, 1981, p.66.

?*Molgula recumbens* Herdman, 1899, p.56.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Victoria (Yarra River — Kott 1976b). ? New South Wales (Port Jackson — Herdman 1899). Queensland (Brisbane River — Kott 1976b). Japan (Takehara City, salty pond — Tokioka and Kado 1972; Bay of Hamana-ko, Tokyo Harbour — Nakauchi and Kajihara 1981).

The natural range of the species is apparently on the Atlantic coast of North America, from Maine to Louisiana. It is thought to have been transported by ship to Japan (Tokioka and Kado 1972) and to Australia (Kott 1976b). The species is unusual in that it tolerates a great range of salinities: from 11 ‰ to over 20 ‰ chlorinity (Van Name 1945, Tokioka and Kado 1972 and Kott 1976b).

It is usually taken from shallow waters down to 30 m (Van Name 1945).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are circular to oval, up to 2.5 cm high, usually longer dorso-ventrally than antero-posteriorly. Both apertures are on moderately long and usually divergent siphons from the short upper surface.

FIG. 190: *Molgula manhattensis* (after Kott 1976b) — **a**, external appearance; **b**, branchial sac showing irregular stigmata between folds; **c**, inner body wall showing kidney, gut loop and gonads. (Scales: 1.0 mm)

The test is whitish and rather papery, but translucent and relatively tough. It is covered with sparse, short hairs to which fine sand and mud adhere. On the basal half of the body, the hairs are usually longer and form root-like processes. There are small pointed processes on the rim of the apertures.

INTERNAL STRUCTURE: The body wall is very thin and adheres closely to the test. Longitudinal muscles extend along the siphons and radiate over the anterior half of the body. There is a thin and inconspicuous external layer of circular muscles over the whole of the body. A muscular velum projects into the lumen on each side at the base of both atrial and branchial siphons. The branchial tentacles are very bushy. The dorsal tubercle is a circular cushion with a U-shaped slit, the open interval directed posteriorly and both horns turned inwards. The dorsal lamina is very short.

The branchial sac has 6 narrow and deeply curved folds on each side. There are usually 4 broad, projecting internal longitudinal vessels on the folds, although there are only 3 on the dorsal and ventral folds. No internal longitudinal vessels are present in the wide, flat interspaces, although there are many rather long, irregular stigmata and also narrow accessory infundibula with coiled stigmata, between the primary coils. In the folds, the infundibula are subdivided twice and interstitial coils are also present.

The gut loop is narrow and deeply curved, the distal part of the loop being curved dorsally and posteriorly. The stomach is relatively long, with parallel longitudinal liver pouches oriented obliquely. The anal border has 12 shallow lobes.

The left gonad fits into the curve of the gut loop; the right gonad lies parallel to the dorsal border of the long, narrow and gently curved kidney. The ovary is a long, cylindrical sac with a terminal oviduct opening near the anal opening at the base of the atrial siphon. The groups of crowded, branching male follicles are scattered chiefly along its ventral border. Sometimes they are also present around the proximal end and there may be a few scattered groups of follicles along the dorsal side of the ovary. Vasa efferentia cross the mesial surface of the ovary to join one of the series of very short vasa deferentia arranged along the centre of the ovary. There are fewer vasa deferentia (1 or 2) on the left gonad than on the right (up to 6). The species is oviparous.

REMARKS: Kott (1976b) discusses the relationship of this species with the eastern Atlantic species *M. tubifera* Oersted, which has male follicles all around the ovary (instead of mainly on the ventral side), often a long vas deferens opening near the oviduct (instead of short ducts along the surface of the ovary) and only occasional accessory coils of the stigmata, which are generally shorter than those of *M. manhattensis*. Kott (1976b) concluded that the species are distinct from one another. However, *M. tubifera* tolerates a similar range of salinities and occupies similar habitats to the present species (Berrill 1950).

The gonads and gut of western Pacific *M. calvata* also resemble those of the present species; however the two species are readily distinguished from one another by the branchial sac (see *M. calvata*, Remarks).

Molgula recumbens Herdman, 1899, with its long, diverging siphons and short, rather irregular, stigmata in the interspaces between the branchial folds, also superficially resembles *M. manhattensis*. It may be evidence of an earlier introduction of the species to Port Jackson.

Molgula mollis Herdman, 1899
(Figs 183b, 191)

Molgula mollis Herdman, 1899, p.54. Kott, 1952, p.298; 1964, p.144; 1972a, p.45; 1976a, p.87. (Not: 1975, p.16, < *M. ficus*).
Molgula sydneyensis Herdman, 1899, p.55.
Molgula sabulosa : Millar, 1975, p.320.
Molgula junis : Millar, 1966, p. 374. (Not: Kott, 1952, p.295, < *M. sabulosa*).

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H378 H410 H780 H781, QM G12736 GH1843; off Cape Howe, ZMC 30.9.14). New South Wales (Nelson's Bay). Queensland (Moreton Bay, QM GH2049-2052; Gladstone Harbour, QM G12707; Heron I., QM GH2616).

PREVIOUSLY RECORDED: South Australia (St Vincent Gulf — Kott 1972a). Victoria (Port Phillip Bay — Millar 1966; Western Port — Kott 1976a). New South Wales (Twofold Bay — AM Y8788 Kott 1952; Botany Bay — AM Y1902 Kott 1952; Port Jackson — holotype *M. sydneyensis* AM U276, syntypes *M. mollis* AM G12226 G2052 Herdman 1899). Queensland (Moreton Bay, Noosa, Gladstone — Kott 1964; Mackay — Millar 1975).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are small, (up to 3 cm in diameter) and may be egg-shaped, top-shaped or lens-shaped. The test is very delicate, although the sand embedded in the test can make it hard and rigid. Sand grains also adhere to the fine hairs that project through the sand. The hairs, which are short and inconspicuous in larger specimens, are more crowded around the dorsal and ventral border of the body than on the sides. The sessile apertures are at opposite ends of a thin median strip of sand-free test along the upper margin of the body. Sandy test along each side closes over the top of this median strip when the apertures are withdrawn. In larger specimens (AM Y1902), only a vestige of this thin median strip of test remains, and it is often completely obscured, as the apertures on the surface are completely surrounded by sand and well separated from one another.

INTERNAL STRUCTURE: Very fine longitudinal muscles radiate from each of the apertures and extend about three-quarters of the way down the body. A thin external layer of equally fine circular muscles covers the whole body. The musculature is thicker in larger specimens, rendering the body wall opaque. When the apertures are withdrawn, a sharp fold of the body wall, with the longitudinal muscles curving over it, projects along each side of the mid-line on the upper border of the body. In some specimens (GH1843) there is a tuft of small vascular papillae that project from the

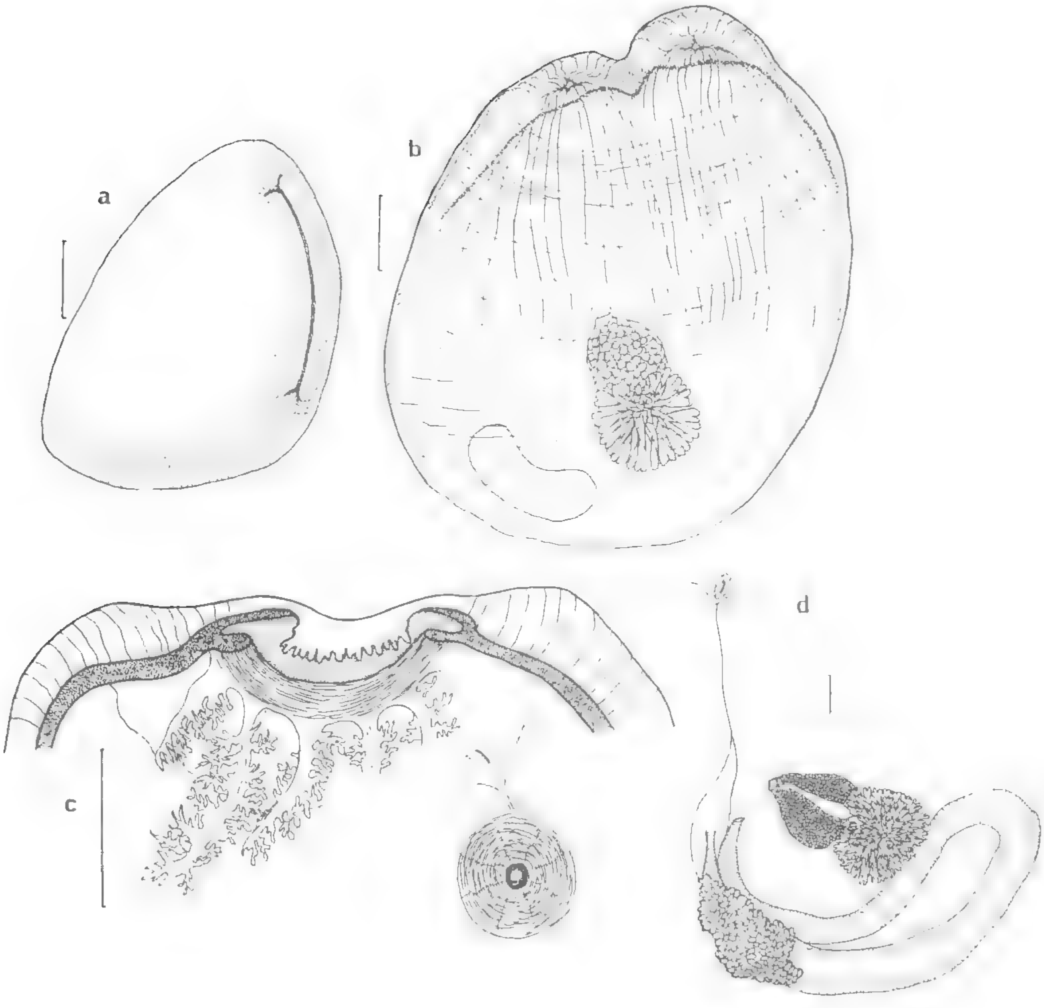


FIG. 191: *Molgula mollis* (NMV H410) — **a**, external appearance; **b**, body removed from test, from right; **c**, anterior part of pharynx (showing rim of test to the right of the apertures, the severed branchial velum and closed atrial velum, branchial tentacles partly removed and dorsal tubercle); **d**, inner body wall, left side. (Scales: **a**, 5.0 mm; **b**, **c**, 2.0 mm; **d**, 1.0 mm).

ventral mid-line at about the level of the pole of the gut loop.

There is a wide velum with circular muscles and a small central opening inside each aperture. The branchial tentacles are long, with relatively long primary and secondary branches. The dorsal tubercle is an oval cushion. The slit is elongate and either straight or with the ends of the slit turned slightly, in opposite directions, to form a very long S. In the largest specimens, the aperture is wide open and almost circular. The dorsal lamina is moderately long, extending to about halfway down the body before passing to the left of the unperforated membranous area that surrounds the oesophageal opening. The enlarged neural gland reported by Herdman (1899) is not always present.

The branchial sac has 7 folds on each side of the body. There are always 2 broad internal longitudinal vessels on the ventral side of the fold, one on the edge and 3 very fine longitudinal vessels toward the edge of the dorsal side of the fold. Longitudinal vessels on the dorsal side of the fold are so fine that they are often difficult to see in smaller specimens, but are quite conspicuous in specimens of 3 cm diameter. There are no vessels between the folds. There are 6 primary meshes along each fold except the ventral one, where there are 12. Each mesh divides into 2 broad, conical infundibula in the fold. The stigmata in the interspace are divided by intermediate transverse vessels and curve up toward the fold at each end of the mesh. The stigmata in the fold are longer, coiling around each cone. Occasionally, there are small accessory coiled stigmata between the primary coils in the interspace at the base of the folds. Only a single stigma coils in the tip of each infundibulum. With age, the stigmata in the interspace become irregular, while those in the folds are interrupted by robust parastigmatic vessels (which do not further subdivide the infundibula).

The gut, which is in the posterior half of the body, forms a gently curved loop, open in its terminal half. The oesophagus is short. The pyloric part of the gut is expanded and its wall is produced into rounded liver pouches. Short, parallel, elongate pouches form a single, small arc at the distal end of the liver only in the largest specimens. The kidney is bean-shaped, but becomes very long and narrow with age.

The proximal end of the left gonad lies hard against the anterior half of the descending limb of the gut loop; the right gonad lies at an angle with the curved kidney. The gonads consist of a relatively short, very broad ovary, narrowing to a short oviduct dorsally. Testis follicles are long and branched, fan-shaped lamellae arranged in a complete circle between the end of the ovary and the intestine. The terminal lobes on the outer arc of each lamella are crowded, forming a hemisphere with a depression in the centre that projects into the atrial cavity. A ligament passes through the depression in the centre of the testis to join the body wall to the branchial sac. The follicles converge to a central point beneath the mesial depression in the hemisphere. Here, short vasa efferentia join the common vas deferens. The vas deferens moves inwards from beneath the testis onto the mesial surfaces of the ovary, where it expands into a wide, seminal vesicle and then gradually narrows to the male opening on the surface of the oviducal opening. In some specimens, the hemisphere of male follicles is cut off sharply where it presses against the gut loop. The diameter of the testis is only slightly greater than the width of the ovary.

REMARKS: The general form of the gonad is similar to that of *M. ficus*. However, in *M. ficus*, the testis forms a semicircle around the end of the relatively long and narrow ovary (rather than forming a circle ventral to the end), and the branchial infundibula are tall, narrow, more numerous and subdivided twice in the folds. *Molgula mollis* is also distinguished by its thin, sandy, brittle test; laterally flattened and circular shape; sessile apertures; relatively long dorsal lamina; wide siphonal vela; crowded and rounded liver pouches with only a small arc of more or less elongate pouches; and a relatively short and gently curved gut loop.

Molgula mortenseni (Michaelsen, 1922)
(Fig. 192)

Ctenicella mortenseni Michaelsen, 1922, p.365.
Molgula mortenseni: Brewin, 1951, p.111; 1952b, p.188; 1957, p.578; 1958, p.440; 1960, p.120. Millar, 1982a, p.97.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV H741 H410; Western Port, QM G9712).

PREVIOUSLY RECORDED: New Zealand (Bay of Islands and south to Stewart I. — Michaelsen 1922, Brewin 1951-1960, Millar 1982a).

This appears to be a southern temperate species with a range between New Zealand and southern Australia. It can be expected to occur off Tasmania.

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are about 2 cm in diameter. There are almost spherical, only slightly laterally flattened. The apertures are on

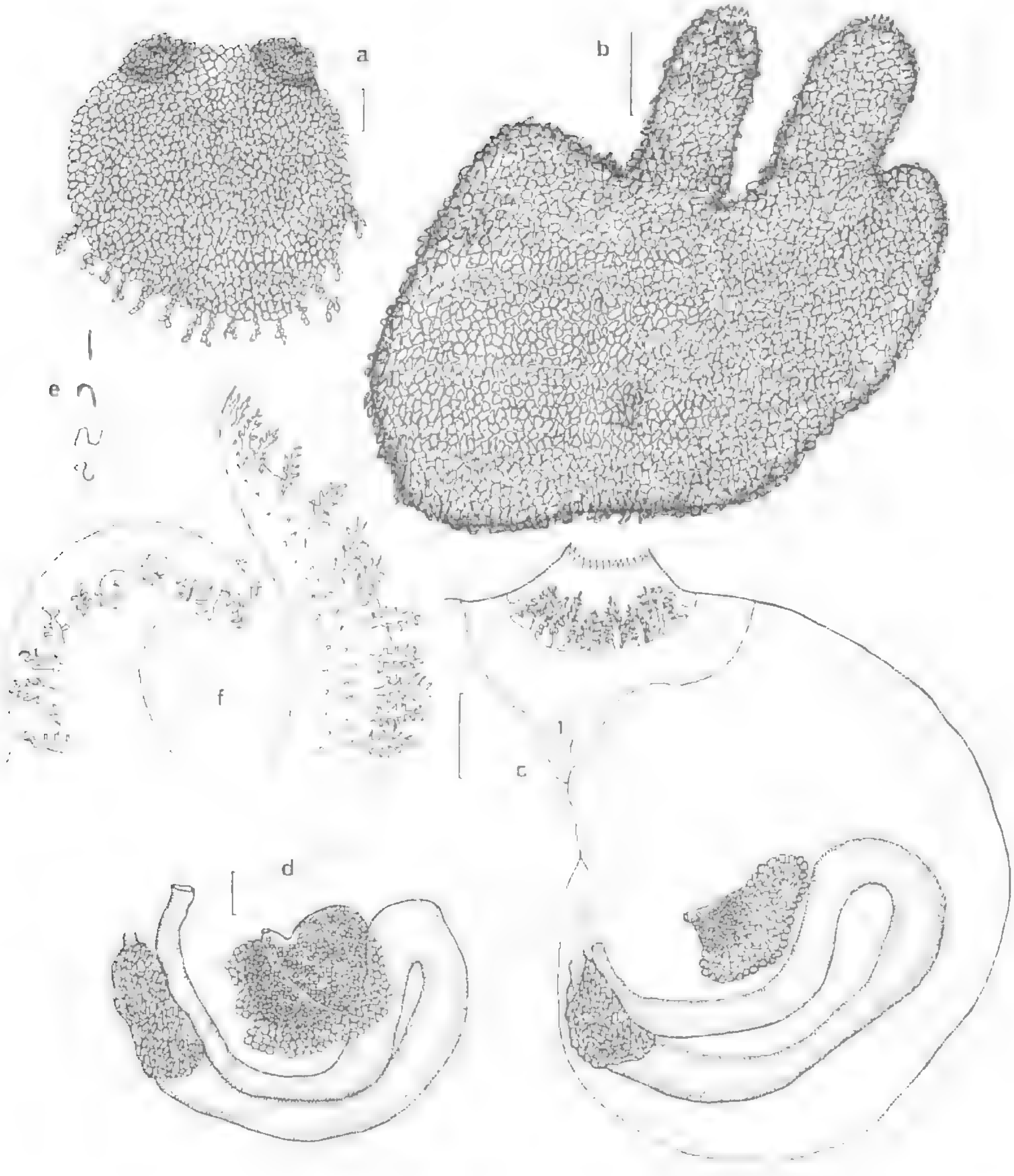


FIG. 192: *Molgula mortenseni* — a, b, external appearance (NMV H742, QM G9712); c, left side inner body wall (NMV H742); d, gut and gonads (QM G9712); e, variation in openings of neural gland; f, branchial tentacles (after Millar 1982a). (Scales: a – c, 2.0 mm; d, 1.0 mm).

siphons of variable length. They are very long indeed (about 4 mm) in one specimen (QM G9712), and project upwards, parallel to one another. In the majority of specimens (all from Bass Strait), the siphons are short and hemispherical, and each has a ring of thin test around the base that allows it to be withdrawn slightly into the surface of the body. They are quite close together on the upper surface. The test is very thin and flexible. It is covered with a layer of sand, which is embedded in and adherent to the external layer and to the very fine test hairs that project from the surface all over the body. There are small, crowded, pointed projections around the rim of each aperture.

INTERNAL STRUCTURE: The body wall is thin, with fine, radiating longitudinal muscles, and a very thin external layer of circular muscles over the whole body. An internal layer of very strong circular muscles is also present in the siphons and in the broad muscular velum at the base of each siphon. Eight relatively short branchial tentacles with both primary and secondary branches alternate with rudimentary tentacles. The prebranchial area is extensive. The small, oval dorsal tubercle is in the centre of a very wide, V-shaped peritubercular area. The opening of the neural gland is a longitudinal slit, developing into a horizontal S-shape. The dorsal lamina is only moderately long, passing to the left of the unperforated, elliptical, membranous area that surrounds the oesophageal opening.

The branchial sac has 7 folds on each side. Anteriorly, the dorsal folds terminate along the sides of the peritubercular area; posteriorly, they terminate around the sides of the membranous area that surrounds the oesophageal opening. A retropharyngeal groove runs between the posterior end of this membranous area and the endostyle. There are 5 or 6 internal longitudinal vessels on most of the folds: 2 near the edge of the dorsal side, 1 on the edge of the fold and 2 or 3 evenly spaced on the ventral side of the fold. The vessels on the edge and on the ventral side of folds are most developed, while those on the dorsal side are delicate and inconspicuous. There are 6 primary meshes in each fold. Each mesh has especially long and almost straight stigmata between the folds. These curve up toward the fold at each end and are divided in the centre by an intermediate transverse vessel. In the folds, the divided stigmata lengthen and coil around two infundibula. There are 2 or 3 parastigmatic vessels extending down each side of each infundibulum and across the interspace. The cones are sometimes subdivided a second time right at their apex in the edge of the fold. Occasionally there are some accessory coiled stigmata between the primary coils. Only a single stigma coils in the tip of each infundibulum.

