

THE FAMILY HEXACROBYLIDAE SEELIGER, 1906 (ASCIDIACEA, TUNICATA)

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Kott, P. 1989 11 13: The family Hexacroblyidae Seeliger, 1906 (Ascidiacea, Tunicata). *Mem. Qd Mus.* 27(2): 517-534. Brisbane. ISSN 0079-8835.

Hexacroblyidae, a family containing seven highly adapted abyssal ascidian species in two genera, is closely related to the Molgulidae. A review of the literature together with examination of 14 newly recorded and some previously recorded specimens including the type of *Hexacroblyus psammatodes* Sluiter, 1905 (the type species of the genus *Hexacroblyus*) shows that the latter species is not congeneric with *Hexacroblyus indicus* Oka, 1913. *Hexacroblyus* Sluiter, 1905, *Gasterascidia* Monniot and Monniot, 1968 and *Sorbera* Monniot and Monniot, 1974 are treated as synonyms of *Oligotrema* Bourne, 1903. A new genus is erected to accommodate *Hexacroblyus indicus* Oka, 1913.

□ Ascidiacea, Molgulidae, *Hexacroblyus*, *Oligotrema*, *Gasterascidia*, *Sorbera*, *Asajirus*, abyssal.

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The family Hexacroblyidae Seeliger, 1906 was erected to accommodate its type species *Hexacroblyus psammatodes* Sluiter, 1905 from the Java Sea. Oka (1913) described a further species, *Hexacroblyus indicus*, from the Indian Ocean near Sri Lanka, noting its similarity to *Oligotrema psammites* Bourne, 1903 from New Britain; and confirming the close affinity of both species with the family Molgulidae — a similarity that both Sluiter and Bourne also had noted. Huus (1936) included these three species, *Hexacroblyus psammatodes*, *H. indicus* and *Oligotrema psammites*, together with *Hexacroblyus arcticus* Hartmeyer, 1923, in the family Hexacroblyidae.

Owing to incomplete diagnoses that have resulted from problems in the interpretation of contracted and often mutilated specimens with novel adaptations, there has been confusion in the taxonomy of members of the family.

In this work the comparison of 14 newly recorded specimens with others previously recorded, and with published descriptions has clarified the phylogeny of the family and the relationships of its species.

The specimens marked with an asterisk in the Distribution section of each species treated have been examined in the course of this study. The following abbreviations have been used preceding museum registration numbers: USNM American National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; AM Australian Museum, Sydney, Australia; AMNH American Museum of Natural History, New York, USA; MV Museum of Victoria, Melbourne, Australia; ZMA Zoological Museum, University of Amsterdam, The Netherlands.

EXAMINATION OF SPECIMENS

Owing to the reduction of the branchial sac, it is not possible to dissect individuals of this family by opening them along the endostyle as in most stolidobranch and phlebobranch ascidians. Small individuals, gently removed from the test, can be examined whole by staining in alcohol soluble stain and clearing in glycerol. If dissection is necessary, most organs can be displayed by opening the left atrial cavity to the left of the mid-dorsal line, and then opening the buccal cavity and pharynx. The stigmata and pouches of the pharyngeal wall can only be observed clearly by removing part of it (including the atrial wall), staining and clearing.

FAMILY CHARACTERISTICS

The family is characterised by the large buccal cavity surrounded by 6, usually large and branched, branchial arms; the large kidney; the reduced pharynx limited to a relatively short band at the proximal end of the gut; the small area of the atrial wall perforated by stigmata; and the small atrial aperture without lobes.

With the exception only of *Oligotrema sandersi* and *O. unigonas* in which they are reduced, the large branchial arms have regular pinnate branches along each side of the central stem. The branches curve in across the flat inner surface of the stem and the whole arm can fold down over the branchial aperture. The extensions of the body wall that form these arms carry with them the extensions of the muscles from the region around the buccal cavity. The arms appear to be homol-

ogous with the branchial lobes of other ascidians. Similar, although less developed, enlargements of the branchial lobes consisting of hollow expansions of the test with evaginations of the body wall extending into them are known in both aplousobranch and stolidobranch, including some molgulid, species (e.g. *Molgula sabulosa*, see Kott 1985).

The buccal cavity is lined with test and is homologous with the branchial siphon of other ascidians. It is completely eversible in one species (*Oligotrema sandersi*), forming a proboscis like structure projecting forward and leaving the branchial arms in a ring around the outside of its base. In *Oligotrema lyra* and *O. unigonas* it is partially eversible.

The musculature of the buccal cavity resembles that of the branchial siphon of other Ascidiacea, with longitudinal bands internal to the strong circular muscles that form a sphincter around the branchial opening. The muscles of the arms branch from the circular muscles of the sphincter. Longitudinal and circular muscles are also present around the atrial siphon. Posterior to the siphonal regions, transverse muscles, sometimes interrupted over the sides of the body, are present only in *Oligotrema*; and longitudinal muscles (in two ventral bands) are present only in *Asajirus* n.gen. (see *H. indicus*).

Branchial tentacles are present around the branchial orifice at the base of the buccal cavity only in the genus *Oligotrema*. They are usually irregular and flattened vertically or horizontally.

Although the pharynx is reduced, it has the usual ciliated peripharyngeal band of the Ascidiacea which forms a V in the mid-dorsal line behind the dorsal tubercle. There often is a dorsal groove, but a projecting dorsal lamina is not developed. There is a shallow groove in the mid-ventral line in some species, but a true endostyle is not present. *Oligotrema unigonas* is the only species in which the stigmata are reported to directly connect the atrial cavity with the lumen of the pharynx (see Monniot *et al.* 1975). *Oligotrema sandersi* is the only species in which ciliated stigmata have not been detected (see Monniot *et al.* 1975). In most species there are relatively few openings from the pharynx into a system of chambers that penetrate the wall of the pharynx and open into the right and left anterior horns of the atrial cavity by ciliated stigmata. The branchial chambers appear to be homologous with the spaces created by the three-dimensional network of curving branchial vessels on the inner wall of the pharynx of molgulid genera such as *Ascopera* and *Paramolgula* (compare Herdman 1882 Pl. 4, fig. 6 with *Oligo-*

trema lyra, Fig. 2c below). The walls of the branchial cavities are very delicate. Difficulties in their interpretation arise if they are regarded as tubules rather than spaces. Their structure can be observed only in whole, stained mounts, or in sections.

Although Kott (1969) and Monniot and Monniot (1973) refer to the proximal part of the gut (including the pharynx) as muscular, the muscles are confined to the wall of the buccal cavity and the parietal body wall, and are not found in the walls of the gut itself.

The gut is well developed in all species. A wide oesophagus often is flat in preserved specimens but may be cylindrical in life. With the exception of *Oligotrema lyra* and *O. sandersi* the oesophagus is long and vertical, entering a curved stomach in the posterior end of the body. In *O. lyra* and *O. sandersi* the oesophagus is short, about the same length as the pharynx, and the length of the gut is almost completely taken up by a remarkably large stomach. The rectum varies in length and the anus, its border divided into two shallow lobes, opens at the base of the atrial siphon. In one genus (*Asajirus* n. gen.) there is a crescent-shaped opening from the stomach into a large sac-like diverticulum. Its function is not known, although it has previously been referred to as a liver (Oka 1913, Millar 1959, Kott 1969). However, in the examined specimens referred to below the wall of this sac-like diverticulum is delicate, transparent, and it does not appear to be glandular. There is a conspicuous gastro-intestinal gland with its branches spreading over the wall of the intestine in all species except those in the genus *Oligotrema* in which the stomach is large and the intestine and rectum reduced or absent (see *O. lyra*).

There is some evidence that the species of this family are carnivores, actively trapping a range of crustaceans and polychaetes as well as foraminifers (Bourne 1903, Millar 1959, Monniot and Monniot 1968, Kott 1969). Nevertheless, as Millar (1970) observed, the gut contents could have been taken in with bottom deposits or could fall in from above. The hairs on the posterior part of the body indicate that individuals of *Asajirus indicus* (Oka) are vertically oriented, although the orientation of other species, all of which have the atrial aperture at the posterior end of the body, is more problematical. Actually very little is known of the feeding habits of these organisms. The stigmata are ciliated, the pharynx perforated, and a current of water probably is directed through from the pharynx into the atrial cavity. However, the perforated area is very much reduced and these

ascidians probably are not filter feeders. The strong musculature of the buccal cavity and branchial arms suggests active capture of food rather than a passive process of food falling into the open buccal cavity.