The gut forms a gently curved loop, open at the pole, across the posterior end of the body. The oesophagus is very short indeed. It opens almost immediately into an expanded, but short, pyloric region, which has oblique glandular pouches that are usually irregularly subdivided into rounded or oval caeca.

The left gonad has its long proximal border against the anterior part of the descending limb of the gut loop. The proximal border of the right gonad is parallel to the oval, barely curved, kidney, but is anterior to the kidney for about half of its length. Both gonads have a very broad but short ovary (about twice as wide as it is long), with a short, wide oviduct in the centre of the long dorsal border. The male follicles radiate around the long proximal or ventral side of the ovary, and the broad male duct extends across the middle of the ovary to open just above the female opening. The male follicles are very long and branched, forming a very wide arc of crowded lobes on the ventral side of the ovary

REMARKS: The New Zealand specimens closely resemble those from Australia in all respects, except for their greater number of internal longitudinal branchial vessels (up to 10). The short oesophagus is similar to that of *M. ficus*, but the present species does not have the same bipartite liver, the tall, narrow and numerous infundibula, the long, deeply curved gut loop, very short dorsal lamina and elongate ovaries. The dorsal lamina, short gut loop, and branchial sac resemble those of *M. mollis* but the liver pouches and gonads are different.

The species is characterised by its wide siphonal vela; the length of its dorsal lamina; its wide branchial meshes and tall, but not narrow, infundibula; short oesophagus; short pyloric region and obliquely arranged liver pouches; short gut loop; very short and wide ovary; and long, branched male follicles.

The long siphons of the Western Port specimen resemble those sometimes found in *M. manhattensis* (Tokioka and Kado 1972) and those described by Herdman (1899) for *M. recumbens*. However, other characters, particularly the branchial sac, are identical with those in the Bass Strait specimens of the present species. It is possible that the long siphons are a response to environmental pressures, as they appear to be in the Japanese specimens of *M. manhattensis*.

Molgula rima Kott, 1972
(Fig. 193)

Molgula rima Kott, 1972c, p.250.

DISTRIBUTION

NEW RECORDS: None.

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1972c).

This species is recorded from sand, shell-grit and sandy mud down to 10 m. Data from Moreton Bay suggest that the individuals have a 6-month life span (Kott 1972c).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are small, oval, and laterally flattened. The thin, transparent test has very long, hair-like processes to which a coating of sand and mud adheres. This coating conceals the rather long siphons that project through it. The siphons are separated from each other by about one-third of the body length.

INTERNAL STRUCTURE: The body wall is delicate:the only strong muscles are those around the siphons and the bands of short, parallel muscles along each side of the dorsal and ventral mid-lines. The latter are probably associated with the lateral flattening of the body. Only very narrow vela are present at the base of each siphon. There are 8 branchial tentacles, with long primary and small secondary branches, alternating with rudimentary tentacles. The dorsal tubercle is a small cushion in a wide peritubercular V. Its C-shaped slit is turned to the right. The dorsal lamina is long, the oesophageal opening being almost at the posterior end of the branchial sac.

Each side of the body has 6 branchial folds, each with a row of 8 tall, conical infundibula. Sometimes these are subdivided (but never more than once) at the top of the cone. Up to 10 internal longitudinal vessels are present on each fold, some on each side of the fold. The long stigmata coil around the infundibula for most of their height in the folds.

The gut loop is long and deeply curved, open at the pole. It extends anteriorly almost to the prepharyngeal groove. There are irregularly arranged longitudinal and circular glandular pouches in the pyloric region. The kidney is bean-shaped.

The gonads are long, deeply curved, sometimes S- or U-shaped, the concavity of the U directed posteriorly. The right gonad extends anteriorly from the kidney and then curves back towards the atrial aperture. The left gonad, which is in the curve of the gut loop, is deeply curved. Long and much-branched male follicles form wide bands in the body wall, usually all around the ovary, but sometimes absent from part of its border. The vas deferens extends along the middle of the mesial surface of the ovary to open near the oviducal opening.

FIG. 193: *Molgula rima* (QM G6235) — inner body wall. (Scale: 2.0 mm).

REMARKS: Characteristics of the species are the long test hairs, lateral flattening, thin and flexible test, long siphons, almost entire and only slightly subdivided infundibula, long coiled stigmata, deeply curved right gonad and long, narrow and much-branched male follicles.

The gonads resemble those of *M. malvinensis*, but are in a different position. The proximal end of the left gonad never curves anteriorly parallel to, and sometimes around the top of, the pole of the gut loop (as it does in *M. malvinensis*), but always curves posteriorly. Both species have similar branchial sacs, with 8 tall, undivided infundibula in each fold. However, the present species has fewer muscles and more internal longitudinal vessels and its liver lacks the regular and narrow parallel folds of that of *M. malvinensis*.

Molgula sabulosa (Quoy and Gaimard, 1834)
(Fig. 194)

Ascidia sabulosa Quoy and Gaimard, 1834, p.614. Dujardin, 1837, p.586; 1840, p.536.

Cynthia sabulosa: Gervais, 1840, p.405.

Astropera sabulosa: Pizon, 1898a, p.343; 1898b, p.273.

Molgula sabulosa: Kott 1972b, p.190; 1975, p.16; 1976a, p.86. (Not: Hartmeyer and Michaelsen, 1928, p.449, < *M. ficus*. Kott, 1952, p.298; 1964, p.144; 1972c, p.248, < *M. ficus*. Millar, 1960b, p.136; 1966, p.374, < *M. ficus*; 1975, p. 320, < *M. mollis*).

Caesira parasitica Macdonald, 1859a, p.367.

Molgula nodosa Hartmeyer, 1922, p.304. Hartmeyer and Michaelsen, 1928, p.445. Kott, 1952, p.293.

Molgula janus Kott, 1952, p.295.

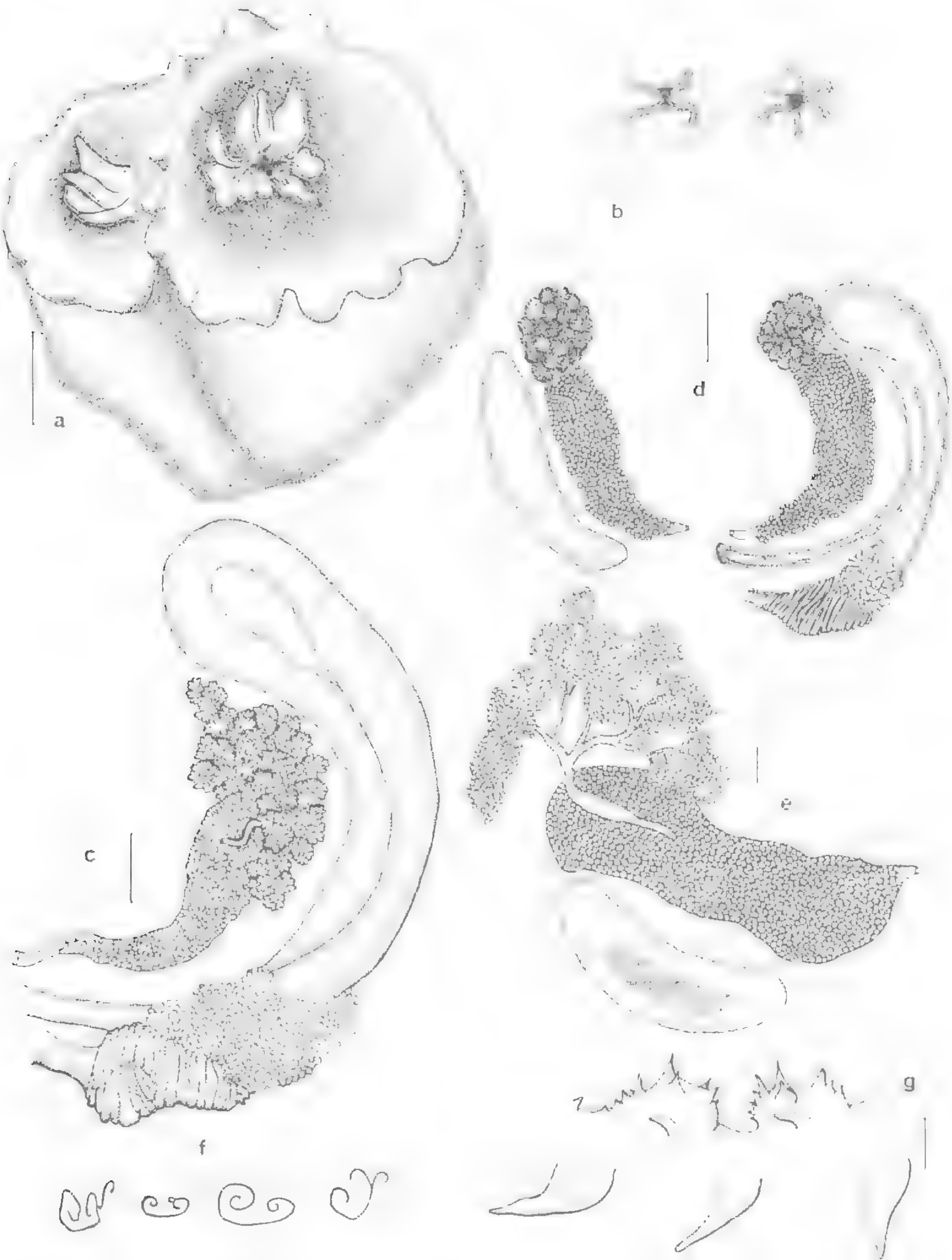


FIG. 194: *Molgula sabulosa* — **a**, external appearance nodose specimen (NMV H448); **b**, apertures of smooth specimen with hollow lobes closed (NMV F51585); **c**, gut and gonad showing clumps of male follicles at proximal end of ovary (QM GH1847); **d**, inner body wall showing gut, kidney and gonads with clumps of male follicles crowded together (NMV H448); **e**, kidney and gonad with clumps of male follicles well-separated from one another (WAM 99.75); **f**, variations in opening of neural gland; **g**, projections of the body wall on the rim of the apertures (NMV H448). (Scales: **a**, **b**, 5.0 mm; **c**, **e**, 2.0 mm; **d**, 1.0 cm; **g**, 1.0 mm).

DISTRIBUTION

NEW RECORDS: Western Australia (Bremer Bay, WAM 99.75). South Australia (Elliston Bay, QM GH1847). Victoria (Western Port, F51585; Pt Leo, AM Y1890; Bass Strait, NMV H448).

PREVIOUSLY RECORDED: Western Australia (Cockburn Sound, Bunbury — AM Y791-2 Kott 1952; Hartmeyer 1922; King George Sound — Macdonald 1859a). South Australia (St Vincent Gulf — Kott 1952; Elliston Bay — Kott 1972b 1975). Victoria (Western Port — Quoy and Gaimard 1834, Kott 1976a).

DESCRIPTION

EXTERNAL APPEARANCE: Specimens are spherical, 2 to 3 cm in diameter. The sessile apertures, which are fairly close together on the upper surface, are surrounded by large, hollow, flattened test lobes. There are 6 of these around the branchial aperture and 4 around the atrial aperture. They are, however, variable and sometimes subdivided and irregular, so that the primary number of lobes is obscured. Each aperture and its surrounding lobes can be withdrawn slightly into the body. The hollow lobes (pointed, rounded or straight-ended) fold in over the apertures when they are withdrawn.

A wide area of the body around each aperture is often flattened, with a slight rim of test standing up around each flat, circular area. This rim is sometimes produced into evenly spaced, hollow swellings, or into almost spherical, hollow nodules. In Western Australian specimens these nodules are also present over the rest of the body, with protruberances of the body wall fitting into them. The nodules are not always present, however, and their occurrence may represent a cline in populations of the species from east to west. Spherical specimens without nodules are from Western Port, Pt Leo (Victoria) and Elliston Bay and Victor Harbour (South Australia). Specimens from Bass Strait (NMV H448) have a wide circle of hollow swellings around each aperture, while larger specimens from Western Australia (west of the Great Australian Bight) have nodules all over the body. There are also smaller, inconspicuous, fleshy-processes around the rim of the apertures, which alternate with the external lobes. Each of these fleshy processes have 2 central pointed papillae (one inside the other), a series of smaller lateral points down each side, and an external point near the centre base.

The test is thin, but stiff and brittle with embedded sand. Specimens often occur in aggregates.

INTERNAL STRUCTURE: The longitudinal muscle bands, which extend from the apertures, branch over the projections of the body wall that fit into the hollow test processes surrounding the apertures. At the base of these projections, the fibres reform into bands, which extend about halfway down the body. There are circular muscles around each aperture (especially around the rim, where there is a distinct sphincter muscle) and a fine layer around the anterior part of the body. Circular muscles also extend down into the siphons inside the longitudinal bands, and are present in the broad siphonal velum at the base of each siphon. The branchial tentacles have primary, secondary and some tertiary branches. The dorsal tubercle is a large, circular cushion in the prebranchial area just behind the base of the tentacles. It either has a U-shaped slit, with the open interval directed forward and sometimes both horns rolled in; or it is more complex, with a branched slit. The peritubercular area is very shallow, or absent altogether, the prepharyngeal groove extending straight across the anterior end of the dorsal lamina. The dorsal lamina is fairly long, extending halfway down the length of the branchial sac before passing to the left of a long, elliptical, membranous area that contains the oesophageal opening.

The branchial sac has 7 narrow folds on each side of the body, with only 3 internal longitudinal vessels on each: 1 on the edge and 2 on the ventral side of each fold. The stigmata are very short and straight. They form tall, narrow infundibula in each fold. The primary meshes are very numerous, and there are 4 infundibula per mesh.

The gut forms a gently curved loop, slightly open at the pole. The oesophagus is moderately long. The pyloric region is expanded. The liver pouches are bipartite, with long, parallel oblique pouches proximally, and a long band of fan-shaped pouches with rounded terminal lobes distally. The plain-bordered anus projects out through the atrial velum.

The left gonad lies in the curve of the gut loop, parallel to the descending limb. The right gonad is parallel to the long, narrow and slightly curved kidney. The gonads consist of a long and sometimes sinuously curved ovary, terminating near the anus in a short oviduct. The testes are behind the proximal end of each ovary. The male follicles, which are long and branched, are packed into spherical clumps, converging toward the centre of the sphere. The spherical clumps of male follicles are sometimes tightly grouped into a single rounded mass, but the more numerous follicles of other specimens remain separate and spread out over a wide area at the end of the ovary. Vasa efferentia from the centre of each spherical clump of male follicles join the short vas deferens, which extends up onto the surface of the proximal end of the ovary where it opens into the atrial cavity. Usually the vas deferens is embedded in the body wall, with only the short terminal part projecting into the atrial cavity. In one specimen, however, it is free of the body wall for most of its length (Western Port, NMV F51585).

REMARKS: The species resembles *M. ficus* in its numerous, tall branchial infundibula, its short stigmata and its bipartite liver. However, the two parts of the liver are more distinctly different from one another than they are in *M. ficus*. Moreover, *M. ficus* has a long vas deferens, opening with the oviduct, as well as more numerous branchial vessels, some present on the dorsal sides of the branchial folds. The present species, unlike *M. ficus* and *M. mollis*, has numerous spherical clumps of male follicles with ducts joined in the centre of each clump (rather than at the base of a single, hemispherical clump).

Molgula sphaera Kott, 1972
(Fig. 195)

Molgula sphaera Kott, 1972c, p.251.
Molgula discogona Millar, 1975, p.325

DISTRIBUTION

NEW RECORDS: Western Australia (Albany, AM Y2010).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1972c). Singapore (Millar 1975).

The species is taken from sand, shell grit and sandy mud down to 10 m.

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are small and absolutely spherical. The sessile apertures are close together on the upper surface. Although there are sparse, long test hairs, sand is mainly embedded in the test, causing it to be hard and brittle.

INTERNAL STRUCTURE: The body wall adheres closely to the test. Fine external circular muscles are present over the whole body, overlying longitudinal bands that radiate from each siphon and become diffuse over the ventral surface. Narrow siphonal vela lie the base of each siphon. There are 8 larger branchial tentacles alternating with rudimentary ones. Although the primary and secondary branches are rather long, they are sparse, so the tentacles are not bushy. The dorsal tubercle is a simple, circular opening. The dorsal lamina is about half the length of the branchial sac.

On each side of the body, there are 7 branchial folds. Each of the 6 most dorsal folds on each side has a row of 6 infundibula; the ventral folds have 12. There are 3 or 4 internal longitudinal vessels on the folds, but none in the interspaces. The infundibula are broad basally. In larger specimens, they subdivide irregularly at the top of the cone.

The gut loop is moderately long and curved, but is quite wide. In the large, expanded pyloric region, irregularly oriented clumps of parallel, glandular folds often subdivide into circular pouches. The oesophagus is very short. The kidney is long and curved.

The gonads are almost circular, with an almost spherical ovary surrounded by a wide band of crowded, radially arranged, long and branched male follicles. Vasa efferentia join to form 3 to 5 separate ducts, which join a seminal vesicle in the centre of the mesial surface of the ovary. The vas deferens extends across the surface of the ovary to open above the almost sessile oviducal aperture.

REMARKS: Characteristic of the species are its spherical shape; sessile apertures; hard, brittle, sandy test; irregularly subdivided and largely free-standing infundibula; and circular gonads with a seminal vesicle.

The species is unusual; there do not appear to be close relatives. The short oesophagus resembles that of *M. ficus*, which has no other character in common with the present species.

Genus **Eugyra** Alder and Hancock, 1870

Type species: *Molgula arenosa* Alder and Hancock, 1848

Molgulids in which the branchial sac is without folds, but has projecting infundibula with long, spiralling stigmata, that form square meshes around the base of the cone.

There are usually 8 rows of infundibula. All except the dorsal row have a single, internal, longitudinal vessel extending down the centre of the row. Each row has 6 infundibula, except for the ventral row (which has 12) and the short dorsal row (which has 5). In the Australian specimen examined, the sickle-shaped main stem of the branchial tentacles have especially long bases that radiate out across the prebranchial area. There is a long, rather spindle-shaped, dorsal ganglion in many of the species (e.g., *E. mammillata* n.sp., *E. malayensis* Millar, 1975), which also occurs in *Pareugyrioides exigua*. The stomach is small, with broad, parallel, longitudinal glandular folds that are not usually subdivided (as they often are in *Molgula* spp.). The proximal end of the left gonad is enclosed in the gut loop, but its distal end sometimes crosses the descending limb. The vas deferens is usually, but not always, short, opening

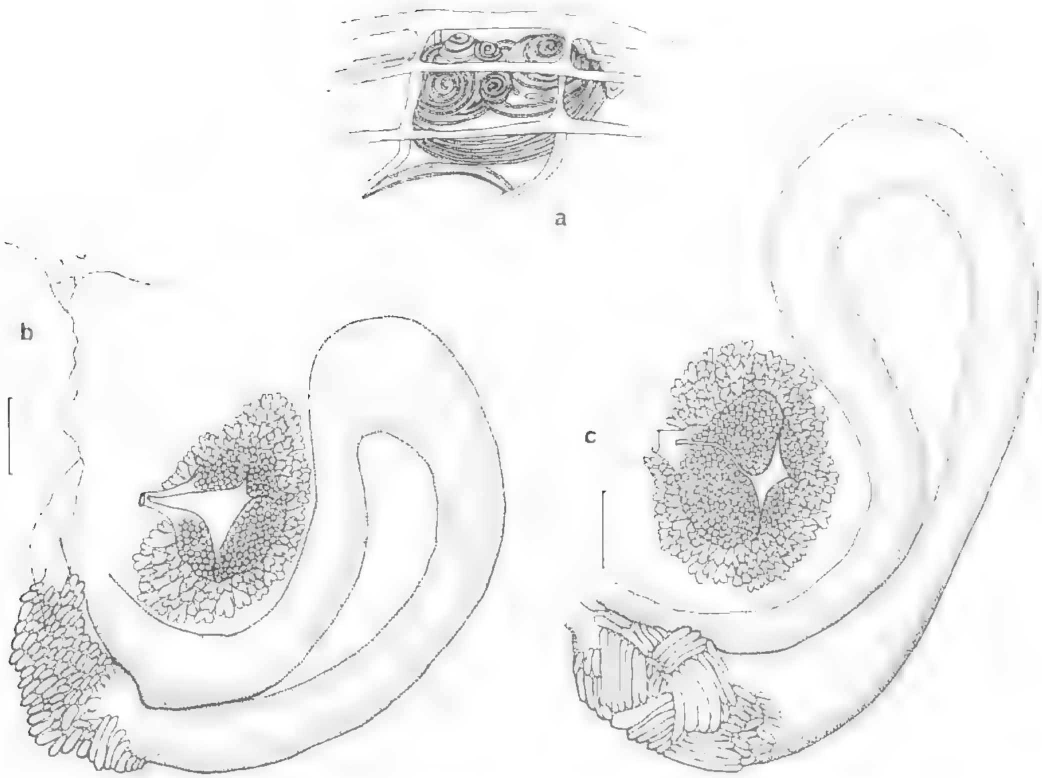


FIG. 195: *Molgula sphaera* — **a**, portion of branchial fold showing subdivision of infundibulum (QM G6319); **b**, **c**, gut and gonad showing variations in liver pouches (QM G6319, G6317). (Scales: **b**, **c**, 1.0 mm).

at the proximal end of the ovary. It sometimes has multiple openings.

The synonymy of *Bostrichobranchus* Traustedt, 1822 and *Eugyra* (see Huntsman 1912b, Arnback 1928) is justified by the condition of the branchial sac in *E. mammillata* n.sp., in which the proliferation of infundibula in many of the branchial meshes is seen to occur with growth; it is not, therefore, a character that indicates generic distinction. The highly retractile siphons of *Eugyra pellucida* are also a feature of many other species of *Eugyra* and the monotypic genus *Bostrichobranchus* (*B. pilularis* Verrill, 1871).

Neither species nor records of this genus are numerous, although they are recorded from all oceans. It is possible that the usually small individuals have been overlooked in the sandy habitats that they occupy.

KEY TO THE SPECIES OF *EUGYRA* RECORDED FROM AUSTRALIA

1. Right gonad curves posteriorly .... *E. millimetra* n.sp.
   Right gonad does not curve posteriorly 2
2. Test around apertures forms firm cones; long transverse muscle present between apertures................ *E. mammillata* n.sp.
   Test around apertures soft and wrinkled; no long transverse muscle between apertures .... *E. pellucida*

Species reported from adjacent areas but not recorded from Australia are:

Eugyra hexarhiza Tokioka, 1949 from Japan has similar gonads to those of *E. pellucida*, but has sessile apertures and a more muscular body.

Eugyra kerguelenensis Herdman, 1882 from the sub-Antarctic is a sessile species with multiple openings of the vas deferens. Its external appearance closely resembles that of *E. pellucida*.

Eugyra malayensis Millar, 1975 from Singapore has male follicles around the whole length of the long ovary.

Eugyra molguloides Sluiter, 1904 from Indonesia has gonads resembling those of *E. mammillata* n.sp. and *E. pellucida*. However, its gut loop is confined to the posterior end of the left side. Other distinguishing features are not known.

Eugyra mammillata n.sp.
(Fig. 196)

Eugyra molguloides: Millar, 1975, p.326. (Not: Sluiter, 1904, p.113).

DISTRIBUTION

TYPE LOCALITY: Northern Australia (Gulf of Carpentaria, Albatross Bay, coll. E. Camburg, 20.1.62, holotype WAM 83.75).

NEW RECORDS: Queensland (Euri Creek, paratype QM GH757).

PREVIOUSLY RECORDED: New Guinea (Port Moresby — Millar 1975).

DESCRIPTION

EXTERNAL APPEARANCE: The holotype has a flat, oval base, 1.7 cm long and about 1 cm broad. The body gradually narrows toward the upper surface, where the apertures are about one-third of the body length apart. They project on two wide cones, their bases meeting in the centre of the upper surface. The test is firm, gelatinous and translucent. The surface of the type specimen is naked, with fine mammillations, especially on the ventral half of the left side. These small swellings become less conspicuous toward the upper half of the body and on the right side. The paratype is 1.3 cm in diameter. It has some fine hairs with adherent sand around the base of the siphons, and is more rounded than the holotype. It has the same firm test on the upper surface. The test on the flat, basal surface of both specimens is very thin and flexible.

INTERNAL STRUCTURE: The body wall is delicate and transparent. It is not easily removed from the test, the siphons and upper part of the body being very firmly attached. Longitudinal muscle bands extend down each long siphon and terminate around and near the internal circular sphincter muscle. There are external circular fibres around each siphon, but apparently nowhere else on the body. There are no siphonal vela. Transverse muscles cross the mid-line between the siphons and behind the atrial siphon. The transverse bands that extend across the median line between the siphons are very short, except for one that extends halfway down each side of the body. There are also about 7 short transverse bands on each side of the anterior end of the endostyle. The branchial tentacles have long, narrow bases that radiate from the circular sphincter muscle across the prebranchial space almost to the prepharyngeal groove. The main stem is the usual sickle-shape. The 7 or so primary branches along each side of the main stem are also sickle-shaped, and have long, flat bases attached transversely across the side of the main stem to form a series of flat lamellae up each side of the tentacle. There are short, papilla-like secondary branches along the convex anterior side of the primary branches and short papillae along each side of the concave anterior edge of the main stem. There are no tertiary branches. There is no peritubercular area. The dorsal tubercle, which is in the middle of the prebranchial area, is an oval, protruberant cushion with a long, C-shaped slit. The long base of a branchial tentacle extends along each side of the dorsal tubercle, which is exposed when the tentacles are parted. The neural gland is long and elliptical. The dorsal lamina is a very wide membrane, which divides about halfway down the branchial sac to enclose the wide, elliptical, membranous area surrounding the oesophageal opening.

There are 7 rows of square-based, deep, projecting infundibula in the branchial sac. A single, wide, longitudinal vessel extends along the centre of each row except the dorsal row. Each row has 6 infundibula, except for the ventral row, which has 12. Occasionally there are accessory infundibula between the primary coils, and in some meshes of the paratype, the stigmata are broken up and form the multiple, small, projecting coils that characterised the genus *Bostrichobranchus*. The infundibula are conspicuously deep, and 2 stigmata coil together around them about 8 times.

The gut forms a long, straight loop for most of its length, although its posterior end, consisting of oesophagus and rectum, curves sharply anteriorly to form a pronounced J. The loop reaches anteriorly to the prepharyngeal groove. The oesophagus, which is of moderate length, opens into a short stomach, with about 12 broad, glandular folds, at the posterior end of the body. A group of about 3 glandular folds from the anterior border curve posteriorly around the distal end of the stomach on its mesial surface. The intestinal loop extends forwards from the pyloric

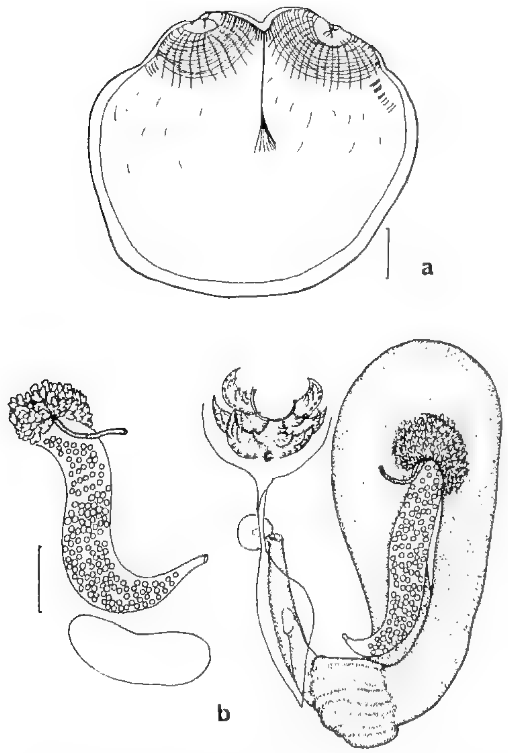


FIG. 196: *Eugyra mammillata* n.sp. (QM GH757) — **a**, body in test showing muscles; **b**, inner body wall. (Scales: 2.0 mm).

end of the stomach. The gut loop is open at the pole, where it encloses the proximal end of the left gonad. The anus is near the atrial aperture. Its border has small, pointed lobes on its ventral lip, but longer, rounded lobes dorsally.

The ovary is long and tubular. Its short terminal oviduct lying on the mesial surface of the descending limb of the intestine is curved dorsally toward the atrial aperture. The testis follicles are long and very branched, and radiate in an arc around the proximal end of the ovary. Their terminal branches on the mesial surface of the follicles are rounded and very crowded. The short male duct extends up over the end of the ovary to turn dorsally before opening into the peribranchial cavity distant from the atrial aperture. It is embedded in the body wall for most of its length. The right gonad is mostly anterior to the curved kidney, the ovary curving dorsally just at the antero-dorsal end of the kidney.

REMARKS: Like the paratypes, but unlike the naked holotype, Millar's small specimen (up to 3 cm) has test hairs and adherent sand.

The dorsal lamina and anal border of the present species resemble those features in *E. japonicus* Oka, 1934 (see Tokioka 1949a), but the latter species has multiple openings of the vas deferens, and its male follicles surround the ovary.

Eugyra mammillata is characterised by firm, translucent, naked siphons; the protruberant dorsal tubercle between the bases of the tentacles; the single, long, transverse muscle that crosses the mid-line between the siphons; deep conical infundibula; and small, pointed anal lobes.

Eugyra millimetra n.sp.
(Fig. 197)

DISTRIBUTION

TYPE LOCALITY: Victoria (Bass Strait, 40°09.2′S, 147°31.9′E, SM, shell substrate, Bass Strait Survey, syntypes NMV F51475).

The syntypes were taken from a sandy bottom at 51 m.

DESCRIPTION

EXTERNAL APPEARANCE: These very small individuals are up to 2.5 mm long and almost spherical, but the contracted specimen has conspicuously protruding apertures on conical prominences. The apertures are at opposite ends of the upper surface, and there is a very narrow stalk from the centre of the postero-ventral corner of the body. Both apertures are 4-lobed; in one specimen, the branchial lobes radiate from the aperture like the points of a star. The test is very delicate and completely transparent. It is slightly thicker anteriorly around the siphons, where it adheres closely to the muscular part of the body wall. There are a few fine, short test hairs, especially on the stalk.

INTERNAL STRUCTURE: A wide band of circular muscles around each aperture extends nearly halfway down each side of the body, to almost meet in the dorsal mid-line between the apertures. The posterior muscles in each circle appear to be interrupted on the right and left sides to form bands that cross the mid-line over the ventral and dorsal surfaces of the body. Longitudinal muscles radiate from the apertures and stop abruptly just posterior to the circular muscles. There is a rather short, single, narrow transverse muscle across the dorsal line between the two sets of circular muscles. Well-separated, fine transverse muscles also cross the ventral line (across the endostyle) and extend a little distance down each side of the body. The 8 branchial tentacles of varying sizes have short primary branches. Their long bases extend across the prebranchial area. The neural

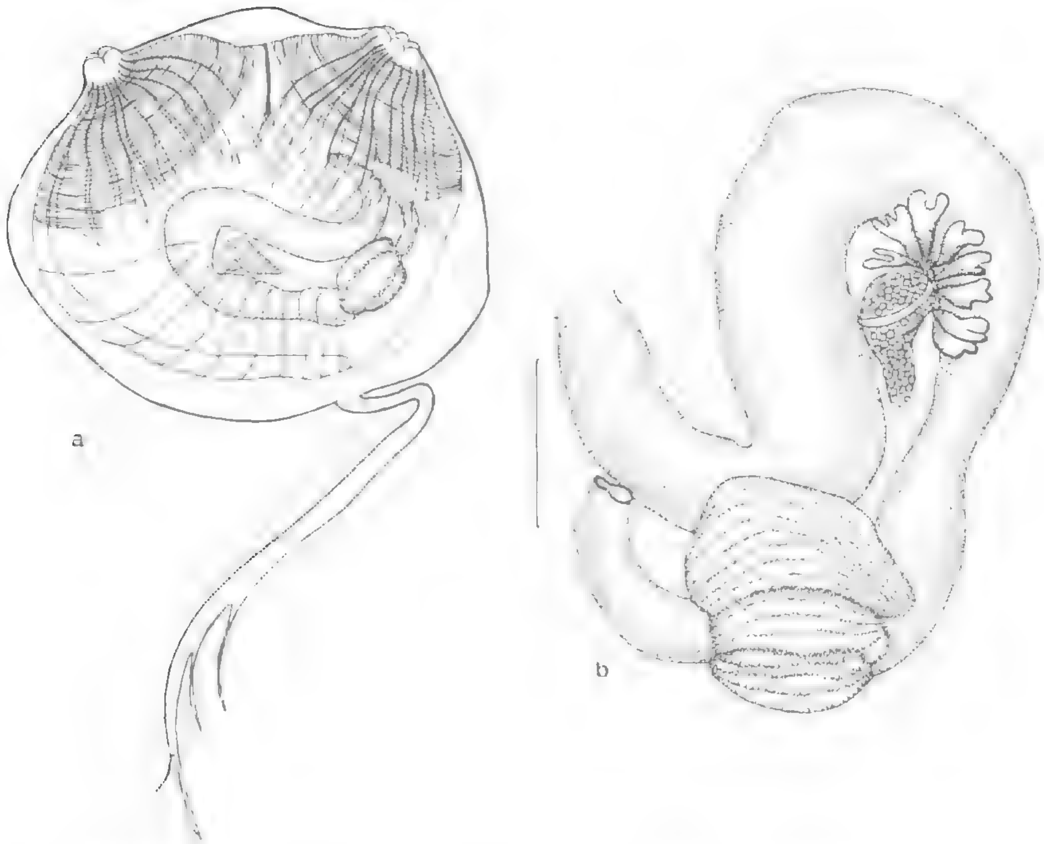


FIG. 197: *Eugyra millimetra* n.sp. (NMV F51475) — **a**, whole body in test; **b**, gut and gonad. (Scales: 0.5 mm).

gland is oval, and there is a simple opening of the neural duct. The dorsal lamina is very short.

The branchial sac has 7 internal longitudinal vessels, each extending along the centre of one of the 7 rows of infundibula. Generally there are 6 infundibula in each row, although there are fewer in the dorsal row and twice that number in the ventral row. The infundibula have 2 stigmata coiling together around them.

The gut forms a narrow, deeply curved loop that occupies about two-thirds of the left side of the body. The stomach is large and green in these preserved specimens. It is very much longer along the anterior than the posterior border. It has fine, parallel, glandular folds and is also folded into 4 longitudinal compartments or groups. The compartment of glandular folds on the anterior or inner curve of the gut is especially long and swollen, and curves across the distal end of the stomach on its mesial surface. There is a duodenal area, which narrows slightly before entering the intestine.

The right gonad is anterior to the large, oval kidney. The left gonad is enclosed in the primary gut loop. The gonads consist of a rather long, flask-shaped ovary that extends dorsally and then posteriorly to a short, wide opening. The testis follicles are long and lobed, and radiate from around the proximal end of the ovary. There is a single, short vas deferens that extends dorsally across the surface of the proximal end of the ovary.

REMARKS: This very small species is distinguished from others of the genus by its size, its delicate test and narrow stalk, and by the orientation and curve of ovary. The left gonad appears to be entirely contained within the primary gut loop. It is embedded in the body wall, and the distal end of the ovary was not seen to cross the intestine. However, the opening of the oviduct was not detected. The transverse muscle across the dorsal mid-line between the apertures is not robust and long, as it is in *E. mammillata*.

Eugyra pellucida (Macdonald, 1859)
(Fig. 198)

Caesira pellucida Macdonald, 1859a, p.369.
Eugyra molguloides Sluiter, 1904, p.111.
Eugyra moretonensis Kott, 1972c, p.252.

DISTRIBUTION

NEW RECORDS: Western Australia (Cockburn Sound, AM Y790, WAM 34.72). Victoria (Bass Strait, NMV H771). Queensland (Moreton Bay, QM G5961-77 G6328-9 G8587 G9490 G9493 G9505-6 G9988-90; AM Y937 Y979 Y982; Townsville).

PREVIOUSLY RECORDED: Western Australia (Shark Bay — Macdonald 1859a). Queensland (Moreton Bay — Kott 1972c). Indonesia (Sluiter 1904).

From 1 to 200 specimens were taken in Van Veen grab samples from various locations in southern Moreton Bay between August 1975 and September 1976. Their average size was 3 mm, with a maximum of 1.5 cm. Kott (1972c) observed that (in 1970 and 1971) the species appeared in June and that specimens of 1 cm had well-developed anural embryos in the atrial cavity in September.

DESCRIPTION

EXTERNAL APPEARANCE: The body is soft and laterally flattened, covered with long, hair-like test extensions to which sand and mud adhere (although these may be absent posteriorly). The apertures are close together on the upper surface in an area of soft, sand-free test that is often slightly depressed into the upper surface. The atrial siphon is about 3 times the length of the branchial siphon when it is extended. However, in most specimens examined, both siphons are contracted, and the soft siphonal test is gathered along and around them. All of the test is extremely thin and flexible, but tough. In preservative, individuals are flat and look ragged.

INTERNAL STRUCTURE: The body wall is thin, delicate and transparent. The short longitudinal muscles around the siphons terminate at their base. There are also delicate circular muscles around the siphons, and short transverse muscles are present in the mid-line posterior to the atrial siphon and between the siphons. Short transverse bands are also present on each side of the anterior part of the endostyle. The branchial tentacles are delicate, but they have a long base radiating across the prebranchial area from a circular sphincter at the base of the branchial siphon. The tentacles are flat and sickle-shaped, with wide primary branches, and small, papilla-like secondary branches. The V-shaped peritubercular area, has a small, protruberant tubercle with a longitudinal or

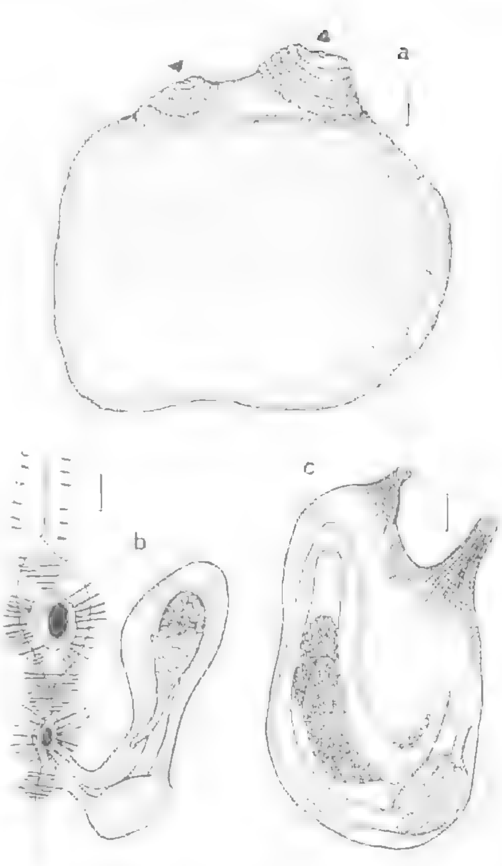


FIG. 198: *Eugyra pellucida* — **a**, external appearance (QM G5961); **b**, inner body wall showing musculature across the anterior mid-line of the body (AM Y790); **c**, body removed from the test from the left (WAM 34.72). (Scales: 1.0 mm).

circular opening. The dorsal ganglion is narrow and spindle-shaped. The dorsal lamina is wide, but very short, dividing to extend each side of the long, membranous area that surrounds the oesophageal opening.

There are 7 rows of infundibula, with an internal longitudinal vessel extending along the centre of each row. There are 12 infundibula in the ventral row, and 6 in each of the next 6 rows. There is also an eighth dorsal row with 5 infundibula, but no internal longitudinal vessel.