Individuals are monoecious, and the gonads usually are paired, one on each side of the body. They are characteristically molgulid-type gonads with a tubular or sac-like ovary opening near the atrial aperture and usually a single cluster of elongate, branched testis follicles, converging to the vas deferens at the proximal end of the ovarian tube. The vas deferens diverges from the ovary, and opens into the atrial cavity independently of the oviducal opening as in many molgulid species (see Kott 1985). In most other families of the Ascidiacea the male and female gonoducts are associated and open adjacent to one another.

The kidney is large and oval, and contains a large concretion. It is found either on the right side of the body anterior to the right gonad or across the ventral part of the body anterior to the stomach. Its exact position varies according to the development of the gut.

The neural complex consists of the usual dorsal ganglion and gland. Although Monniot *et al.* (1975) believe its position to be particularly superficial, it is in the same position in all families of the Ascidiacea — in the body wall beneath the epidermis between the base of the atrial and branchial siphons. The gland is dorsal to, or dorsal and to the right of the ganglion (as in the Molgulidae and other Stolidobranchia) in *Oligotrema* spp. In the new genus *Asajirus* (> *Hexacrobylus*; Oka, 1913) the gland is ventral to the ganglion as in aplousobranch and phlebobranch ascidians (see Goodbody 1974). The neural ganglion has two anterior short, thick nerve trunks, each dividing into three to serve the six branchial arms. Posteriorly there is the usual median visceral nerve (dorsal nerve cord; Monniot *et al.* 1975) and other smaller paired nerves to the atrial siphon and body musculature as in other species of the Ascidiacea (see Goodbody 1974).

The median visceral nerve in *Oligotrema* spp. has nerve cells anteriorly which become less abundant posteriorly, suggesting the posterior extension of the ganglion as in other stolidobranch species with the atrial aperture at the posterior end of the body (see Kott 1985).

PHYLOGENETIC AFFINITIES OF THE FAMILY

As observed by Bourne (1903), Sluiter (1905), Oka

(1913), Hartmeyer (1923) and Kott (1969), genera of the Hexacrobylidae are related to genera in the family Molgulidae, having a kidney primarily on the right side of the body, six branchial lobes (four in other stolidobranch families) and characteristic molgulid gonads. It is distinguished from the Molgulidae by the reduction of the branchial tentacles and branchial sac, and the development of the branchial lobes into muscular branchial arms which are present consistently in the two known genera of the family.

Seeliger (1906), in erecting the family Hexacrobylidae, placed it in a pleurogonid suborder Aspiraculata, characterised by the absence or rudimentary nature of the stigmata, the presence of the branchial arms, and the position of the gut — behind the pharynx. However, although it is behind the pharynx, the gut bears the same relationship to the atrial cavity as it does in other stolidobranch ascidians; and the other body organs, *viz.* gonads and kidney, embedded in the parietal body wall alongside rather than posterior to the atrial cavity and the gut as in all stolidobranch ascidians. Thus, the position of the gut in relation to the pharynx is the result of the reduction in the size of the pharynx rather than some plesiomorphic change that could justify the establishment of a new suborder.

Perceiving differences in the nervous system, the gut and the position of the kidney, Monniot *et al.* (1975) and Monniot and Monniot (1978) elevated the Hexacrobylidae to a separate class of the Tunicata — the Sorberacea. However, as discussed below, the characters invoked to support this separation cannot be confirmed as real plesiomorphic differences between Hexacrobylidae and the rest of the Ascidiacea.

The principle distinction between Sorberacea and Ascidiacea (Monniot *et al.* 1975) is based on the view that the posterior median nerve in the Sorberacea is homologous with the dorsal strand (sometimes called dorsal cord) of the Ascidiacea. However, the dorsal strand of the Ascidiacea has no neural elements. It extends posteriorly from the duct of the neural gland rather than the ganglion (Goodbody, 1974). Although associated closely with the visceral nerve it consists of histologically undifferentiated cells, and develops independently of the adult nervous system. There is no justification for regarding the posterior median nerve in the Hexacrobylidae as other than the homologue of the median visceral nerve present in all taxa of the Ascidiacea. The nerve cells in the anterior part of this median nerve in *Oligotrema* spp. appear to

indicate a lengthening of the neural ganglion — a commonly occurring phenomenon in species with posteriorly positioned atrial apertures (see *Pyura elongata*, *P. molguloides*: Kott 1985). The neural complex is in the same position beneath the epidermis as it is in other families of stolidobranch and aplousobranch ascidians. The minute cell masses on the posterior median nerve called accessory ganglia (Monniot *et al.* 1975) that were invoked in support of the new class were observed to resemble the cells of the neural gland (Monniot *et al.* 1975) and there seems no reason to regard them as other than 'small accessory neural glands' (Monniot and Monniot 1978, p.206).

The histology and morphology of the gut are variable throughout the Ascidiacea. In the Hexacrobylidae the large stomach is found in only two species, while in others the gut has the usual subdivisions. The branchial sac is reduced, but is not absent in Hexacrobylidae; and differences in the structure of the branchial sac between aplousobranch and molgulid species are greater than those between Hexacrobylidae and Molgulidae. The kidney is usually on the right side of the body, as in the Molgulidae, although variations in development of the gut sometimes force it ventrally and toward the left. The gonads and gonoducts of species of the present family are identical with those found in many species of the Molgulidae (see Kott 1985).

The members of the family Hexacrobylidae are highly adapted, presumably for life at great depths (having been recorded from 94m to about 5000m). Although it is not yet positively demonstrated, they may be adapted for a carnivorous and active predatory habit. Nevertheless the members of the family have closer plesiomorphic characters in common with the Molgulidae than the members of that family have with other families of the Stolidobranchia, especially in regard to the morphology of the branchial sac and gut, the presence of a kidney, the arrangement of the gonads, and the nature of the thin but tough and fibrous test.

The justification for the family Hexacrobylidae separate from the Molgulidae is somewhat problematical. It is retained here as a reflection of the apparently close relationship between its two genera rather than an indication of its phylogenetic distance from the Molgulidae.

The type genus of the family Hexacrobylidae is *Hexacrobylus* Sluiter, 1905 < *Oligotrema* Bourne, 1903.

KEY TO SPECIES OF THE HEXACROBYLIDAE

1. Branchial tentacles present; sac-like divertic-

ulum of gut not present (*Oligotrema*) 2
Branchial tentacles not present; sac-like
diverticulum of gut present (*Asajirus* n. gen.)
..... 5

2. Branchial arms with pinnate branches 3
Branchial arms without pinnate branches 4
3. Testis divided into two; oesophagus short;
rectum vestigial *O. lyra*
Testis not divided into two; oesophagus long;
rectum not vestigial *O. psammatodes*
4. Testis and ovary present on both sides of
body; male follicles not branched; oesopha-
gus short *O. sandersi*
Testis present on both sides of the body, ovary
present only on one side of body; male
follicles branched; oesophagus long
..... *O. unigonas*
5. Ventral longitudinal muscle bands present
along length of body *A. indicus*
Ventral longitudinal muscle bands not present
along length of body 6
6. Testis follicles in two separate clusters
..... *A. dichotomus*
Testis follicles not in two separate clusters ..
..... *A. gulosus*

Asajirus n. gen.

Type species: *Asajirus indicus* (Oka, 1913) > *Hexacrobylus indicus* Oka, 1913.

The name *Hexacrobylus* is preoccupied by *H. psammatodes* Sluiter, 1905, type species of the genus *Hexacrobylus*, which is a junior synonym of the genus *Oligotrema* Bourne, 1903. The name of the new genus commemorates Dr Asajiro Oka, the author of its type species.

The genus is characterised by the complete absence of branchial tentacles, a long oesophagus, a large sac-like diverticulum of the gut with a crescent-shaped opening at the base of the oesophagus, a relatively small stomach, a very short pharynx with one or two openings on each side, two stigmata in each anterior horn of the atrial cavity, the atrial aperture projecting forward from halfway down the body, and the neural gland ventral to the ganglion.

The atrial cavity, extending ventrally from the atrial aperture at mid-dorsal level and dividing into

two pouches one passing each side of the oesophagus to terminate anteriorly beneath the pharynx, is smaller than in the genus *Oligotrema* (in which it extends almost the whole length of the body).

The body musculature is strong around the siphonal regions. However, on the sides of the body the longitudinal muscles usually extend only to the level of the posterior end of the pharynx. Only in one species (*Asajirus indicus*) are there also two strong bands of longitudinal muscles, one each side of the mid-ventral line, extending to the postero-ventral part of the body. Unlike the genus *Oligotrema*, *Asajirus* has no transverse muscles on the body other than those around the siphons.

There are 3 species known in this genus.

Asajirus indicus (Oka, 1913) known from 1000 to 5000 m in the central and western Indian Ocean, the tropical eastern Pacific, the Arctic and all parts of the northern Atlantic, and tropical-central and south-western Atlantic. It is very possible that the species will be found to occur in all the oceanic basins. Undoubtedly its remarkable depth range has contributed to gene flow and prevented isolation of its populations.

Asajirus gulosus (Monniot and Monniot, 1984) is known only from 11 specimens from 1800 to 2500 m in the tropical western Indian Ocean.

Asajirus dichotomus (Monniot and Monniot, 1984) is known only from 3 specimens from 3550 m in the Cape Basin (S.E. Atlantic).

Asajirus indicus (Oka, 1913)

Hexacrobylus indicus Oka, 1913, p. 6. Millar, 1959, p. 203; 1970, p. 147. Monniot, C., 1969, p. 184. Monniot, F., 1971, p. 458. Monniot and Monniot, 1968, p. 32; 1970, p. 334; 1973, p. 457; 1974, p. 777; 1984a, p. 198; 1985a, p. 35; 1985b, p. 307.

Hexacrobylus arcticus Hartmeyer, 1923, p. 133. Arnback, 1928, p. 76. Van Name, 1945, p. 442. Monniot and Monniot, 1984b, p. 141; 1985a, p. 34.

Hexacrobylus eunuchus Monniot and Monniot, 1976, p. 658.

Hexacrobylus sp. Kott, 1957, p. 147. Monniot and Monniot, 1982, p. 128 part (specimen 4.5 cm).

Oligotrema psammites: Kott, 1969, p. 168.

DISTRIBUTION

NEW RECORDS: Western Pacific Ocean (34°27'S, 51°27'E — 1200m, AM Y2125, 1 spec*; 38°16.40'S, 149°27.60'E — 800m, MV F53949, 1 spec*; 38°19.6'S, 149°24.3'E — 930m, MV F53948, 2 specs*; 38°21.9'S, 149°20.00E — 1000m, MV F53947, 3 specs*; 42°2.20'S, 148°38.70'E — 800m, MV F53950, 2 specs*).

PREVIOUSLY RECORDED: Indian Ocean (Sri Lanka —

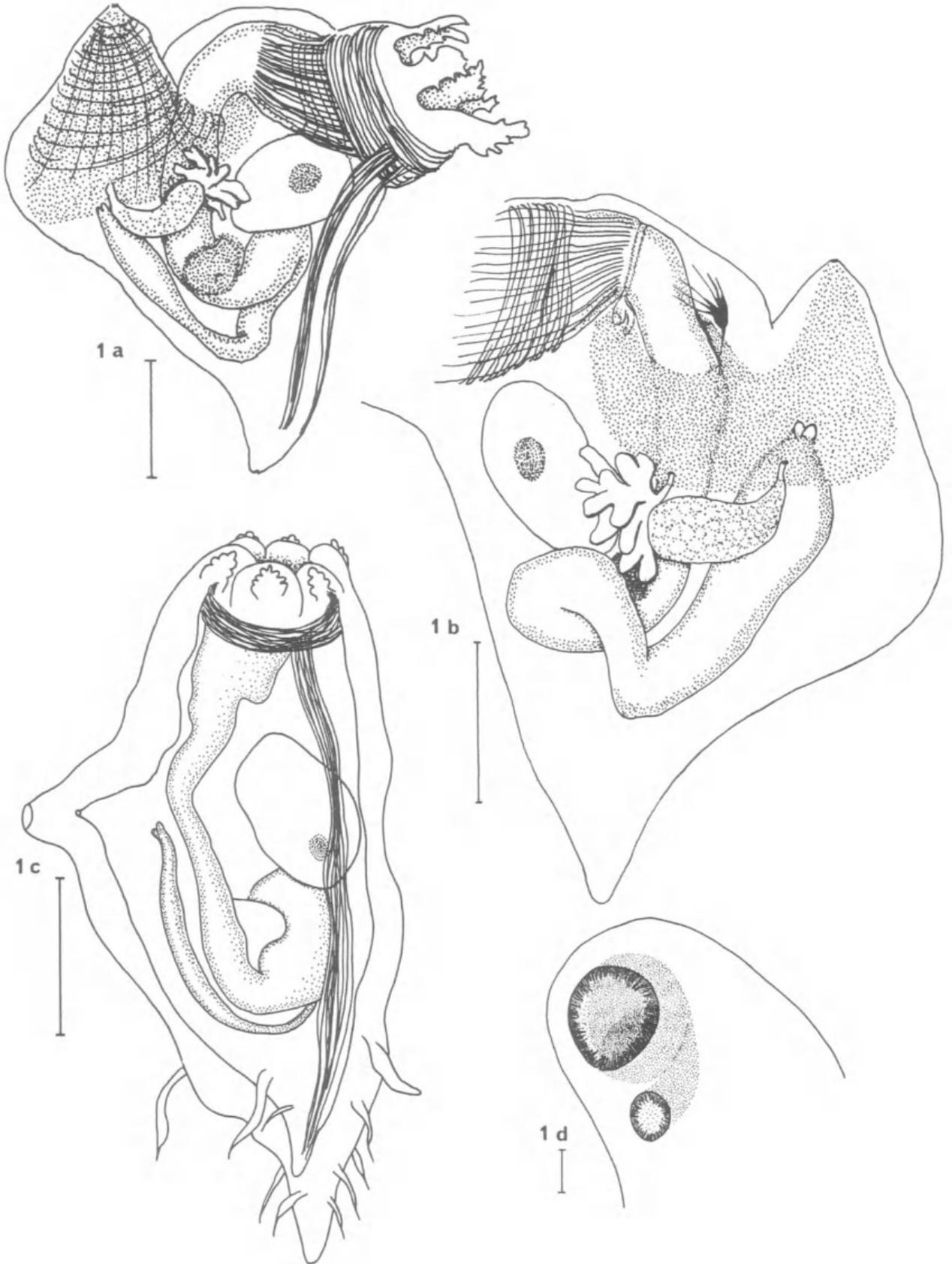
3500 m, Oka 1913. Seychelles — 4340–50 m, Millar 1959, ? Southern Arabia — 2000 m, Kott 1957. Central and western Indian Ocean — 1300–4283 m, Monniot, C. and F. 1984a; 4280 m, 1985b). Pacific Ocean (tropical E. Pacific — 1892 m, 3659 m, AMNH 2257* 2258 (part)* Millar 1970). Atlantic Ocean (Faroes and Iceland — 891–1264 m, Hartmeyer 1923. N.E. Atlantic — 900 m, Monniot, C. 1969; 2134–4400 m, Monniot, C. and F. 1974; 4190–4480 m, Monniot, C. and F. 1984b; 3859–4435 m, Monniot, C. and F. 1985a. N. central Atlantic — 1200–4692 m, Monniot, C. and F. 1973. N.W. Atlantic — 2496 m, Monniot, C. and F. 1968; 4400 m, Monniot, C. and F. 1985. Tropical central Atlantic — 2022–4892 m, Monniot, C. and F. 1970; 1493–3806 m, Monniot, F. 1971. S.W. Atlantic — 2672–3030 m, USNM 12646* Kott 1969; 2000–5000 m, Monniot, C. and F. 1976; 2195–2323 m, Monniot, C. and F. 1985a).