The gut forms a narrow, J-shaped loop, its posterior end curved anteriorly. It is open at the pole, where it contains the proximal part of the left gonad. The stomach is short, with about 10 fairly broad, straight glandular folds, which are green in preservative. A group of 2 or 3 glandular folds from the anterior border curve posteriorly across the distal end of the stomach on its mesial surface. The anal border is smooth.

The gonads consist of a long, tubular ovary with, at its proximal end, a circle of long, branched male follicles converging to the centre to join a short vas deferens. The vas deferens runs dorsally across the proximal end of the ovary and the surface of the descending limb of the gut loop before opening into the atrial cavity.

REMARKS: The species is less robust than *E. mammillata*, and is distinguished from it by the very thin, wrinkled test around its long siphons, which are 'capable of considerable retraction' (Macdonald 1859a, p. 369); very short dorsal lamina; absence of the long transverse muscle across the middle of the body that occurs in *E. mammillata*; rather shallow infundibula; and smooth anal border. The species have in common the form of the gonads, the longitudinally folded stomach, and the form of the tentacles, although these are less robust in the present species.

Genus **Pareugyrioides** Hartmeyer, 1914

Type species: *Eugyrioides dalli* Ritter, 1913

The genus is closely related to *Eugyra*. It is distinguished by the position of the left gonad, which is in the secondary curve of the gut loop, outside the primary loop. The liver pouches are usually rounded and short, and the vas deferens is relatively long, always opening with the oviduct.

The species reported on below, together with *P. longipedata* (Sluiter, 1904) and *P. flagrifera* (Sluiter, 1904), both from Indonesia, have 2 internal longitudinal vessels along each row of infundibula. Millar (1982a) has observed that the 2 vessels reported for *P. filholi* are in fact a single vessel that is folded. This could not be confirmed for *P. exigua*, which has 2 closely set vessels along most of the rows of infundibula.

The genus is not diverse; only a single species is known from the northern hemisphere (Alaska). From the Pacific and Southern Oceans, there are one abyssal, 2 Subantarctic (New Zealand and Macquarie I.), one Antarctic and 3 tropical western Pacific species. The western Pacific *Pareugyrioides longipedata* and *P. flagrifera* and the Antarctic *P. arnbackae* have long, wiry stalks, and *P. exigua* often has a fine, hair-like stalk, but this is not characteristic of the genus.

Pareugyrioides exigua (Kott, 1972c)
(Fig. 199)

Molgula exigua Kott, 1972c, p.249.
Eugyra flabelligona Millar, 1975, p.328.

DISTRIBUTION

NEW RECORDS: Victoria (Bass Strait, NMV F51561 F51562 F51566; off Cape Howe, ZMC 30.9.14). Queensland (Moreton Bay, QM GH2693).

PREVIOUSLY RECORDED: Queensland (Moreton Bay — Kott 1972c). Indonesia (Millar 1975).

Only a single specimen is known from Indonesia, where it was taken on a sandy bottom at 70 m (Millar 1975). The species is found on sand and shell grit down to 10 m in Moreton Bay, at which location there is some mortality of larger specimens following the onset of summer rain. Populations disappear from Moreton Bay during March, at the end of rainy period. They reappear in the following month, and rapidly reach sexual maturity at 0.5 mm diameter (Kott 1972c).

DESCRIPTION

EXTERNAL APPEARANCE: Individuals are small and rounded. Those from Queensland are up to 1.0 cm in diameter, with fine, hair-like test extensions over the whole body to which rather large sand grains adhere. The extensions are longer around the apertures and on the posterior end of the body. The apertures are on very short siphons almost at opposite ends of the upper surface, the branchial siphon turned away from the upward projecting atrial siphon. In juvenile specimens, the apertures are closer together. The test is relatively firm and stiff. The specimens from Bass Strait are spherical, and only 2 mm in diameter. They have sessile apertures; a brittle, sandy test; and a very fine, hair-like stalk that has not been observed on either the Queensland or Cape Howe specimens. The atrial aperture is on the upper, free surface, while the branchial aperture is on the side of the body directed down toward the substrate.

INTERNAL STRUCTURE: The body wall is thin and delicate. Circular muscles are present around the apertures. Longitudinal muscles radiate from the apertures and extend down both sides, crossing one another in the middle of each side. They divide into branches posteriorly. There are some very delicate circular muscles on the rest of the body, which are especially conspicuous across the dorsal and ventral borders. The broad velum at the base of each very short siphon has a small aperture in the centre. There are 8 larger branchial tentacles alternating with rudimentary ones. Their primary and secondary branches are short and sparse. The main stem of the tentacles is sickle-shaped, but not broad; the small branches are along each side of the concave anterior edge. The dorsal tubercle is a small cushion with a simple, circular aperture. The dorsal ganglion is long, narrow and spindle-shaped. The dorsal lamina is long, the oesophageal opening being at the posterior end of the branchial sac.

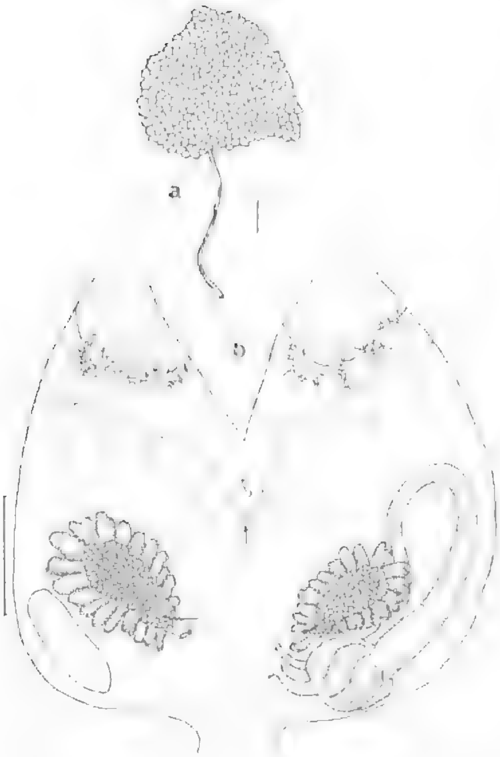


FIG. 199: *Pareugyrioides exigua* — a, external appearance of stalked specimen (NMV F51566); b, inner body wall (NMV F51562). (Scales: 1.0 mm).

There are 7 rows of infundibula, each formed of 2 stigmata coiled together. There are 2 internal longitudinal vessels close together along the centre of each row of infundibula, except for the most dorsal row (which has no overlying vessels) and the second dorsal and most ventral row (each of which has a single longitudinal vessel). The infundibula in the ventral row often number 12, while the other rows have 6 or 7 infundibula each. The infundibula project only slightly. Between the primary infundibula are interstitial coils of stigmata. In the minute specimens from Bass Strait, the stigmata coil only 3 times.

The gut forms a long, moderately wide, curved loop, open at the pole. Elongate, irregular, sometimes subdivided, oblique glandular folds are present in the pyloric region.

The gonads are oval. The right gonad is almost parallel to, but separate from, the short, oval kidney. The left gonad lies in the curve of the gut loop and is almost parallel to it. Each gonad consists of a short, broad ovarian sac with a very short duct and long branched male follicles surrounding the proximal end, along both sides and sometimes on the surface of the ovary. Vasa efferentia join on the mesial surface of the ovary to form a vas deferens that opens slightly anterior to the oviducal opening. The eggs are relatively large, about 0.1 mm in diameter.

REMARKS: Characteristics of the species are its rather firm, but not hard, test; widely separated sessile apertures; almost flat infundibula; broad siphonal vela; and the shape and orientation of the gonads. The hairy test of the Queensland specimens and the fine, hair-like stalk of the Bass Strait specimens do not seem to justify their separation into two species.

Pareugyrioides arnbackae Millar, 1960b from the Antarctic is a very similar species, differing only in having a single internal longitudinal vessel along each row of infundibula. Occasionally (but not always) the vas deferens opens by mutiple openings on the surface of the ovary (Millar 1960b, Kott 1969a, Monniot and Monniot 1976c).

Pareugyrioides longipedata (Sluiter, 1904) has a similar branchial sac and a similar arrangement of gonads and gut to the present species. However, it has male gonads only along the posterior border of the ovarian tube. *Pareugyrioides flagrifera* (Sluiter, 1904) has shorter gonads set at right angles to the gut loop and kidney respectively and, although it is very small (3 mm), it has about 7 coils of each pair of stigmata around the infundibula.

Species	Range beyond Australian waters	Arafura Sea, Darwin, Dampier Arch.	Shark Bay, Abrolhos	Cockburn Sound	Geographe Bay, Esperance	Great Australian Bight	Spencer Gulf, St. Vincent Gulf	Victoria, Tasmania	New South Wales	S. Qld., Hervey Bay	Gladstone, Rockhampton Capricorn Gp., Swains	Mackay, Townsville	Townsville, Cape Flattery	Cape Flattery, Torres St., Gulf of Carpentaria
		Range in Australian waters												
Amphicarpa duploplicata	WP	■												
Polyandrocarpa abjornseni		■	■	■										
Ecteinascidia flora			■											
Polycarpa sobria	WP		■											
Cnemidocarpa posthuma			■											
Stolonica aluta n sp.			■											
Chorizocarpa michaelsensi														■
Perophora namei	WP													■
Ecteinascidia imperfecta	WP													■
Ecteinascidia sluiteri	WP												■	■
Perophora modificata n.sp.													■	■
Metandrocarpa miniscula n.sp.													■	
Ascidia parasamea n.sp.													■	
Microcosmus pupa	IWP												■	
Metandrocarpa agitata n.sp.			■										■	
Stolonica reducta	WP			■									■	
Amphicarpa nodula n.sp.													■	
Cnemidocarpa oligocarpa	WP											■		
Polycarpa contecta	WP											■		
Polycarpa decipiens	IWP											■		
Polycarpa intonata n.sp.												■		
Polycarpa papyra n.sp.												■		
Botrylloides violaceum	WP											■		
Microgastra granosa	IWP											■	■	
Polycarpa longiformis	WP											■	■	
Stolonica agnata n.sp.												■	■	■
Pyura arenosa	WP		■									■	■	■
Eugyra mammillata n.sp.												■	■	■
Phallusia millari n.sp.	WP	■										■	■	■

FIG. 200: Tropical species with south-eastern limits N of the Tropic of Capricorn.

BIOGEOGRAPHY

In the following discussion, the biogeographical affinities of 192 phlebobranch and stolidobranch ascidian species in the Australian fauna are considered. *Pyura pantex* and the probably introduced species, *Styela clava* and *Molgula manhattensis* are excluded from the discussion. Species range is set out in Figs 200–4.

TROPICAL SPECIES (Figs 200–2)

Of the 118 species recorded from the tropics, there are 66 with a range that spans the Tropic of Capricorn, most occurring at least as far south as Moreton Bay and/or Cockburn Sound (Fig. 202). This group of species includes most of the pantropical and many of the wide ranging Indo-West Pacific species, probably reflecting their generic diversity and flexibility. The Australian continent appears to constitute a bridge between tropical and temperate waters for these species.

Seventeen of the species that span the Tropic of Capricorn are apparently indigenous and may be temperate species extending into the tropics in the Northern part of their range. They are discussed below (see Temperate Species, 1).

1. INDO-WEST PACIFIC COMPONENT: This is a conspicuous feature of the Australian fauna, which contains 80 recorded species with a range in the Indo-West Pacific. Ten are pantropical. Seven have not yet been recorded in Australian tropical waters, although since they do occur south of the Tropic of Capricorn, they will probably be found to occur further north on the Australian coast: *Ecteinascidia thurstoni*, *Styela plicata*, *Polycarpa sobria*, *Polycarpa thelypanes*, *Stolonica vesicularis*, *Botryllus purpureus* and *Molgula sphaera*.
2. INDIGENOUS TROPICAL SPECIES: There are 20, mostly newly described, species recorded from relatively few, mainly tropical locations (species marked * extend south of the Tropic of Capricorn on the western or eastern coast): *Ascidia pandora* n.sp., *A. nerea* n.sp., *A. parasamea* n.sp., *A. glabra**, *Perophora modificata* n.sp., *Cnemidocarpa posthuma*, *Polycarpa intonata* n.sp., *P. nota* n.sp., *P. papyra* n.sp., *Amphicarpa nodula* n.sp., *Stolonica agnata* n.sp., *S. aluta* n.sp., *Metandrocarpa miniscula* n.sp., *M. agitata* n.sp., *Chorizocarpa michaelseni*, *Pyura confragosa* n.sp.*, *P. viarecta* n.sp., *Microcosmus tuberculatus* n.sp., *Molgula lucidata* n.sp.*, *Eugyra mammillata* n.sp. Some of these may be indigenous, although some of the smaller species (especially in the Perophoridae and Polyzoinae) could be components of the Indo-West Pacific fauna previously overlooked). It is in this group of species that any truly indigenous tropical species will be found.

TEMPERATE SPECIES (Figs 203–4)

In addition to the 49 tropical species that also occur in temperate waters (Fig. 201–2), there are 91 temperate species (Figs 203–4).

1. INDIGENOUS SPECIES: in contrast to the tropical fauna, where wide ranging Indo-West Pacific species prevail, the strictly temperate ascidian fauna of Australia is dominated by indigenous species. There are 63 confined to temperate locations and a further 17 that extend into tropical waters.

   The 17 probably indigenous species, that have the northern limits of their range north of the Tropic of Capricorn, are most often recorded from the mainland coast rather than reefal locations: *Ascidia decepta* n.sp., *A. latesiphonica*, *Phallusia obesa*, *Cnemidocarpa personata*, *C. intestinata* n.sp., *C. lobata*, *C. aculeata* n.sp., *C. stolonifera*, *Polycarpa fungiformis*, *P. lucilla* n.sp., *Polyandrocarpa australiensis*, *Amphicarpa diptycha*, *Hartmeyeria formosa*, *Microcosmus stoloniferus*, *Molgula diversa*, *M. mollis*, *Eugyra pellucida*.
2. SUBANTARCTIC COMPONENT: This is a small group of 6 species, several with a circumpolar range. Only *Corella eumyota* and *Agnesia glaciata* have been recorded north of Bass Strait. The species are: *Adagnesia charcoti*, *Ascidia challengeri*, *Corella eumyota*, *Molgula mortenseni*, *Molgula malvinensis* and *Agnesia glaciata*.
3. SOUTHERN TEMPERATE COMPONENT: An equally small group of species that have a wide range in southern temperate seas: *Ascidiella aspersa*, *Botryllus stewartensis*, *Perophora hutchisoni*, *Asterocarpa humilis* and *Pyura stolonifera*. They all extend at least to New Zealand but South Africa and South America are also included in the range of the latter 2 species.

GEOGRAPHICAL AFFINITIES OF ASCIDIAN TAXA

The tropical fauna is dominated by species of the genus *Polycarpa* and the family Ascidiidae and

Species	Range beyond Australian waters	Arafura Sea, Darwin, Dampier Arch.	Shark Bay, Abrolhos	Cockburn Sound	Geographe Bay, Esperance	Great Australian Bight	Spencer Gulf, St. Vincent Gulf	Victoria, Tasmania	New South Wales	S. Qld., Hervey Bay	Gladstone, Rockhampton Capricorn Gp., Swains	Mackay, Townsville	Townsville, Cape Flattery	Cape Flattery, Torres St., Gulf of Carpentaria
Ascidia empheres	WP										■			
Ascidia kreagra	WP										■			
Ascidia nerea n.sp.											■			
Ascidia pandora n.sp.											■			
Polycarpa nota n.sp.											■			
Polyandrocarpa sagamiensis	WP										■			
Symplegma reptans	WP										■			
Halocynthia papillosa	IWP										■			
Microcosmus tuberculatus n.sp.											■			
Pyura viarecta n.sp.											■			
Polyandrocarpa australiensis				■							■	■	■	
Cnemidocarpa intestinata n.sp.		■									■	■	■	
Ecteinascidia nexa	WP										■	■	■	
Polycarpa stirpes n.sp.	WP										■	■	■	
Polycarpa argentata	WP	■									■	■	■	
Pyura curvigona	WP		■								■	■	■	
Polycarpa biforis	WP			■							■	■	■	
Polyzoa violacea	IWP			■							■	■	■	
Polycarpa nigricans	WP			■							■	■	■	■
Phallusia arabica	IWP	■	■								■	■	■	■
Polycarpa reniformis	WP			■							■	■	■	■
Polycarpa aurata	IWP										■	■	■	■
Molgula diversa										■	■			
Botryllus tuberatus	WP			■						■	■	■	■	
Pyura confragosa n.sp.										■	■	■	■	
Polycarpa fungiformis										■	■	■	■	
Polycarpa ovata	WP									■	■	■	■	
Cnemidocarpa floccosa	WP	■								■	■	■	■	
Phallusia julinea	IWP	■								■	■	■	■	
Styela canopus	pan tropical		■	■						■	■	■	■	■
Eusynstyela latericius	IWP	■	■	■						■	■	■	■	■
Ascidia munda	WP	■	■						■	■				
Ascidia archaia	WP								■	■	■			
Ascidia liberata	WP								■	■	■			
Ascidia capillata	WP	■			■				■	■	■	■		
Ascidia glabra			■						■	■	■	■		
Ecteinascidia rubricollis	WP								■	■	■	■		
Molgula calvata	WP			■	■				■	■	■	■		
Cnemidocarpa stolonifera									■	■	■	■	■	
Chorizocarpa sydneyensis	WP								■	■	■	■	■	
Molgula incidata n.sp.									■	■	■	■	■	
Ecteinascidia diaphanis	WP	■							■	■	■	■	■	
Perophora multiclathrata	IWP		■	■					■	■	■	■	■	
Polycarpa aurita	WP	■	■	■					■	■	■	■	■	■

FIG. 201: Tropical species with south-eastern limits between the Tropic of Capricorn and New South Wales.

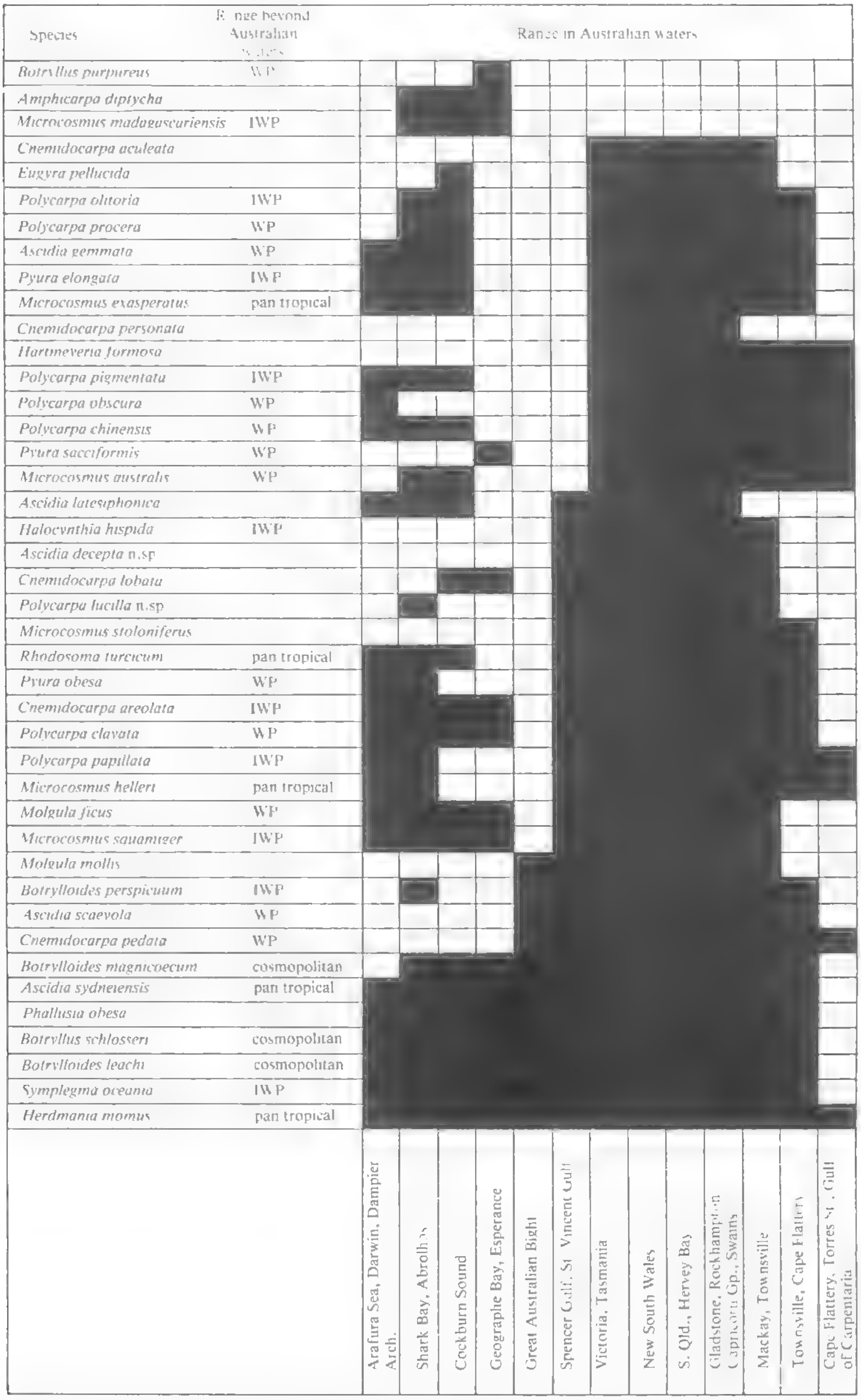


FIG. 202: Tropical species with southern limits S of New South Wales or Cockburn Sound.