DESCRIPTION (Fig. 1a–c)

The body is sac-like, usually rounded posteriorly with a beard of fine hairs, to which foraminifers and other particles adhere. In one specimen (MV F53949) the posterior end of the body is drawn out to a point; and one specimen from the tropical Atlantic (Monniot and Monniot 1970) has a long narrow stalk from the posterior end of the body. The branchial opening at the anterior end of the body is a wide, transverse aperture surrounded by branchial arms with regular pinnate branches along each side of the central tapering stem. There are four arms on the ventral side of the branchial opening and two larger arms on the dorsal side. The largest specimen of this species for which the length has been recorded is 2.3 cm long (Monniot, C. and F. 1984a), although one of 4.5 cm (Monniot, C. and F. 1982) may be of this species. The test is thin and translucent.

The atrial siphon is largely internal, only a relatively small conical protrusion being apparent on the surface. Internally it is very variable in length, occasionally being as long as half the body length. It opens about level with the base of the crown of the branchial arms. It is probable that in life the atrial aperture is directed upwards and the branchial aperture to the side.

The base of the buccal cavity is surrounded by a sphincter muscle where it passes into the pharynx. Strong longitudinal muscles are present in the walls of the buccal cavity inside the circular muscles. There are also circular and longitudinal muscles on the atrial siphon, the longitudinal ones extending onto the sides of the body over the atrial cavity. Circular muscles are absent from the remainder of the body and the longitudinal musculature is confined to two ventral bands, one each side of the ventral mid-line, that extend into the



(sometimes pointed) postero-ventral corner of the body which is attached to the test, and which fits into the posterior projection of the test when this is present (MV F53949). The atrial cavity envelops the oesophagus from the dorsal surface, separating the parietal body wall from the oesophagus. It extends anteriorly, ventral to the pharynx, in two horns, one on each side.

The neural gland is ventral to the neural ganglion in the interval between the two siphons at the base of the buccal cavity. Its short duct extends ventrally to open into the pharynx by a transverse slit on the small dorsal tubercle. A peripharyngeal groove around the anterior part of the pharynx forms a V in the dorsal mid-line behind the dorsal tubercle. The very short pharynx has on each side, ventrally, a small aperture opening into an anterior and posterior pharyngeal chamber.

The structure of the branchial apparatus in this species is not completely understood. Monniot *et al.* (1975) have demonstrated two openings in a depression (interpreted here as a single opening) on each side of the pharynx, each leading into two large interconnected conical pharyngeal chambers. Each pharyngeal chamber opens into a pocket in the atrial cavity through a horse-shoe shaped ciliated opening (stigmatum). Similar horse-shoe shaped stigmata opening into the anterior horns of the cloacal cavity on each side can be observed in the relatively robust (but rather mutilated) specimen from the South Atlantic (1.5 cm long, USNM 12646). In the smaller (1.0 cm) long specimen from the tropical eastern Pacific (Millar 1959, AMNH 2258) there are two round stigmata, a larger one anterior to a smaller one, in each anterior horn of the atrial cavity. A similar arrangement of stigmata can be seen in one side of the atrial cavity of a small, newly recorded specimens (MV F53948, 4 mm long), although on the other side there is only a single vertically oriented oval stigmatum. The longer stigmata seem to be depressed into the atrial wall for at least part of their length, possibly resulting in the atrial pouches referred to by Monniot *et al.* (1975).

The oesophagus is long, extending most of the length of the body. It opens into a U-shaped stomach enlargement which curves dorsally and to the left before narrowing to the rather long intestine which loops around in the postero-dorsal curve of the body to the base of the atrial siphon where it opens by a two-lipped anus. In larger

specimens (USNM 12646) the anal lips have small secondary lobes. At the base of the oesophagus there is a crescentic opening to a sac-like diverticulum lying transversely across the anterior limb of the stomach between the intestine and the kidney.

The kidney is large and oval, lying anterior and slightly to the right of the gut loop.

The gonads consist of long, branched male follicles in a single clump at the proximal end of each long, tubular ovary. The male follicles converge into the centre of the clump where they join a short vas deferens which opens directly into the atrial cavity. The female openings are near the anus at the base of the atrial siphon.

REMARKS

The specimen from 2672-3030 m north of the South Shetlands (USNM 12646; Kott 1969) was described as having a muscular oesophagus, a glandular diverticulum from the gut, and two large sacs from the pharyngeal region that Kott (*loc. cit.*) interpreted as branchial sacs. This specimen has been re-examined. As Millar (1970) suggested, what Kott called 'pharyngeal sacs' are indeed the atrial cavity. There is a single opening from each side of the gut into the two interconnected chambers each opening into the atrial cavity by a very long curved stigmatum. The more numerous openings (Kott 1969, Fig. 239) appear to be sections of the long curved stigmata. The gut diverticulum and the oesophagus are the same as in the present specimens. The larger of the two specimens from the Antarctic assigned to *Hexacrobylus* sp. by Monniot and Monniot (1982), with its buccal cavity turned to the side, may also be a specimen of *A. indicus*. If so, it is the largest specimen known, having a length of 4.5 cm.

Specimens ascribed to *Hexacrobylus arcticus* Hartmeyer, 1923 have only one distinction from the majority of recorded specimens of this species — they have a longer spermduct. However, they have been recorded from the Faroes and Iceland, and the Bermuda Basin, the north-east Atlantic Basin and North West Atlantic. Thus, specimens with this long oviduct attributed to *H. arcticus* are not from a single isolated population and, in fact, Monniot and Monniot have observed both long and short sperm ducts in specimens from the eastern Atlantic (see Millar 1970). It is more likely, in a species with the wide range of the present one, that there is some genetic diversity, and that the

FIG 1. *Asqirus indicus* (Oka, 1913): a, individual from right side (AM Y2125); b, body from left side, branchial arms not shown (AM Y2125); c, individual attenuated posteriorly (MV F53949); d, opening of stigmata into the atrial cavity (MV F53948). Scales: a-c = 1.0 mm; d = 0.1 mm.

long oviduct is a reflection of this diversity, found especially in populations from all parts of the north Atlantic as far south as the Bermuda Basin.

In one of the newly recorded specimens (AM Y2125) there is a large parasitic copepod embedded in the right parietal body wall near the base of the atrial cavity.

***Asajirus gulosus* (Monniot and Monniot, 1984)**

Hexacrobylus gulosus Monniot and Monniot, 1984a, p. 203.

DISTRIBUTION

Indian Ocean (tropical W. Indian Ocean — 1800–2500 m, Monniot C. and F. 1984).

DESCRIPTION (after Monniot and Monniot 1984a including Figs 4 A–D, 5A–B)

Eleven very damaged specimens are known. They are oval, the largest 1.25 cm long. The body has the same branchial arms, test with fine hairs to which foraminifers attach, and mid-dorsal atrial aperture as *A. indicus*. There is neither a stalk nor ventral longitudinal muscle bands. There are two pharyngeal perforations on each side. A very large distended rectum fills the rounded posterior half of the body. There is the usual diverticulum from the stomach that is characteristic of the genus. Both ovary and testis are present on each side of the body. The ovaries are short and sac-like, and the testes follicles are large and branched. Usually the kidney is anterior to the stomach as in *A. indicus*, however, in all except one of the specimens the gut turns to the right rather than the left, and the kidney appears to be more on the left side of the body (Monniot and Monniot 1984a, Fig 4D) than the right (i.e., to the left of the enlarged intestine).

REMARKS

The absence of ventral muscle bands and the short sac-like ovaries in this species and in *A. dichotomus* from the S.E. Atlantic (see below) distinguish them from *A. indicus*. *A. dichotomus* is distinguished from the present species by its two rather than one clump of male follicles on each side of the body.

***Asajirus dichotomus* (Monniot and Monniot, 1984)**

Hexacrobylus dichotomus Monniot and Monniot, 1984, p. 207; 1985a, p. 35.

DISTRIBUTION

Atlantic Ocean (S.E. Atlantic Cape Basin — 3550 m, Monniot, C. and F. 1984, 1985a).

DESCRIPTION (see Monniot and Monniot 1984a including Fig. 6A–D)

Three (one damaged) individuals from 1.0 to 1.2cm long are known. They are oval, with the usual six branchial arms, a short atrial siphon from the mid-dorsal part of the body, and a thin test with hair-like extensions to which foraminifers are attached. Neither ventral muscle bands nor stalk are present. The rectum is distended, but is not spherical as it is in *A. gulosus*. The ovary is a rather irregular or curved sac. There are two clumps of branched male follicles at the proximal end of each ovary. Each clump of male follicles has a long duct and these join to form a very short vas deferens which opens into the atrial cavity. As in the majority of the specimens of *A. gulosus* the gut appears to turn to the right rather than the left. The kidney, accordingly appears to be the left of the enlarged intestine.