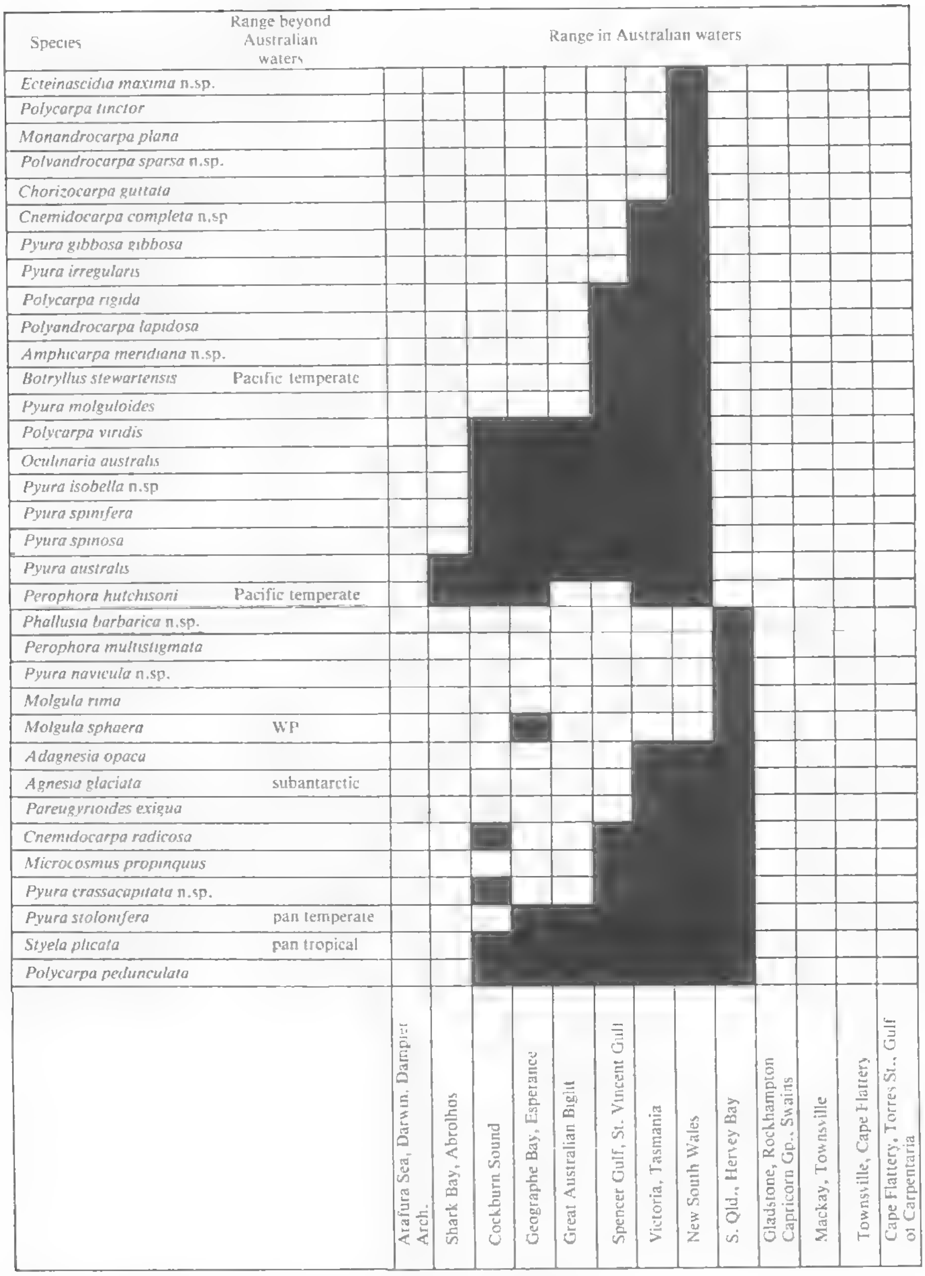


FIG. 203: Temperate species recorded north of Bass Strait.

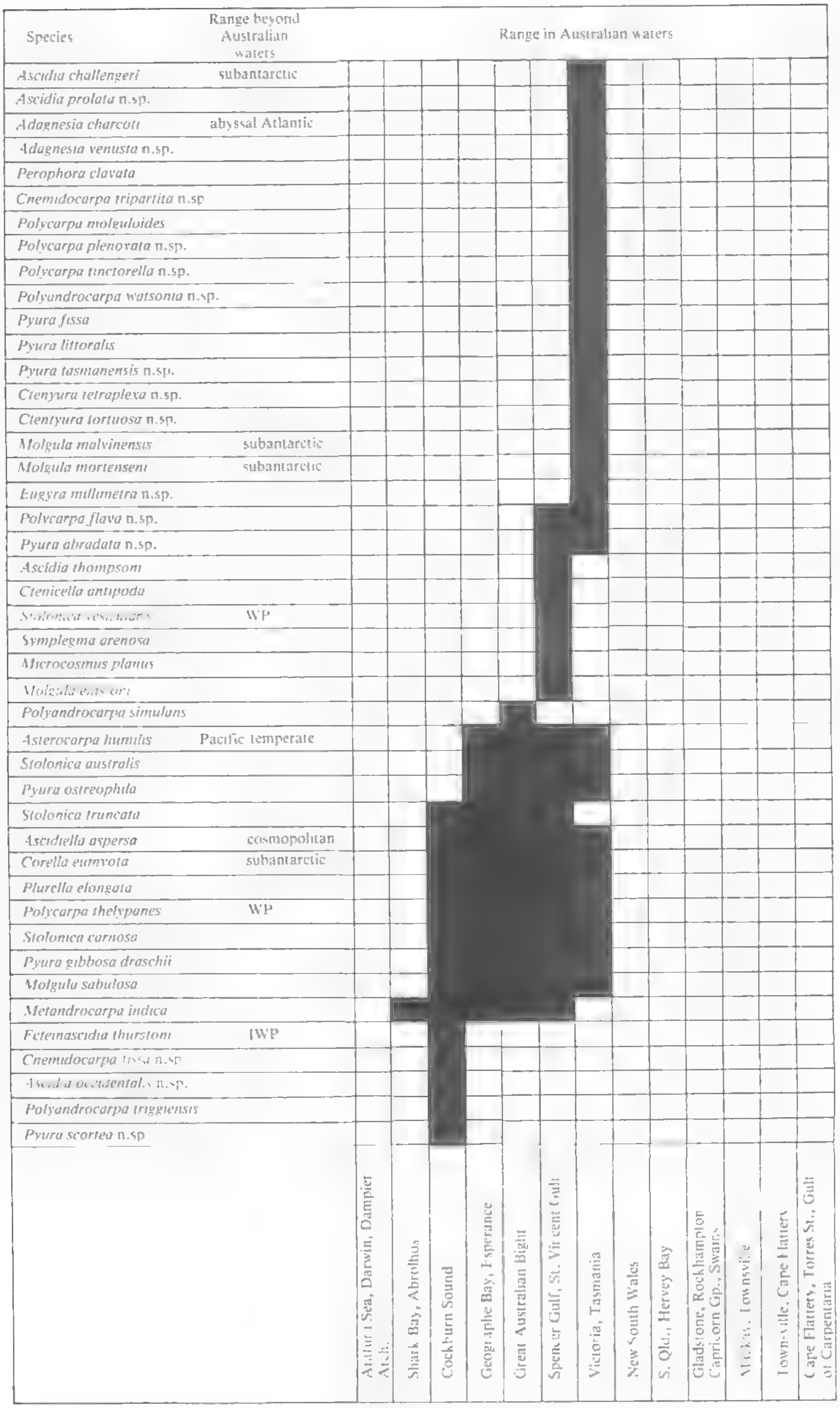


FIG. 204: Temperate species not recorded north of Bass Strait.

subfamily Polyzoinae (Table XIX, columns a, b, c). The tropical *Polycarpa* spp. are largely Indo-West Pacific species (Table XI, columns a and b). The genus is also moderately well represented in temperate seas (Table XIX, columns b, d, and e) where more than half of the tropical species have an extended range and the remainder are apparently indigenous.

Since the genus does not occur in either the Antarctic or the Subantarctic (Kott 1969a) the indigenous Australian *Polycarpa* spp. probably have affinites with the tropical fauna, becoming isolated from one another and from the tropical populations in temperate seas.

Cnemidocarpa spp. are not so numerous. The genus is not well represented in the Antarctic but does occur. In Australia there is a relatively large number of indigenous species in temperate waters. Although these have quite wide geographic ranges, extending into tropical latitudes, it appears that species of this genus also have a tendency to speciate in the temperate waters of Australia.

The vegetatively reproducing family Polyzoinae is conspicuous in both temperate and tropical Australian seas. However, only two species *Polyandrocarpa lapidosa* and *P. watsonia* n.sp. have temperate affinities, being related to the Subantarctic, *P. placentela* (Herdman) and the South African *P. anguinea* (Sluiter). Other species of *Polyandrocarpa* appear to be more closely related to tropical forms: of the other genera of this subfamily, only *Polyzoa* is known from both Australian, Antarctic and Subantarctic waters. Generally, the Australian genera and species of the *Polyzoinae* have closer affinities with those in the tropics than with Southern Ocean forms. The distribution of species of the subfamily is similar to that observed for *Polycarpa* spp., many having a wide range over tropical and temperate latitudes, while others apparently become isolated in temperate waters to account for the large number of indigenous species.

Microcosmus is another genus that does not occur in the Antarctic or Subantarctic. Like *Polycarpa* and the Polyzoinae, species of wide Indo-West Pacific occur in Australian waters. There are also a number of species of pantropical range and relatively few indigenous species. Species of this genus do not, generally, appear to be subject to isolation as much as *Polycarpa* and Polyzoinae.

The family Ascidiidae is well represented in the tropics. It has a relatively large number of tropical species extending into temperate waters where there are also a number of indigenous species. However, unlike the Polyzoinae, *Polycarpa* and *Microcosmus*, some of the latter appear to have affinities with species of the Southern Ocean. (Table XIX, column e).

In temperate waters the fauna is dominated by species of the genus *Pyura* (Table XIX, columns b, d and e), many of which are indigenous and appear to be related to southern temperate species known from other continents. In particular, the *pachydermatina* group, which is well represented in New Zealand and south of the subtropical convergence, is also well represented in temperate Australian waters. *Pyura stolonifera* is also significant, with populations in South Africa and Chile as well as Australia that are very likely relicts of a Gondwanaland fauna. The genus is more common in Antarctic and Subantarctic waters than in the tropics and appears to be the major component of the Australian fauna with southern rather than tropical affinities.

Australian species of the families Molgulidae and Agnesiidae also appear to have southern affinities, but neither are very well represented in the Australian fauna.

It is suggested (see *Polycarpa*, above) that the loss of a larval ocellus may have contributed to the isolation of *Polycarpa* spp. in temperate waters, where there is not such a profusion of suitable habitats as in the tropics; and where selective pressures favouring population maintenance are so stringent that they have resulted in viviparity. Similar selective pressures for population maintenance may be invoked to explain similar distribution patterns in the family Polyzoinae. The wide range and lesser number of indigenous species of the largely tropical genus *Microcosmus* spp. (which is never viviparous and does have a larval ocellus) support this hypothesis.

Nevertheless, the composition of the Australian indigenous ascidian fauna suggests that species of all genera, including those with temperate affinities (*Pyura*) tend to speciate in the temperate waters of the Australian continent. It is probable that this results from physical isolating pressures in these waters. Biological factors such as reproductive strategies for population maintenance (including viviparity and loss of the larval ocellus) may increase vulnerability to isolation.

It is not known how gene flow is maintained to account for the wide range of the great majority of species that occur in the tropical western Pacific. The longest known life span of an ascidian larva is 24 hours, but usually it is less (see Berrill 1950, Anderson *et al.* 1975, Olson 1983). This is

TABLE XIX: COMPOSITION OF THE AUSTRALIAN ASCIDIAN FAUNA

Total	a*	b*	c*	d*	e*	Total
Ascidiidae	5	6	8	3	2	24
Plurellidae	1	—	—	1	—	2
Corellidae	—	1	—	—	1	2
Agnesiidae	—	—	—	2	2	4
Perophoridae	4	4	1	4	1	14
Styela	1	1	—	—	—	2
Cnemidocarpa and *Asterocarpa*	2	2	6	4	1	15
Polycarpa and *Monandrocarpa*	10	10	5	9	—	34
Polyzoinae	5	4	9	14	—	32
Botryllinae	2	5	—	—	1	8
Pyura	1	3	2	16	1	24
Microcosmus	1	5	2	2	—	10
Other Pyuridae	1	1	1	3	—	6
Molgulidae	—	3	5	5	2	15
Total	35	46	37	63	11	192

a* Western Pacific tropical species not extending south of the Tropic of Capricorn.
b* Western Pacific tropical species extending south of the Tropic of Capricorn.
c* Indigenous and new species present north of the Tropic of Capricorn.
d* Indigenous species not present north of the Tropic of Capricorn.
e* Antarctic and Pacific temperate species.

too short a time for them to span the great expanses of deep ocean that separate the groups of islands and reefs. It is known (Olson 1983) that larvae of the aplousobranch *Didemnum molle* delay metamorphosis in the dark and in the absence of the shaded habitats into which all light sensitive ascidian larvae are attracted before settlement (Berrill 1955). It is possible, therefore, that ascidian larvae are all able to delay metamorphosis when suitable settlement sites are not available; and that ascidians will be found to have two strategies: one, a short free-swimming life (for population maintenance); and the other, a long free-swimming life (for gene flow). Long-lived larvae in which metamorphosis is delayed are most likely to occur if release is at times when currents wash them off reefs and into deeper water before they settle (see Kott 1980).

SUMMARY

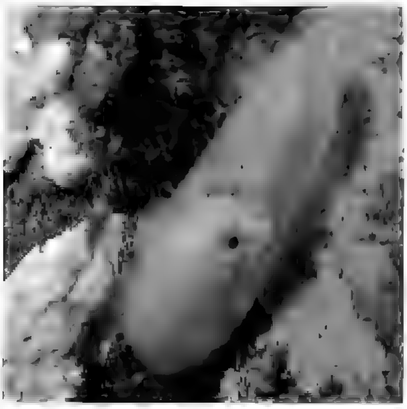
Data on the distribution of the Australian stolidobranch and phlebobranch ascidian fauna suggest that the Australian continent acts as a bridge between tropical and temperate waters, and that the geographic position of Australia, in the centre of the Indo-West Pacific tropical region, has influenced the nature of the ascidian fauna around the whole of the continent:

(a) Species of vast geographic range dominate the Australian tropical fauna and the majority have a range that includes the tropical waters of the western Pacific (Ascidiidae, *Polycarpa*, Polyzoinae, *Microcosmus*).

(b) Many tropical species extend into temperate waters around the southern coast of the continent, where there are also a number of indigenous species of tropical affinities that appear to have evolved as a result of speciation from the tropical fauna (*Polycarpa*, Polyzoinae, *Cnemidocarpa*).

(c) In addition to tropical species in the southern part of their range and indigenous species of tropical affinities, the temperate fauna contains indigenous species of temperate affinities (*Pyuridae*), a few Subantarctic species and some southern temperate species including one (*Pyura stolonifera*) that is possibly a Gondwanaland relict.

PLATE I — ASCIDIIDAE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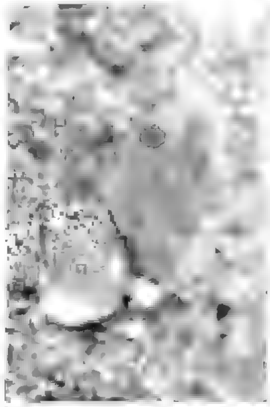
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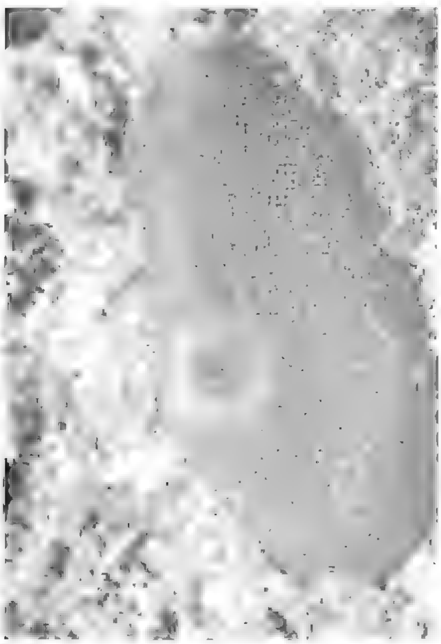
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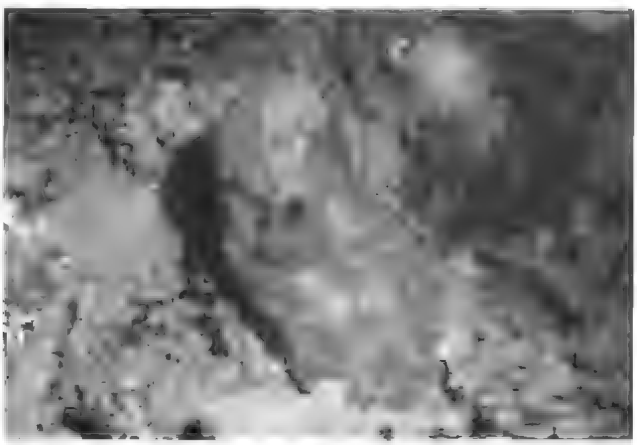
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See following page for caption.

PLATE I — ASCIDIIDAE

a: *Ascidia challengeri* (about 9.0cm long) Port Davey, Tasmania (photo, D. Cropp).

b: *Ascidia kreagra* (about 3.0cm long) Heron I., Queensland (photo, D.L. Parry).

c: *Ascidia liberata* (about 2.5cm long) Lizard I., Queensland (photo, P. Frederickson).

d: *Ascidia sydneyensis* (about 6.0cm long) Tasmania (photo, D. Cropp).

e: *Phallusia arabica* (about 6.0cm long) Heron I., Queensland (photo, D.L. Parry).

f: *Phallusia julinea* (about 6.0cm long) Heron I., Queensland (photo, D.L. Parry).

g: *Phallusia obesa* (about 10.0cm long) Port Hacking, New South Wales (photo, P. Frederickson).

PLATE II — PEROPHORIDAE AND STYELINAE (1)

a,b: *Ecteinascidia diaphanis* (zooids about 1.0cm long) — a, Heron I., Queensland (photo, D.L. Parry); — b, QM G10154, Swain Reefs, Queensland (photo, N. Coleman).

c: *Ecteinascidia maxima* n. sp. (zooids about 2.0cm long) QM GH50 (holotype), Lord Howe I., New South Wales (photo, N. Coleman).

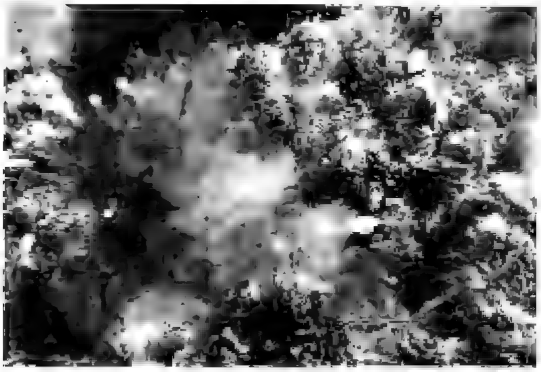
d-f: *Ecteinascidia nexa* (zooids about 6.0mm long) Heron I., Queensland — d, QM GH3484, zooids prostrate, transparent (photo, D.L. Parry); — e, zooids prostrate, opaque (photo, P. Frederickson); — f, QM GH3483, zooids upright, crowded, opaque (photo, D.L. Parry).

g: *Perophora modificata* n. sp. (zooids about 1.0cm long) Lizard I., Queensland (photo, N. Coleman).

h: *Styela plicata* (about 5.0cm high) Port Hacking, New South Wales (photo, P. Frederickson).

See following page for Plate II.

PLATE II — PEROPHORIDAE AND STYELINAE (1)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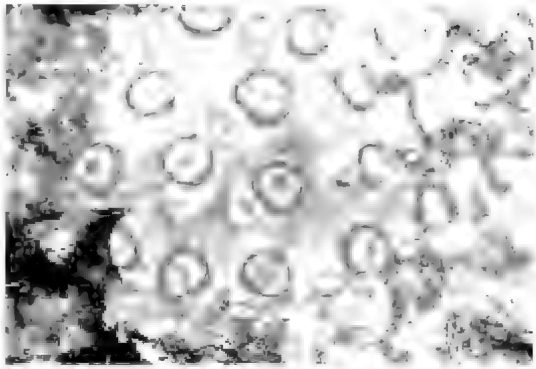
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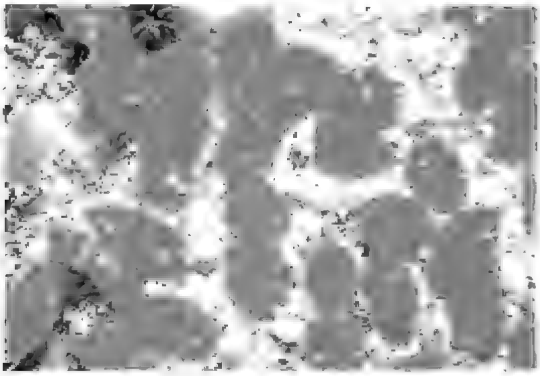
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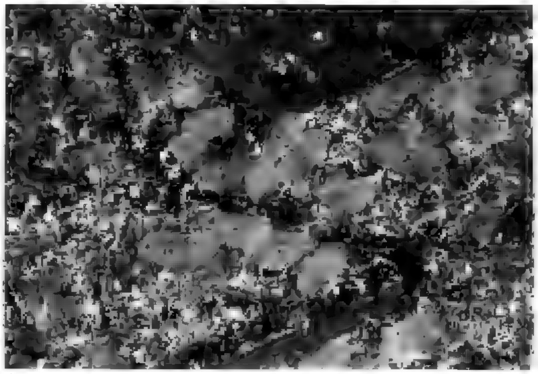
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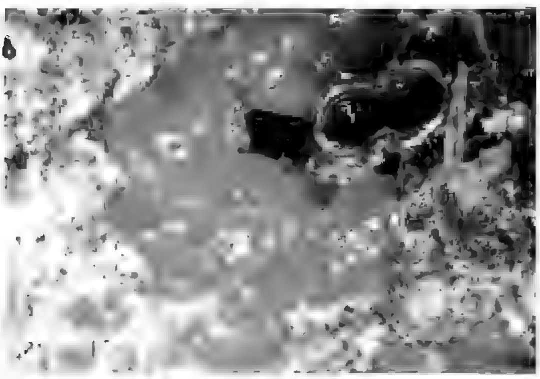
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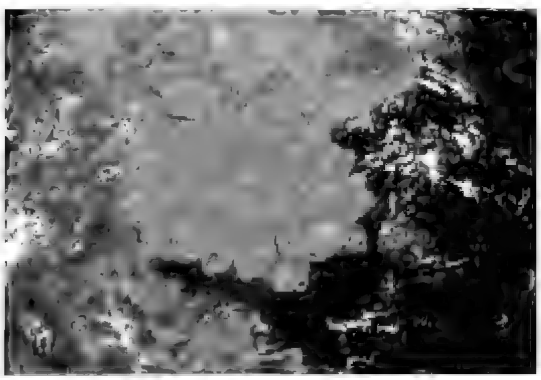
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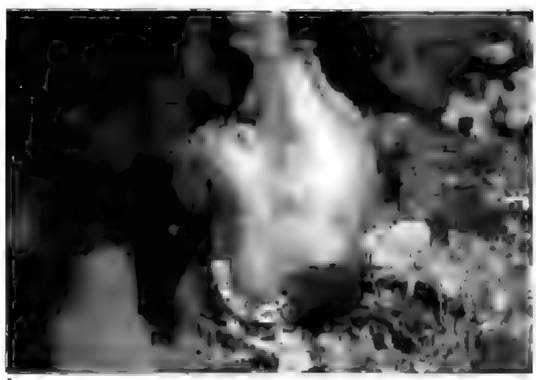
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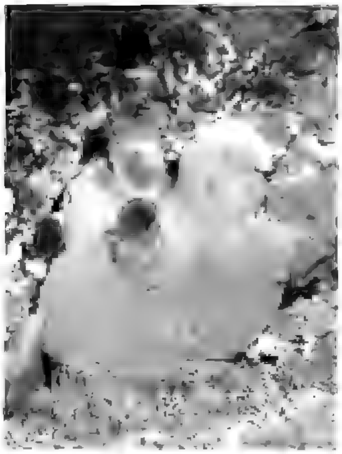
PLATE III — STYELINAE (2)



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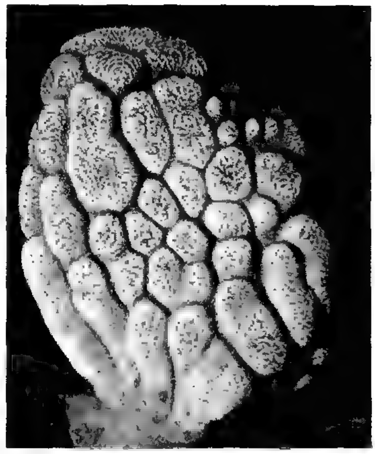

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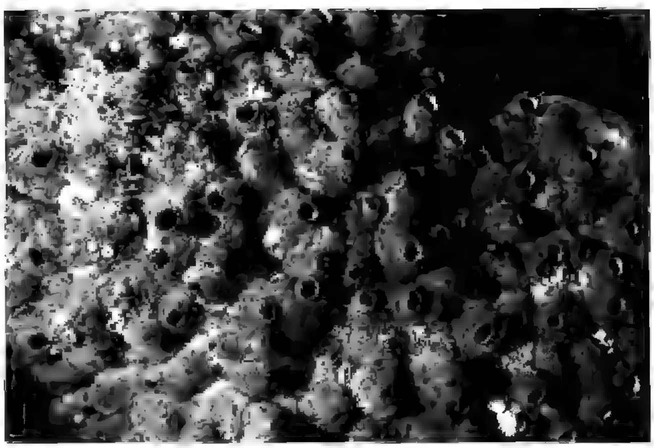

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See following page for caption.

PLATE III — STYELINAE (2)

a: *Cnemidocarpa pedata* (about 5.0cm high, covered with sponge) Batemans Bay, New South Wales (photo, P. Frederickson).

b: *Cnemidocarpa stolonifera* (about 6.0cm high, basal part of body embedded in substrate) QM G9368, Wistari Reef, Queensland (photo, N. Coleman).

c: *Polycarpa aurata* (about 8.0cm long) Lizard I., Queensland (photo, P. Frederickson).

d,e: *Polycarpa clavata* (length, without stalk about 6.0cm) — d, QM GH2375, on sea grass, Roxby I., South Australia (photo, N. Holmes); — e, QM GH274, Lihou Reef, Coral Sea (photo, E. Lovell).

f: *Polycarpa nigricans* (individual about 3.0cm long) northern Great Barrier Reef, Queensland (photo, E. Lovell).

g: *Polycarpa papillata* (about 6.0cm long) QM G11998, Great Keppell I., Queensland (photo, N. Coleman).

PLATE IV — STYELINAE (3) AND POLYZOINAE

a: *Polycarpa pigmentata* (about 10.0cm long, body obscured by epibionts) northern Great Barrier Reef, Queensland (photo, E. Lovell).

b: *Polycarpa procera* (individuals about 3.0cm long) QM G9390, Byron Bay, New South Wales (photo, N. Coleman).

c: *Polycarpa viridis* (individuals about 3.0cm long) QM G9578, Cockburn Sound, Western Australia (photo, N. Coleman).

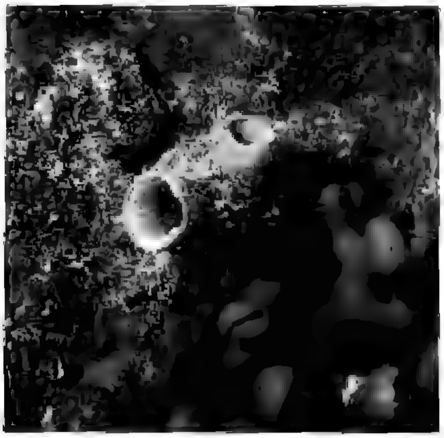
d,e: *Polyandrocarpa lapidosa* (zooids about 5.0mm diameter) — d, QM GH35, Portland, Victoria (photo, N. Coleman); — e, QM GH2381, E Great Australian Bight, South Australia (photo, N. Holmes).

f,g: *Eusynstyela latericius* (zooids about 1.0cm long) Heron I., Queensland (photos, N. Coleman).

h: *Amphicarpa meridiana* n. sp. (zooids about 8.0mm long) QM G10172 (paratype), Port Stephens, New South Wales (photo, N. Coleman).

See following page for Plate IV.

PLATE IV — STYELINAE (3) AND POLYZOINAE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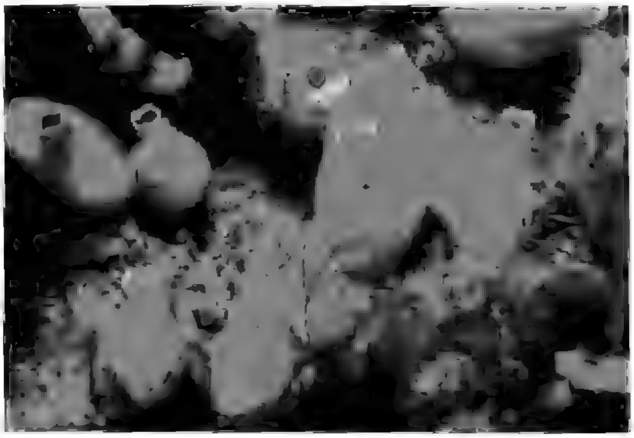
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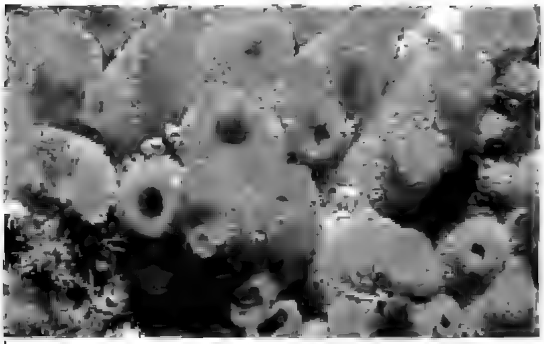
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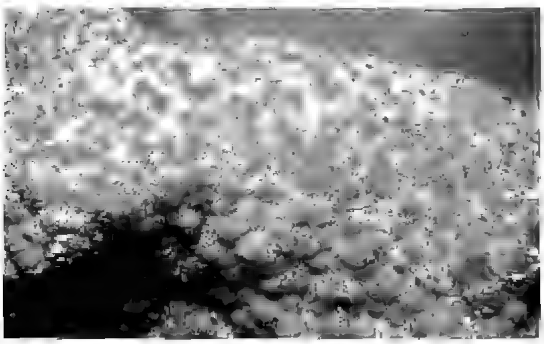
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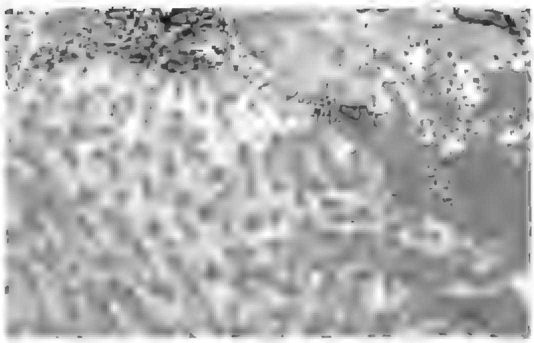
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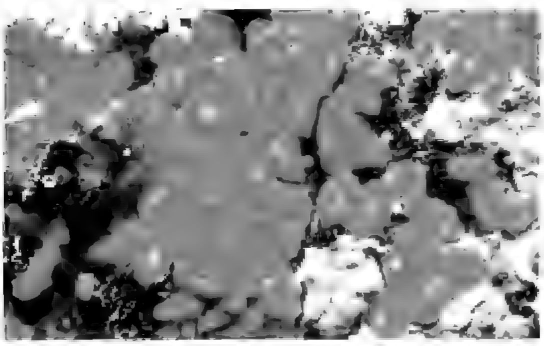
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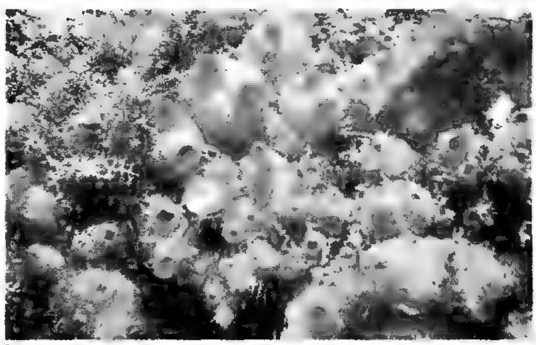
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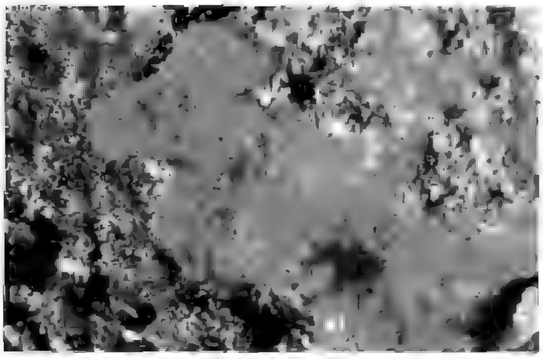
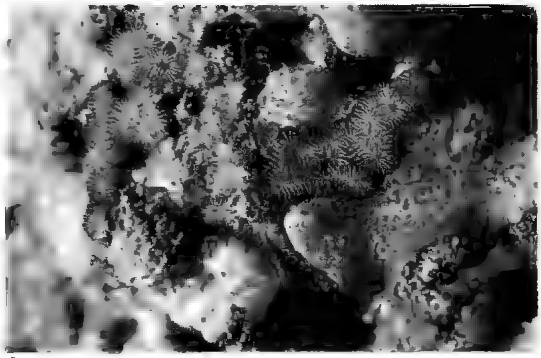
PLATE V — POLYZOINAE (2) AND BOTRYLLINAE (1)


a


c


b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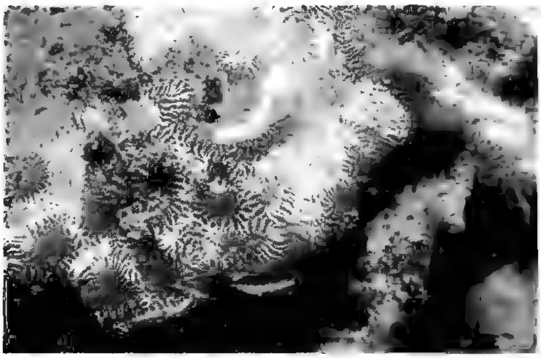
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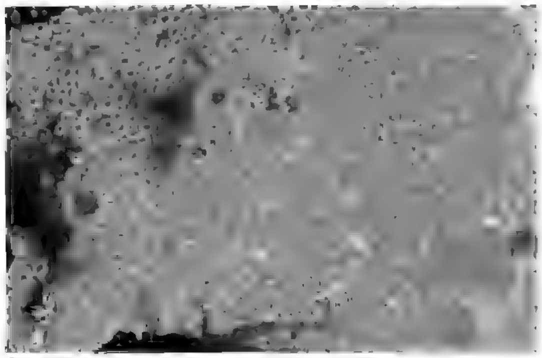
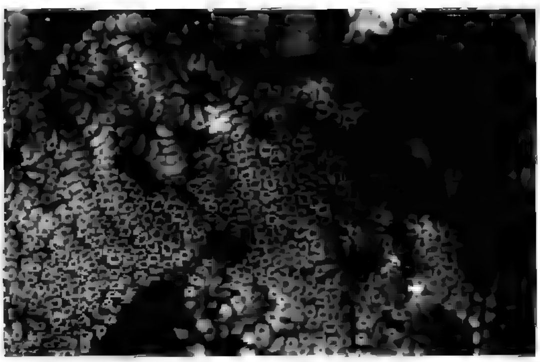

f


g


h

See following page for caption.

PLATE V — POLYZOINAE (2) AND BOTRYLLINAE (1)

a: *Symplegma oceania* (zooids about 3.0mm long) Heron I., Queensland (photo, P. Frederickson).

b: *Symplegma reptans* (circles of zooids about 6.0mm diameter) Heron I., Queensland (photo, P. Frederickson).

c: *Botryllus schlosseri* (zooids about 1.0mm diameter) QM GH2315, E Great Australian Bight, South Australia (photo, N. Holmes).

d-h: *Botrylloides leachi* (zooids about 1.0mm diameter) — d, QM G10099, Heron I., Queensland (photo, P. Frederickson); — e, QM G9394, Port Hacking, New South Wales (photo, N. Coleman); — f, Cockburn Sound, Western Australia (photo, J. Watson); — g,h, Masthead I., Queensland (photos, P. Frederickson).

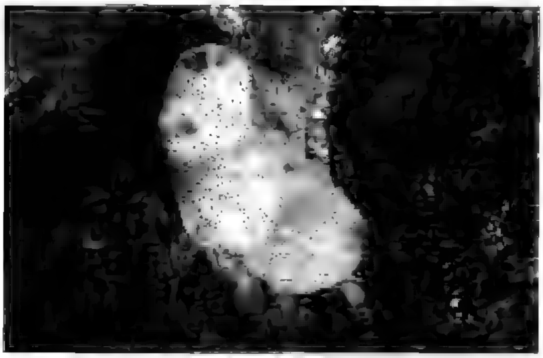
PLATE VI — BOTRYLLINAE (2)

a-d: *Botrylloides magnicoecus* (colony lobes 2 to 3.0cm in diameter) — a, QM GH2301 Port Davey, Tasmania (photo, D. Cropp); — b, Port Kembla, New South Wales (photo, J. Watson); — c, Portland Breakwater, Victoria (photo, J. Watson); — d, Houtman's Abrolhos, Western Australia (photo, E. Lovell).

e-h: *Botrylloides perspicuum* (colony lobes 1 to 2.0cm diameter) — e, Roxby I., South Australia (photo, N. Holmes); — f, Kingston, South Australia (photo, J. Watson); — g, E Great Australian Bight, South Australia (photo, N. Holmes); — h, QM GH2380, Roxby I., South Australia (photo, N. Holmes).

See following page for Plate VI.