REMARKS

The distinctions between *A. dichotomus* and *A. indicus* are discussed above (see *A. gulosus*). Both *A. gulosus* and the present species have a large swollen rectum. The paired clumps of male follicles constitute the principal character separating *A. dichotomus* from *A. gulosus*. The reversed gut loop reported in this species and in *A. gulosus* appears to be an intraspecific variation, at least in the former species.

***Oligotrema* Bourne, 1903.**

Type species: *Oligotrema psammites* Bourne, 1903.

The genus is characterised by the presence of branchial tentacles which are covered with unusual 'flagellated' epithelium (Bourne 1903). There is no sac-like diverticulum from the stomach, which is sometimes very large. The atrial aperture is always posterior, and posteriorly directed. Individuals are never stalked. Longitudinal muscles are confined to the anterior half of the body, and along the atrial siphon, and long ventral muscles (as in *Asajirus indicus*) are never present. Circular muscles are present along the length of the body, but sometimes are interrupted ventrally over the gut. They are particularly strong across the dorsal border. A limited number of openings from the relatively short pharynx lead into chambers which

open into the top of the right and left horns of the atrial cavity by varying numbers of deep circular ciliated stigmata. Occasionally stigmata open into pouches in the wall of the atrial cavity rather than directly into it (see Bourne 1903, Fig. 26, and *O. lyra*, below). The complexity of the pharyngeal wall appears to increase with the size of the specimens. The walls of the chambers between the pharynx and atrial cavity are very delicate and cannot be observed without staining and clearing. The statement that the 'thick lateral walls (of the pharynx) are honey-combed by a number of irregular, canals and chambers, which recall, more than anything else, the incurrent and excurrent canals of a sponge' (Bourne 1903, p. 255) is to some extent misleading in view of the delicacy of the tissues. In the two smaller species there are variations from the usual condition of the branchial wall — *O. unigonas* has stigmata opening directly from the pharynx to the atrial cavity; and in *O. sandersi* ciliated stigmata have not been detected.

Although he found the neural duct, Bourne apparently did not find the neural gland in *Oligotrema psammites*. He found a 'few small tubules closely applied to the nerve ganglion' containing cells with deeply staining nuclei (Bourne 1903, p. 264). In his specimen neither the ganglion nor the gland were well preserved, and Bourne, expecting the latter to be subneural (as it usually is in other than stolidobranch ascidians), may have overlooked it. None of the published figures in Bourne's work include sections across the neural complex, although there is one across the opening of the duct. In view of the agreement in other characters, it is probable that the arrangement of the neural complex in *O. psammites* would be the same as in *O. psammatodes* with the neural gland dorsal to the ganglion.

Bourne's sections (Bourne 1903, Pl. 20, Fig. 7, Pl. 22, Fig. 26) show stigmata and tentacles that are not incompatible with the circular stigmata and vertically flattened and crowded tentacles found in *Hexacrobylus psammatodes* Sluiter, 1905. Thus, despite his reconstructions of elongate stigmata and branched tentacles (Bourne 1903, Pl. 21 Fig. 16, Pl. 23 Fig. 34), it is probable that neither the stigmata nor branchial tentacles of *O. psammites* type specimen were essentially different from those of *H. psammatodes*. Both species have the characteristic posteriorly-positioned atrial aperture, similar gut, gonads, branchial arms, buccal cavity, and transverse body musculature. Although (on the basis of the shape of the stigmata) there is some doubt about the synonymy

of *O. psammites* with *H. psammatodes*, there is none concerning the synonymy of the genera.

The synonymy suggested by Kott (1969) is incorrect in that *Hexacrobylus indicus* Oka, 1913 is not a synonym of either *Oligotrema psammites* or *O. psammatodes*. Further, Oka's species is wrongly assigned to *Hexacrobylus* (see *Asajirus*, above).

Generally the species formerly assigned to *Sorbera* Monniot and Monniot, 1974 and *Gasterascidia* Monniot and Monniot, 1968 have all the characters of *Oligotrema*, and their differences do not appear to justify generic status. *Oligotrema psammites*, *Oligotrema psammatodes* (> *Hexacrobylus psammatodes*) and *O. lyra* (> *Gasterascidia lyra*) have identical large pinnate branchial arms and similar gonads with branched male follicles. *Oligotrema sandersi* (> *Gasterascidia sandersi*) and *O. unigonas* (> *Sorbera unigonas*) have characters that probably are associated with their small size — *O. sandersi* having simple branchial arms and an undivided testis, and *O. unigonas* irregularly branched arms and a single branched male follicle. Other characters (in addition to the variations in the pharyngeal wall referred to above) show a gradation throughout the known species: the pharynx is completely eversible in *O. sandersi*, partially eversible (as in *Asajirus*) in *O. lyra* and *O. unigonas*, is not known to be eversible in *O. psammatodes*; and the rectum is very large in *O. unigonas*, of moderate size in *O. psammatodes* and *O. sandersi* and vestigial in *O. lyra*. It is not unlikely that the swollen stomach in species formerly assigned to *Gasterascidia* is an apomorphic character as is the swollen gut in *Ascidia sydneyensis*. Thus both *Gasterascidia* and *Sorbera* are here regarded as junior synonyms of *Oligotrema*.

Monniot and Monniot (1974, 1975) suggest that the minute black sphere that is usually (but not always) present in the neural gland of species assigned to *Sorbera* Monniot and Monniot, 1974, viz. *S. digonus* (< *Oligotrema psammatodes*) and *S. unigonas* (< *Oligotrema unigonas*) may be an otolith, as it resembles the larval otolith present in most larvae of the Ascidiacea. However, unless the embryology of these species is different from that known in other ascidians, this cannot be the larval otolith persisting in the adult organism. In those species in which the development of the nervous system has been studied, the cerebral vesicle (the right half of the divided anterior end of the embryonic neural tube) and the posterior end of the embryonic neural tube both degenerate on metamorphosis. The elements of the adult neural

complex (including the neural gland) develop from the persisting left half of the anterior end of the embryonic neural tube (see Berrill 1950). Thus, the neural gland is normally an exclusively adult organ, and the black sphere usually present in some species of *Oligotrema* is probably secondarily acquired. Unfortunately this question cannot be resolved until histological and embryological evidence is available.

Five species of the genus *Oligotrema* are known, of which one, *Oligotrema psammites* Bourne, 1903 is very possibly a synonym of *Oligotrema psammatodes* (Sluiter, 1905). All the species appear to be fairly closely related.

Oligotrema lyra (Monniot and Monniot, 1973) is known from numerous specimens, taken from about 2000 to 5000 m in the north-eastern to north-central Atlantic, the tropical eastern and south-eastern Atlantic, the tropical West Indian Ocean, and the eastern Pacific Antarctic Basin. This species has a wide depth range and appears to have almost as wide a geographic range as *Asajirus indicus* — although it has not yet been recorded from the tropical and northern Pacific Ocean.

Oligotrema psammatodes (Sluiter, 1905) is known from about 1000 to 4000 m in the western Pacific Ocean (off the NSW coast), possibly from Indonesian waters (*O. psammites*), from the tropical West Indian Ocean and the southeastern Atlantic. So far it is recorded only from the southern hemisphere. It is sympatric with *O. lyra* in the West Indian Ocean and the south-eastern Atlantic.

Oligotrema sandersi (Monniot and Monniot, 1968) is known from about 2000 to 5000 m from the north-western, north-central, tropical central, and the south-eastern Atlantic. Its depth range is wide and very numerous specimens have been taken in the north-western Atlantic Basin. So far it has not been recorded outside the Atlantic Ocean.

Oligotrema unigonas (Monniot and Monniot, 1974) is a small species known from about 3000 to 5000 m in the north-central to north-eastern Atlantic, the tropical-eastern and south-eastern Atlantic and the tropical to southern West Indian Ocean. Like *Oligotrema lyra* it is not recorded at all from Pacific Ocean Basins.

***Oligotrema lyra* (Monniot and Monniot, 1973)**

Gasterascidia lyra Monniot and Monniot, 1973, p. 457; 1974, p. 777. 1984a, p. 209. 1985a, p. 35.

DISTRIBUTION

NEW RECORDS: Pacific Ocean (E. Pacific Antarctic Basin 56°05'S, 71°07'W — 2028 m, USNM 18252 3 specs*; 70°06'S, 119°44'E — 3553–3575 m, USNM 18251 1 spec*).

PREVIOUSLY RECORDED: Atlantic Ocean (N.E., N. central Atlantic — 3360–4690 m, Monniot, C. and F. 1973; 4196–4700 m, Monniot, C. and F. 1974; 4217–4829 m, Monniot, C. and F. 1985a. S.E. Atlantic — 4180 m, Monniot, C. and F. 1974; 4600 m, Monniot, C. and F. 1984a; 3550–5260 m, Monniot, C. and F. 1985a. Tropical E. Atlantic — 4019 m, Monniot, C. and F. 1974). Indian Ocean (Tropical W. Indian Ocean — 2300–3716 m, Monniot, C. and F. 1984a).

Previously recorded from the eastern Atlantic and the tropical Indian Ocean, the new records are the first from the Pacific Ocean.

DESCRIPTION (Figs 2a–c)

The newly recorded specimen from the Southern Ocean is the largest known in this family. It is 6 cm long, but mature gonads are present from 4 mm (see Monniot and Monniot 1973). In contracted individuals one third of the length is taken up by the anterior buccal cavity and branchial arms. This anterior third of the body is separated from the remainder by a slight constriction over which the thin test has circular folds. This is the area that becomes long and narrow when the animal is extended, anteriorly expanding out into the branchial crown formed by the 6 branched arms. The branchial arms are relatively even in length, with up to 14 pinnate branches along each side that fold in over the inner surface. The posterior end of the sac-like body narrows to the pointed atrial aperture. The test is thin and translucent, especially on the pinnate branches of the branchial arms. On the posterior sac-like portion of the body there are very thin hair-like processes to which particles are attached. The test lining the buccal cavity has numerous upright oval tubercles (up to 1.5 mm long) constricted at their base. Small tubercles are also present on the inside of the branchial arms. The buccal cavity is partially eversible (see Monniot and Monniot 1973).

Circular muscles form a strong band around the outside of the buccal cavity. There are also circular muscle bands over the remainder of the body. These are interrupted over the ventrum and sides of the body but they are conspicuous along the dorsal mid-line. Strong internal longitudinal bands branch off the circular muscles of the buccal cavity and extend anteriorly to the buccal arms. A set of internal longitudinal bands originating from around the branchial aperture extend on each side to the posterior end of the short oesophagus. There are also longitudinal as well as circular muscles on

the atrial siphon. The muscles of the buccal cavity appear to be independent of those on the pharynx and oesophagus and they probably effect the eversion of the buccal cavity and the movement of the arms.

At the base of the buccal cavity there is a variable number of antero-posteriorly flattened tentacles. These vary from long strap-like to short triangular shapes, only sometimes with an

irregular slightly forked tip. The longer tentacles are in the ventral mid-line. In the large (6 cm) newly recorded specimen there are about 16 tentacles, but Monniot and Monniot (1973) found only 4 in their small (up to 4 mm long) specimens. There is a narrow pre-branchial region between the tentacles and a peripharyngeal groove that encircles the pharynx, meeting in a V behind the dorsal tubercle in the mid-dorsal line. Longitudi-

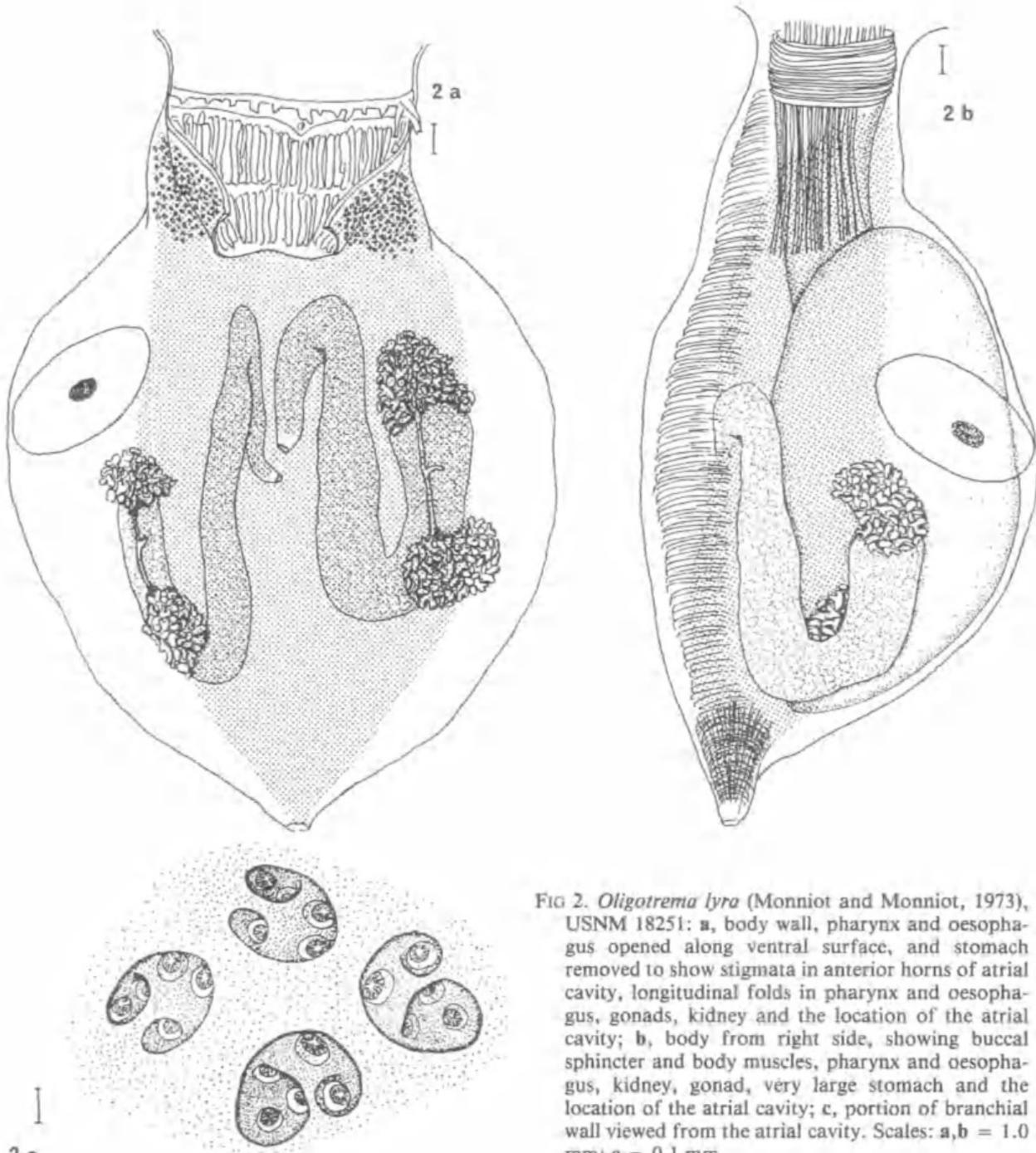


FIG 2. *Oligotrema lyra* (Monniot and Monniot, 1973), USNM 18251: **a**, body wall, pharynx and oesophagus opened along ventral surface, and stomach removed to show stigmata in anterior horns of atrial cavity, longitudinal folds in pharynx and oesophagus, gonads, kidney and the location of the atrial cavity; **b**, body from right side, showing buccal sphincter and body muscles, pharynx and oesophagus, kidney, gonad, very large stomach and the location of the atrial cavity; **c**, portion of branchial wall viewed from the atrial cavity. Scales: **a, b** = 1.0 mm; **c** = 0.1 mm.

nal folds in the pharynx are interrupted in the mid-dorsal line. There is also a shallow groove along the mid-ventral line but there is no endostyle.

The walls of the pharynx are raised into longitudinal folds. Between these folds there are patches of pharyngeal wall where, between the meshes of a complex three-dimensional network of curving vessels, there are interconnected canals and chambers that open by circular ciliated stigmata into pouches in the anterior horns of the atrial cavities on each side of the body. There are about 80 to 100 stigmata on each side. The branchial epithelium tends to lift off in the way Bourne (1903) described for *O. psammites*. Monniot et al. (1975) did not observe cilia lining the stigmata although the atrial and pharyngeal pouches are described (Monniot *et al.* 1975, Pl 5, fig 2).