PLATE VI — BOTRYLLINAE (2)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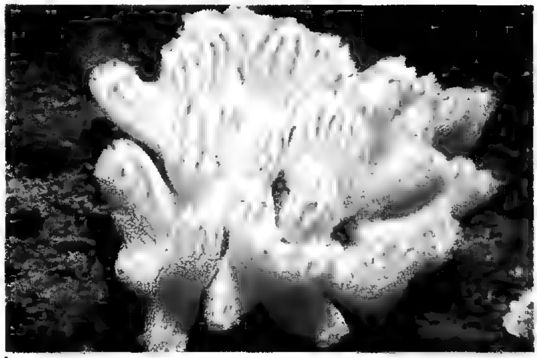
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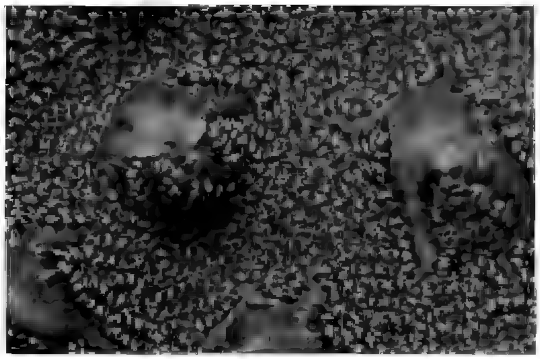
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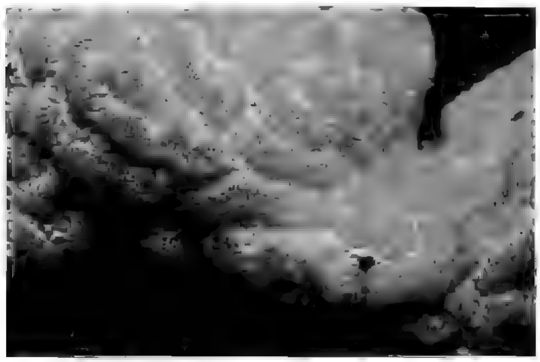

f


g

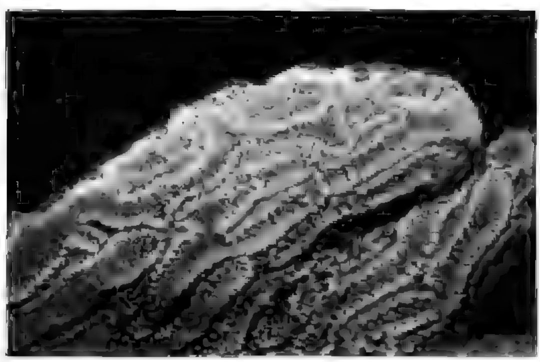
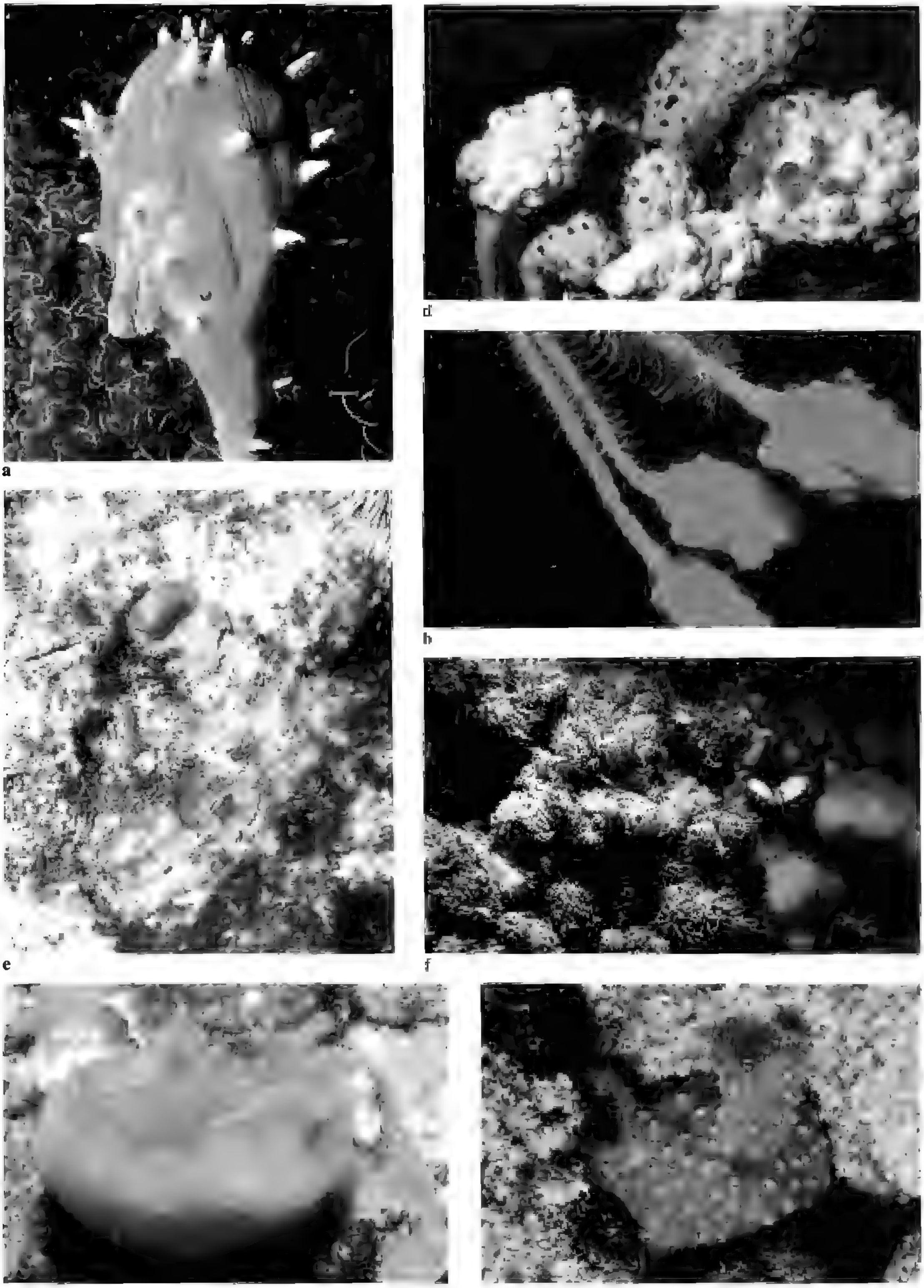

h

PLATE VII — PYURIDAE (1)



See following page for caption.

PLATE VII — PYURIDAE (1)

a: *Pyura gibbosa draschii* (juvenile, head 2.0cm long) QM G10171, Portsea, Victoria (photo, N. Coleman).

b: *Pyura gibbosa gibbosa* (head about 4.0cm long) Port Jackson, New South Wales (photo, P. Frederickson).

c: *Pyura sacciformis* (about 5.0cm long) QM G10174, Port Stephens, New South Wales (photo, N. Coleman).

d: *Pyura spinifera* (heads about 6.0cm long, covered with sponge) Port Hacking, New South Wales (photo, P. Frederickson).

e: *Herdmania momus* (about 8.0cm long, body obscured by epibionts) North Solitary I., New South Wales (photo, P. Frederickson).

f: *Halocynthia hispida* (open siphon, with blue stripes about 1.0cm diameter) with *Amphicarpa meridiana* n. sp, Western Port, Victoria (photo, J. Watson)

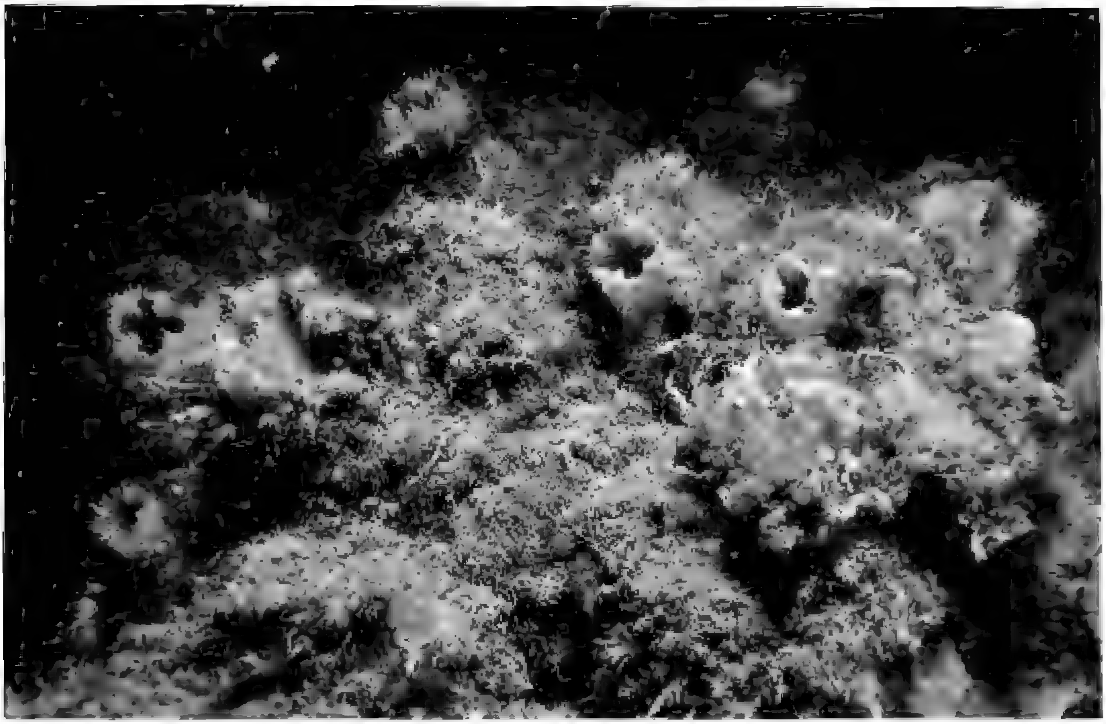
g: *Halocynthia papillosa* (about 3.0cm high) QM G7372, Heron I., Queensland (photo, N. Coleman).

PLATE VIII — PYURIDAE (2)

a,b: *Pyura stolonifera* — a (individuals about 3.0cm diameter) Beaumaris, Victoria (photo, J. Watson); — b, rocky shore at Coolum, Queensland, showing *Pyura stolonifera* in the intertidal zone (photo, D.L. Parry).

See following page for Plate VIII.

PLATE VIII — PYURIDAE (2)



a

b

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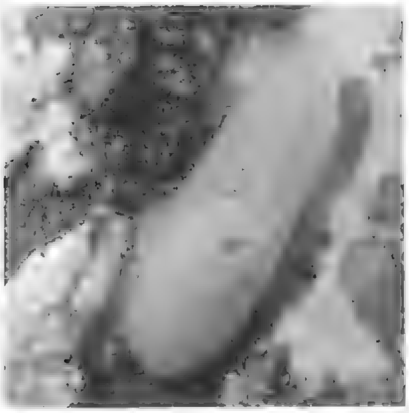
PLATE I — ASCIDIIDAE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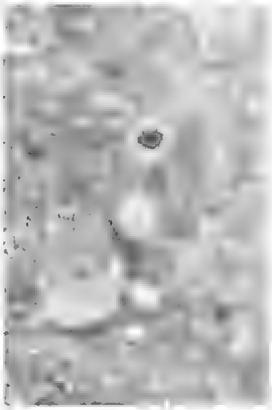
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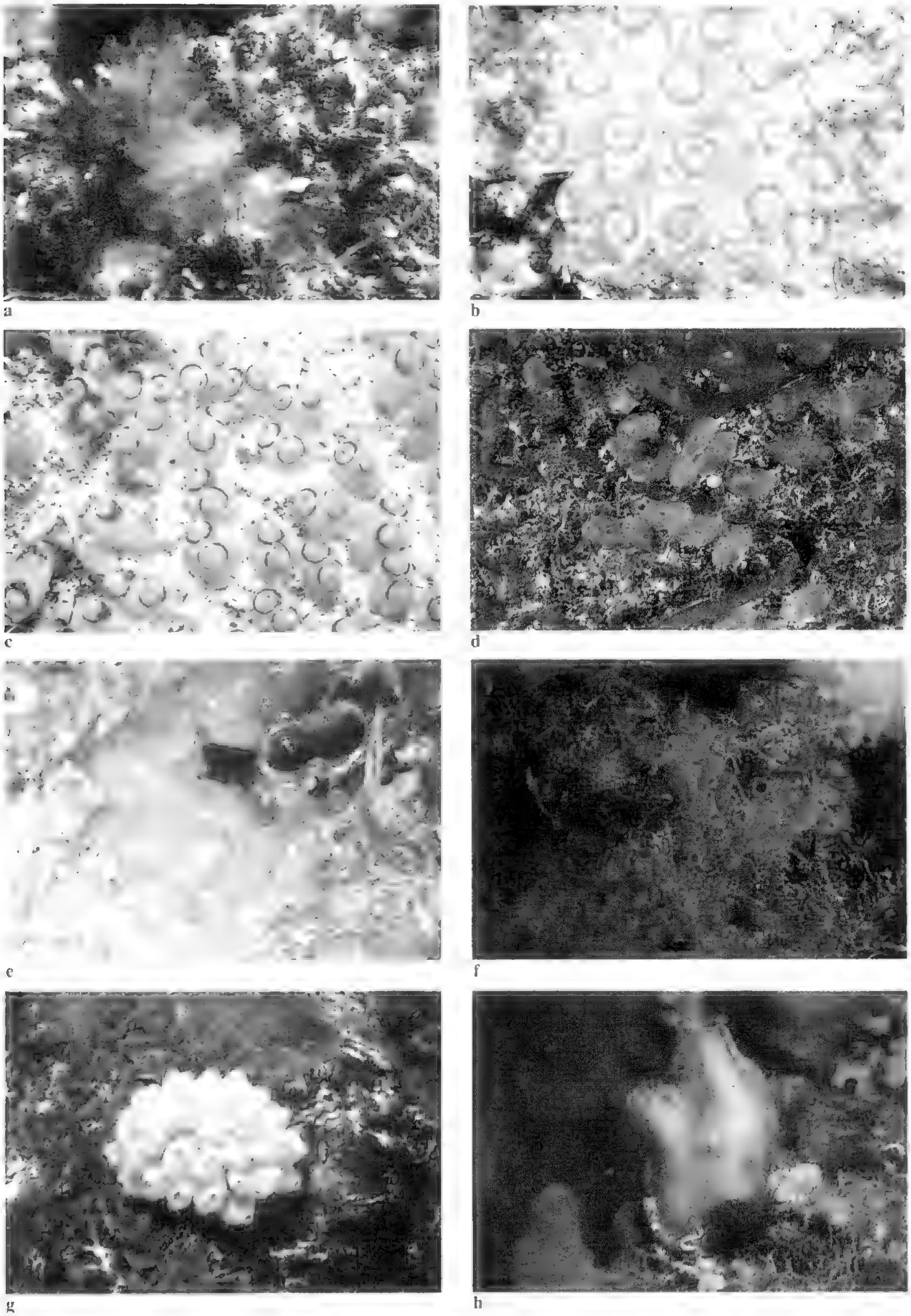
PLATE II — PEROPHORIDAE AND STYELINAE (1)



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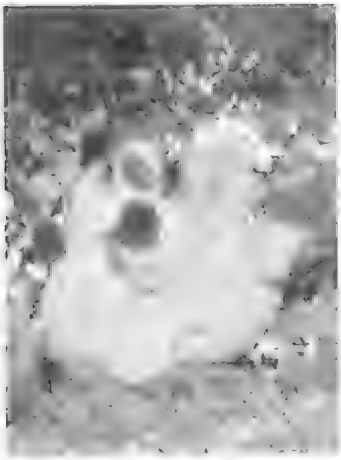
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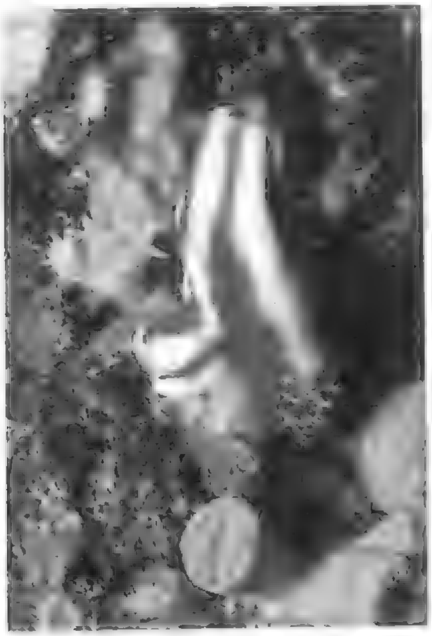
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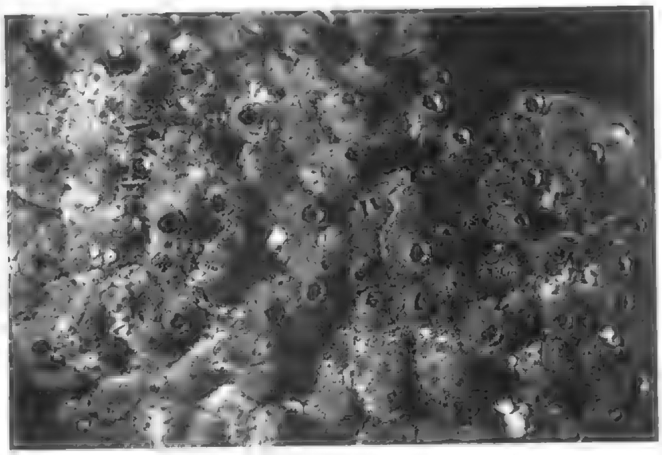
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PLATE IV — STYELINAE (3) AND POLYZOINAE

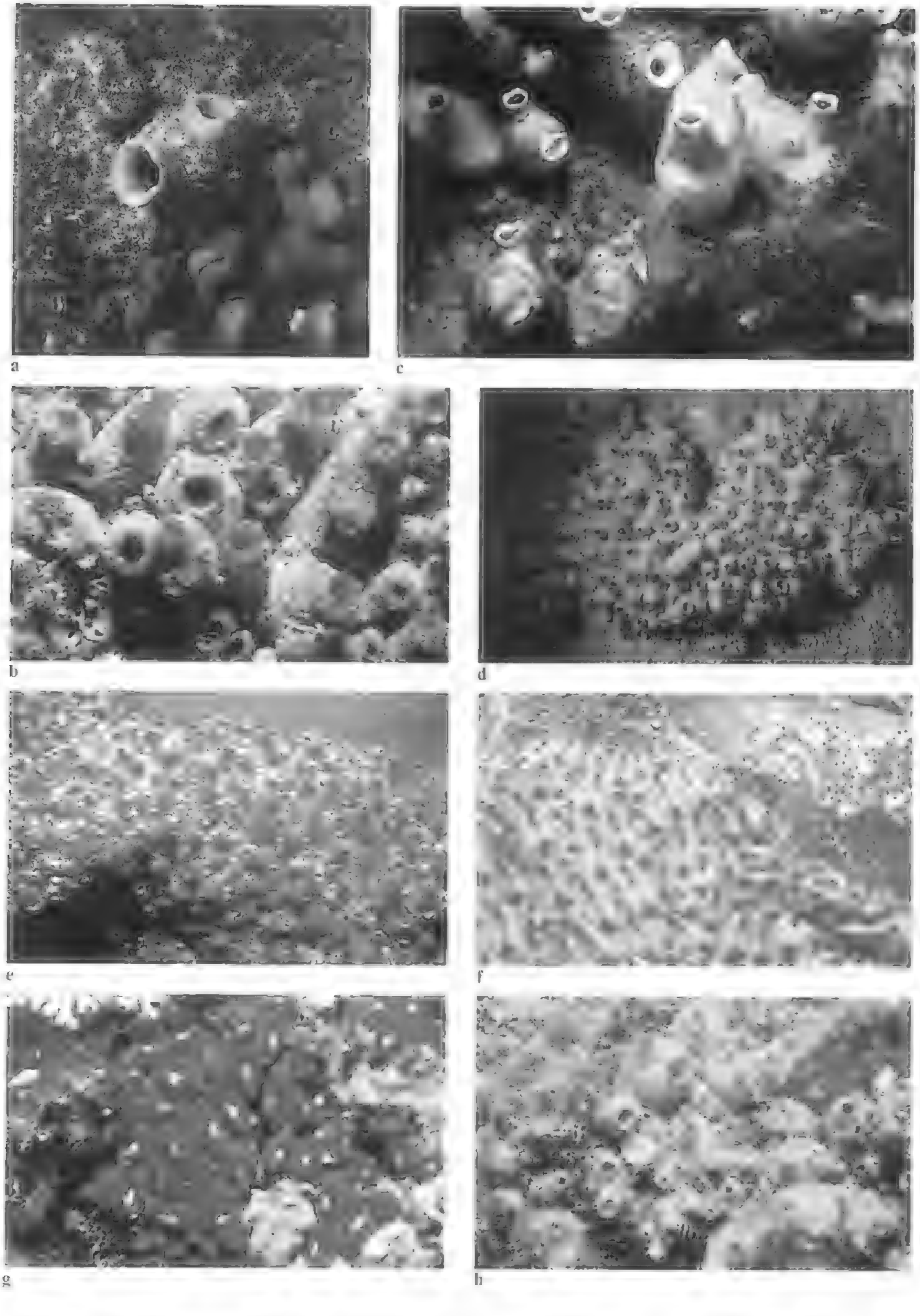

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PLATE V — POLYZOINAE (2) AND BOTRYLLINAE (1)

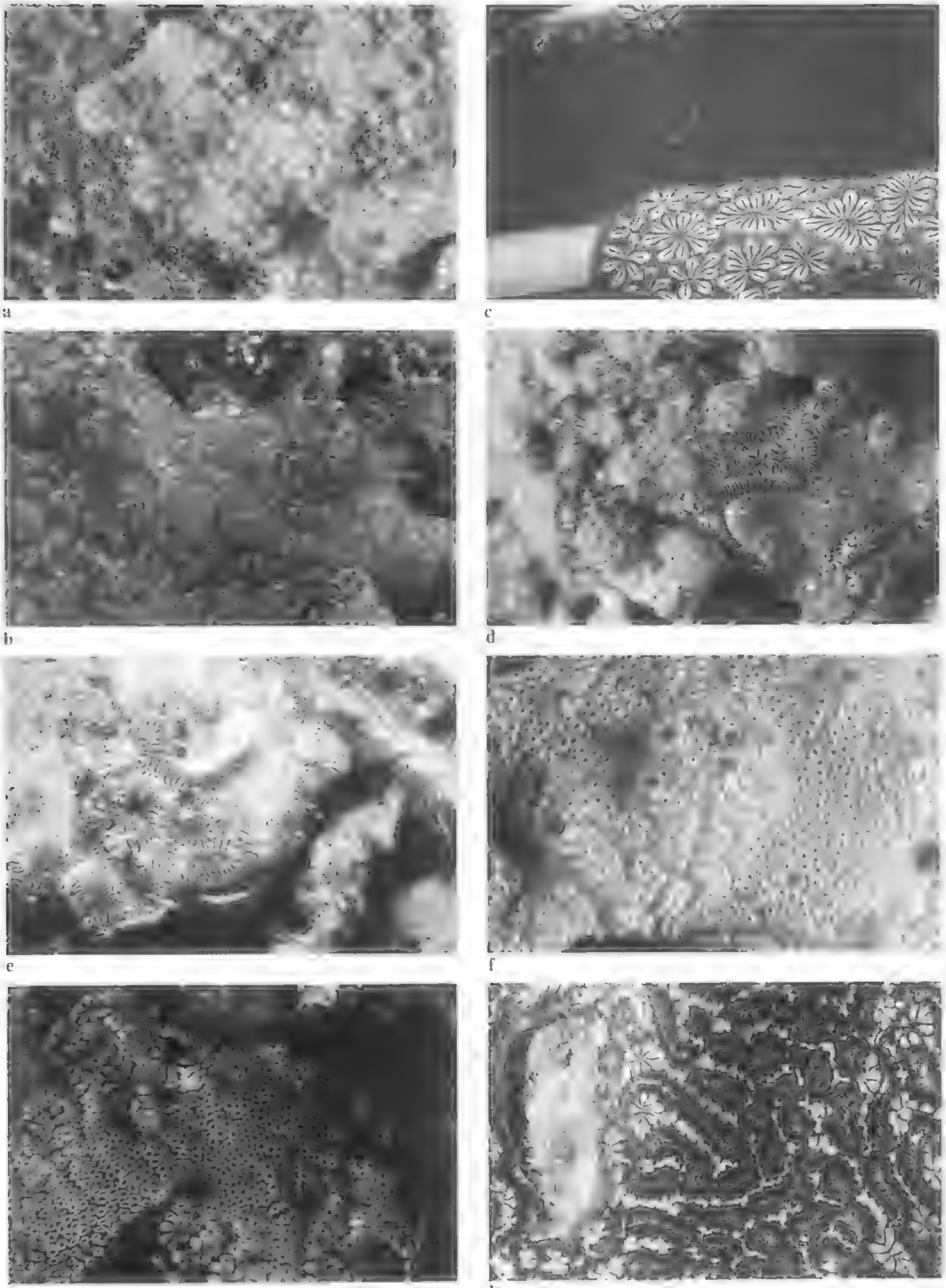

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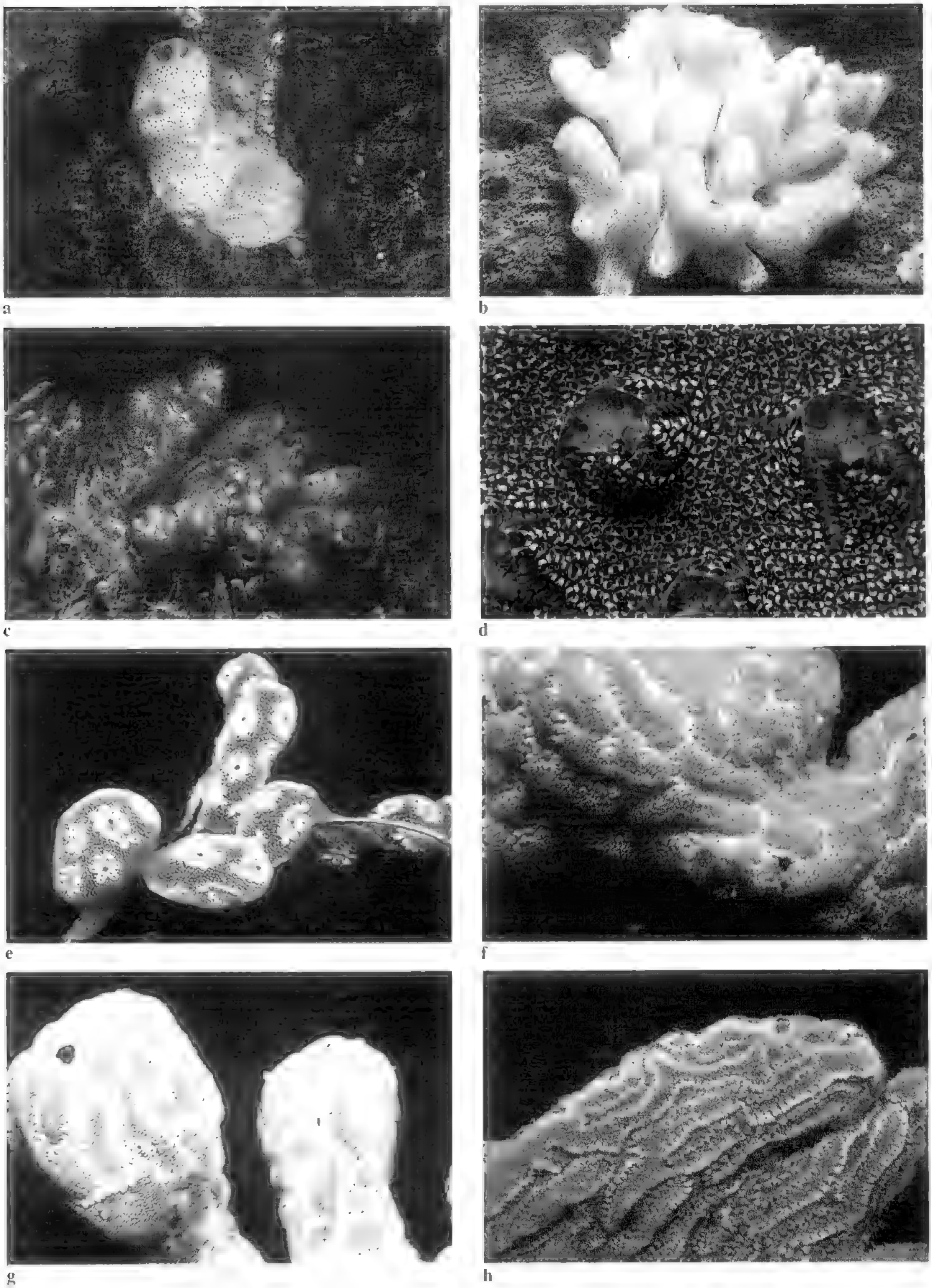
PLATE VI — BOTRYLLINAE (2)



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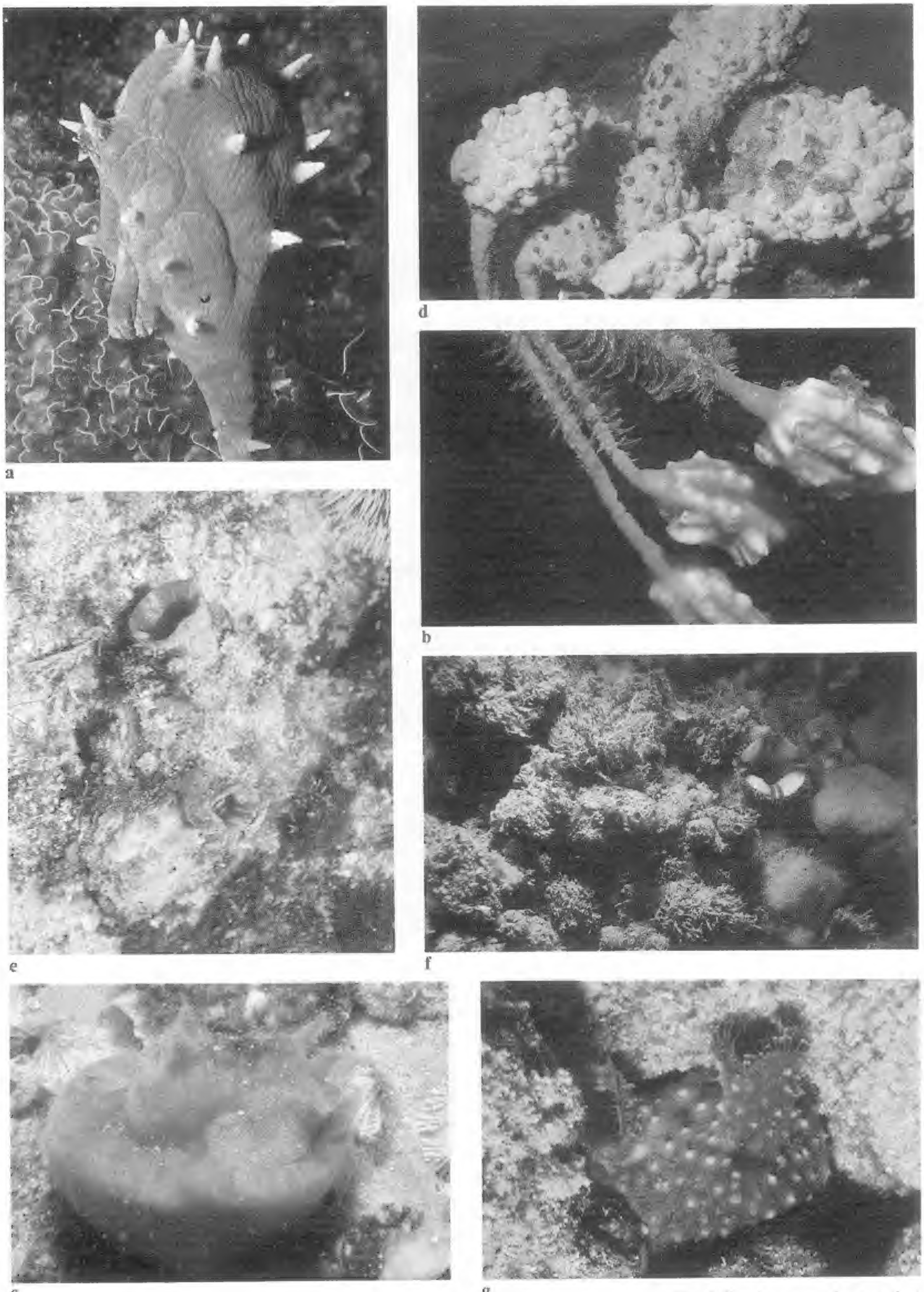

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PLATE VIII — PYURIDAE (2)

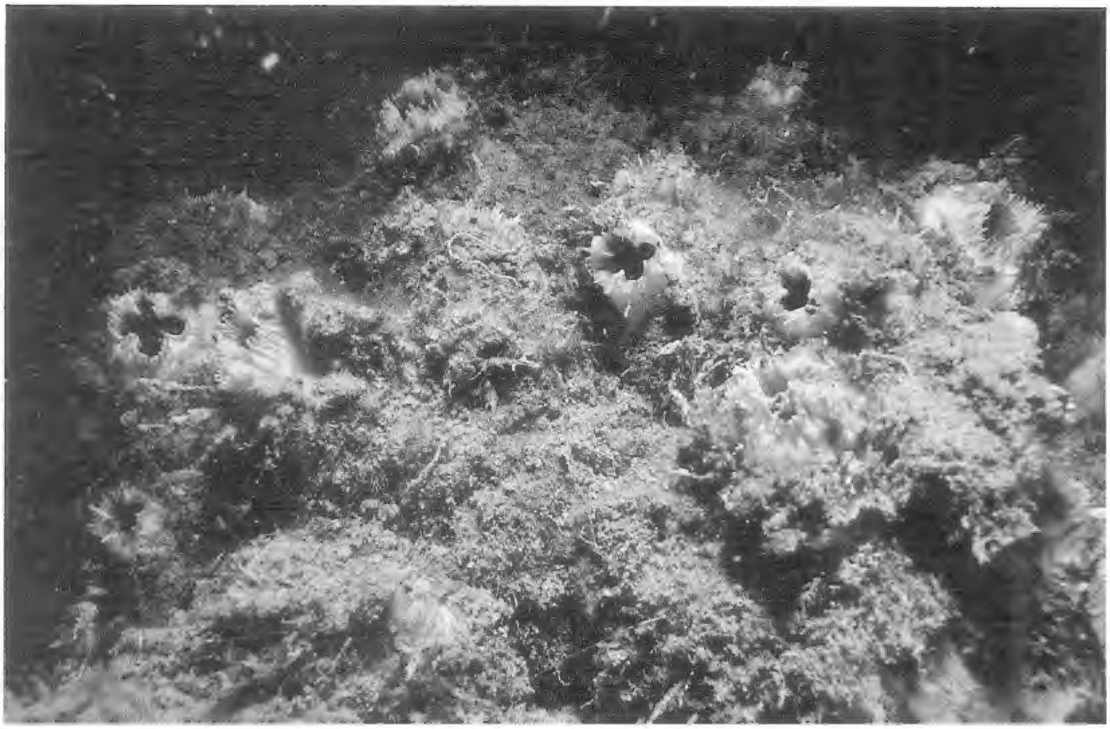

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TABLE XVI SUMMARY OF CHARACTERS OF SPECIES OF *PYURA* RECORDED FROM AUSTRALIA

Species	[1]Range outside Australia	[2]Range in Australian waters	Attachment	Surface	Apertures	Siphonal	Perituber-cular area	Branchial folds	[3]Int gi
P. scortea n.sp.	—	Cockburn Sd	sessile	naked	apart	round scales	shallow	6	
P. elongata	IWP	Dampier Arch. -Mossman	"	"	"	"	deep	"	
P. pantex	Red Sea	Shark Bay	"	"	"	"	?	7	
P. crassacapitata n.sp.	—	Cockburn Sd - Moreton Bay	"	"	"	"	deep	"	
P. molguloides	—	SA–NSW	"	sandy	"	"	"	8–9	
P. navicula n.sp.	—	Moreton Bay	stalked	"	"	"	"	"	
P. abradata n.sp.	—	SA - Bass St	sessile	naked	"	"	narrow, deep	9	
P. viarecta n.sp.	—	Heron I.	"	sandy	"	"	deep	"	
P. confragosa n.sp.	—	Moreton Bay - Lizard I.	"	naked	"	"	wide	"	
P. irregularis	—	Tas. - NSW	"	"	"	"	narrow, deep	7–8	
P. fissa	—	Bass St	"	"	"	"	deep	7	
P. arenosa	WP	Bowen - Abrolhos	"	sandy	close	flattened spines	shallow	6	(
P. tasmanensis n.sp.	—	Tas.	"	"	"	long needles	"	"	
P. obesa	—	Dampier Arch. Cape Melville	stalked or sessile	"	"	"	"	"	(
P. isobella n.sp	—	Cockburn Sd - NSW	sessile	"	"	"	"	"	
P. curvigona	WP	Heron I. - Shark Bay	"	naked	apart	"	"	"	
P. sacciformis	WP	Albany - Cape Kimberley	"	"	"	conical spines	"	6–7	
P. stolonifera	pan-te	Shark Bay - Noosa	"	variable	"	"	"	6–7	
P. littoralis	—	Tas.	"	naked	"	"	none	6	
P. spinosa	—	Cockburn Sd - NSW	stalked or sessile	"	apart	"	shallow	"	(
P. australis	—	Dongara - NSW	stalked	"	"	"	"	"	
P. gibbosa gibbosa	—	Tas - Moreton Bay	"	"	"	"	"	"	(
P. gibbosa draschii	—	Cockburn Sd - Pt Phillip Bay	"	"	"	"	"	"	
P. ostreophila	—	Albany - Bass St	stolons	sponge investment	"	"	"	"	
P. spinifera	—	Carnavon - NSW	stalked	"	"	"	"	6–7	(

[1]Pan-te, pan temperate; WP, western Pacific; IWP, Indo-West Pacific. [2]Range given anti-clockwise around the continent. [3](o folds) between folds. [4]Number of rows; shape; number/row.

TABLE XVI — SUMMARY OF CHARACTERS OF SPECIES OF *PYURA* RECORDED FROM AUSTRALIA (cont.)

	Gut loop	Endocarps on gut	‘Polycarp sacs	Gonad attachment	No. liver diverticula	Additional features
tea n.sp.	closed	absent	2; cuboid;10	ligaments	4	—
gata	open	"	2; rounded; 7–8	"	1+	surface test with thickened scales
tex	"	"	2;7	?	"	"
sacapitata	"	"	2; irregular;12+	ligaments	"	ridge of thick test between apertures
guloides	"	"	2; rounded;12+	"	"	straight branchial folds
icula n.sp.	"	"	2; lobed;5	"	"	sandy papillae on hard test
ıdata n.sp.	"	"	2; lobed;9	"	"	hard wrinkled test
ecta n.sp.	"	"	2; rounded	"	"	sand enmeshed long hairs around surface
fragosa n.sp.	"	present	2; rounded proliferated	"	"	hard wrinkled test often with thickened scales
gularis	"	"	2; rounded;8–10	"	"	dorsal tubercle in posterior end of deep peritubercular area
ı	"	"	2; irregular; proliferated	"	1	surface test with thickened scales
ıosa	closed	absent	2; continuous;8–10	membrane	"	flexible test
nanensis	"	present	2; rounded;12+	embedded	"	hard wrinkled test
sa	"	"	2; continuous;10+	"	"	siphonal spines of 2 sizes; short dorsal lamina; deeply curved gut loop
ɔella n.sp.	"	"	2; lobed;12	membrane	"	siphonal spines inflated basally
vigona	"	"	2; rounded;10+	"	"	siphonal spines with scales
ciformis	"	"	2; continuous;10+	"	4 prs	siphonal spines large striated
lonifera	"	"	1 or 2 cuboid;	embedded	2	very short dorsal lamina
ɔralis	"	"	2; irregular	membrane	4 prs	spherical spicules in test; multiple ♀ openings
ıosa	"	"	2; rounded	"	6 prs	"
tralis	"	"	1; elongate	"	5 prs	stallate spicules in test
bosa gibbosa	"	"	1; elongate;8	"	3 prs	"
bosa draschii	"	"	"	"	5–6 prs	"
reophila	"	°	2; rounded	"	4 prs	aggregates embedded in sponge
nifera	"	"	1; elongate	embedded	3 prs	usually covered by sponge