The pharynx and oesophagus are more or less continuous, and of even diameter. The stomach is very large, occupying most of the body. The kidney lies about half way down the body, across the ventral half of its right side between the stomach and the body wall. In the newly recorded specimen there is a ventral groove in the stomach that terminates in a small pit about one-third of the way up. This pit may be the homologue of the distal opening of the stomach into the rectum. Neither an opening from the stomach, nor a rectum were found in the newly recorded specimen (USNM 18251). Monniot and Monniot (1973) found a very narrow, straight and probably vestigial structure referred to as a rectum, extending dorsally, at first anterior to and then crossing the inside of the right ovary.

The atrial cavity extends from the postero-dorsal aperture around the dorsal half of the stomach (separating it from the gonads which lie in the parietal body wall). Anteriorly it embraces the pharynx and its two anterior horns that receive the openings of the stigmata reach almost to the level of the branchial aperture.

The gonads, one on each side of the body, consist of a long S-shaped ovarian tube which extends postero-dorsally for the middle one third of the length of the body, turns antero-dorsally for an equal distance and then postero-dorsally again before opening into the atrial cavity about halfway down the body near the dorsal mid-line. There are two groups of male follicles. In the newly recorded specimen (USNM 19251), one is at the proximal end of the ovary, and the other at the distal end of the proximal limb. The long ducts from each clump of follicles meet along the mesial surface of the proximal limb of the ovary where they join into a vas deferens of variable length

opening into the atrial cavity. In their small specimens (up to 4 mm) Monniot and Monniot (1973 Fig 32, 33) show the two male glands closer together at each side of the proximal end of the ovary. They have shorter vasa efferentia but a longer vas deferens than in the present large specimen.

The three newly recorded specimens from the eastern Pacific Antarctic Basin (USNM 18252) contain only the two sets of male gonads on each side of the body. The other organs appear to have been resorbed and are replaced by a jelly-like matrix in which the testes are embedded.

In all specimens so far recorded the male openings into the atrial cavity are far removed from the female opening.

REMARKS

The species is distinguished from *Oligotrema sandersi* by its branched rather than simple branchial arms, two rather than one clump of male follicles, longer ovarian tubes bent into S-shapes, more numerous stigmata, and partially rather than completely eversible pharynx. *Oligotrema psammatodes* also has only a single clump of male follicles per side, more numerous tentacles, a longer oesophagus and a smaller stomach than the present species, although it has similar branchial arms. The position of the vestigial rectum of *O. lyra* recorded by Monniot and Monniot (1973) is the same as that of the intestine in *O. psammatodes* with the testis projecting between the stomach and the intestine. However in the newly recorded specimen of *O. psammatodes* the rectum contains faeces, while in the present species it is almost certainly not functional.

The very large stomach and thin vestigial rectum — if one is present at all — are conspicuous features in this species. It is possible that in living specimens the huge stomach is open to the exterior through the wide oesophagus, pharynx and buccal cavity, and that wastes are expelled through the mouth, propelled by the strong muscles across the dorsal surface of the body.

The less numerous branchial tentacles and longer vas deferens of Monniot and Monniot's (1973) small specimens from the north eastern Atlantic may be associated with their size and age, or they may represent intraspecific variations in populations of this widely distributed species.

The 63 unidentified small (0.5–0.7 mm) specimens, *Gasterascidia* sp. Monniot and Monniot, 1976 from the S.W. Atlantic (Argentine Basin), with partly everted buccal cavity and large stomachs almost completely occupying the body,

are possibly this species as Monniot and Monniot (1970) suggest.

Oligotrema psammatodes (Sluiter, 1905)

Hexacrobylus psammatodes Sluiter, 1905, p. 135.
Sorbera digonas Monniot and Monniot, 1984a, p. 209.
 'Hexacrobylidae' juv. intermediate between *Sorbera* and
Gasterascidia Monniot and Monniot, 1984a, p. 212.
 ? *Oligotrema psammites* Bourne, 1903, p. 233.

DISTRIBUTION

NEW RECORD: Pacific Ocean off the NSW coast, 34°27'S, 51°27'E — 1200 m, AM Y2127-8 2 specs*).

PREVIOUSLY RECORDED: Pacific Ocean (? New Britain — 92 m, Bourne 1903; Lauí Banda — 1158 m, ZMA TU564* Sluiter 1905). Indian Ocean (tropical W. Indian Ocean — 3700-3716 m, Monniot, C. and F. 1984a). Atlantic Ocean (Cape Basin — 4,600 m, Monniot C. and F. 1984a).

DESCRIPTION (Fig. 3a-e)

There are 2 newly recorded specimens, both about 2 cm long. The three previously recorded specimens (Monniot and Monniot 1984a) are from 12 mm to 17 mm long, and the type specimen (Sluiter 1905) is the largest known with a length of 3.2 cm. Specimens have the typical appearance of Hexacrobylidae with 6 large branchial arms (with pinnate branches) around the rim of the buccal cavity. The atrial siphon is from the dorsal aspect of the posterior end of the sac-like body. The buccal cavity does not appear to be eversible.

In the two newly recorded specimens and in the type there is a crowded ring of vertically flattened, sessile scale-like projections just inside the mouth opening (at the base of the buccal cavity). They are convex on their outer border and have a finger-like tentacle from the upper border which alternates with similar finger-like tentacles that arise directly from the wall of the lumen of the pharynx. These structures are similar to those described for the hexacrobylid juv. that Monniot and Monniot (1984a) regarded as halfway between *Sorbera* and *Gasterascidia*. They also resemble some of the tentacles that are shown on the tentacular ring of the figured specimen of *Sorbera digonas* (Monniot and Monniot 1984a Fig. 8e).

There is a shallow prebranchial region, and a peripharyngeal groove forming a deep V behind the small dorsal tubercle, on which the short duct of the neural gland opens in a transverse slit. There is an oesophageal groove in the dorsal mid-line. There is a fine very shallow groove in the ventral mid-line but no endostyle. The neural gland is

dorsal and to the right of the neural ganglion. There is a minute black sphere in the dorsal gland of one of the two newly recorded specimens but not in the other. A similar black spot is present in the type specimens of *Sorbera digonas* Monniot and Monniot, 1984a and in the unidentified juvenile from the Cape Basin (Monniot and Monniot 1984a).

The pharynx is short, and its lining is longitudinally folded. Between the folds there are a number of swirling openings leading into the interconnected chambers that open by numerous circular ciliated stigmata directly into the two anterior horns of the atrial cavity around the sides of the oesophagus. Superficially the branchial wall of the newly recorded specimens resembles that figured by Monniot and Monniot for the hexacrobylid they believed to be intermediate between *Gasterascidia* and *Sorbera* (see Monniot and Monniot 1984a Fig. 9c). However, stained and cleared whole mounts of pharyngeal wall show it to have, as in *Oligotrema lyra*, swirling vessels encircling the spaces through which the stigmata are connected to the lumen of the pharynx rather than the branching tubes that Monniot and Monniot (1984a Fig. 9) have figured. The only difference from *O. lyra* is the absence of pouches in the atrial wall of the newly recorded specimens of the present species. The number of stigmata in the present species is variable. Specimens from the Indian Ocean up to 1.7 cm long have up to 20 stigmata on one side and 14 on the other. The largest of the new Australian specimens have about 60, and in the large type specimen (ZMA TU564) they are more numerous.

The oesophagus is long, constricted from the branchial sac, and enters the posterior dorsal half of the stomach about two-thirds of the way down the body. The stomach then curves anteriorly and to the right, its ventral and right wall being deeply convex externally. The long intestine leaves the stomach at the anterior end, extends around the left ventro-posterior curve of the body, gradually expanding into a rather swollen rectum opening near the base of the atrial siphon. In the newly recorded specimens the rectum contains faeces.

The large oval kidney is on the right side of the body in front of the stomach.

A male and a female gonad are present on each side. The male follicle is at the proximal end of the ovary. It consists of long finger like branches converging to a short vas deferens that opens into the atrial cavity — in the vicinity of the pole of the gut loop on the left, and near the posterior end of the kidney and the anterior border of the stomach on

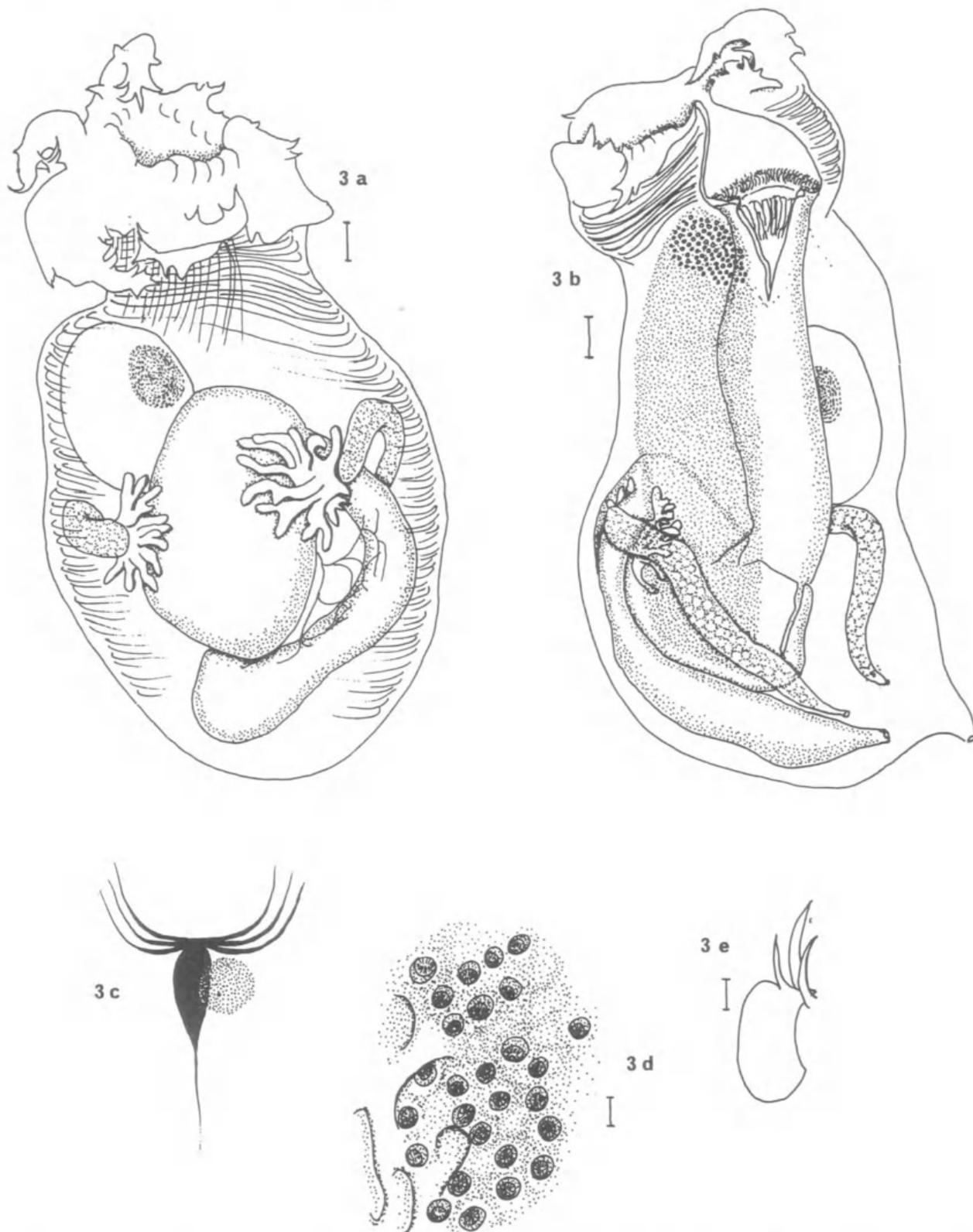


FIG 3. *Oligotrema psammotodes* Sluiter, 1905 (AM Y2127): **a**, individual from the ventral surface; **b**, individual from the left side, with pharynx and anterior part of oesophagus opened, the shaded area representing the ventral ligament that divides the left from the right branches of the atrial cavity; **c**, neural gland and ganglion from dorsal surface; **d**, portion of branchial sac showing openings from pharynx, and stigmata seen through the pharyngeal wall; **e**, branchial tentacle. Scales: **a,b** = 1.0 mm; **d,e** = 0.1 mm.

the right. On the left the branches of the male gland lie on the antero-mesial part of the stomach wall, spreading around between the intestine and the stomach. On the right they spread out over the postero-dorsal part of the stomach and onto the kidney. The right ovarian tube curves antero-dorsally from the middle of the right side of the body, and then posteriorly to the base of the atrial siphon. The left ovarian tube curves around the body parallel and slightly anterior to the intestine and rectum.

The atrial cavity is large, embracing the dorsal surface and sides of the oesophagus, the mesial wall of the stomach on the left and separating the stomach and oesophagus from the kidney on the right. The ventral halves of the right and left horns of the atrial cavities are separated by a long ligament attaching the oesophagus to the ventral body wall.

On each side there is a long endocarp-like thickening of the parietal body wall, one projecting into the atrial cavity along each side of the oesophagus, sometimes with parts of the gonad embedded in them.

REMARKS

The species is characterised by its deep peritubercular V, large atrial cavity, single clump of branched testes follicles that project through the gut loop on the left, numerous stigmata opening into the anterior horns of the atrial cavity, long oesophagus, and the absence of atrial branchial pouches. The number of stigmata and the condition of the branchial tentacles appear to be variable.

The pinnate branchial arms, and transverse muscles across the dorsal surface of the body resemble those of *Oligotrema lyra*.

The single specimen of *Oligotrema psammites* was 17 mm long, falling within the recorded range for this species. Bourne's specimen had numerous branchial tentacles which in the sections figured are consistent with those of the present species. The restraints to considering the species to be a synonym of the present one lie principally in the shape of the stigmata which Bourne (1903) believed to be elongate rather than circular. However, as discussed above (see *Oligotrema*) there is some room for doubt as to their shape and it is not impossible that *O. psammites* is the senior synonym of this species, all other characters being in agreement. Bourne's specimen had endocarp-like thickenings of the body wall as in the newly recorded specimens described above.

The newly recorded specimens agree in every respect with the type specimen (ZMA TU564) — which is in excellent condition.

There is some difficulty in reconciling the account of the branchial sac of the type specimen of *S. digonas* (see Monniot and Monniot 1984a Fig. 8d) with the newly recorded specimens. In the latter specimens and in the type the stigmata open into the extremely concave anterior horns of the atrial cavity, not directly through the walls of branchial pouches as the Monniots' figure implies. It is possible that the pharyngeal pouches figured by the latter authors have evaginated into the atrial cavity obscuring their structure and causing them to appear as sacs (protruding into the atrium?)

Oligotrema sandersi (Monniot and Monniot, 1968)

Gasterascidia sandersi Monniot and Monniot, 1968, p. 36; 1970, p. 334; 1974, p. 777; 1985a, p. 35.
? *Gasterascidia sandersi*; Millar, 1970, p. 148.

DISTRIBUTION

Atlantic Ocean (N.W. and N. central Atlantic — 2200–5020 m, Monniot, C. and F. 1968, 1970, 1974, 1985a; Monniot 1971. Tropical central Atlantic — 1493–3783 m, Monniot 1971. ? S.E. Atlantic — 4618 m, Millar 1970).

DESCRIPTION (after Monniot and Monniot 1968, 1973 Fig. 33B, 1975)

Individuals larger than 3.0 mm have not been taken. The long, cylindrical branchial siphon is about half of that length. The short cylindrical atrial siphon is at the posterior end of the body. The branchial arms around the edge of the buccal cavity are simple pointed and pointed tubercles are present in the siphon lining behind the branchial arms. At the base of the buccal cavity there are four very small tentacles. The neural gland is to the right of the ganglion. The opening of the neural duct is on a small tubercle in the mid-dorsal line behind the ring of tentacles. The pharynx is represented by a narrow band around the proximal end of the gut with its wall thrown up into vertical folds which continue into the short oesophagus. Two non-ciliated openings on each side of the pharynx lead, by short tubules, into the anterior horns of the atrial cavity.

The large stomach occupies most of the body, leaving a small space anterior to it where the kidney is placed horizontally across the ventral surface. The oesophagus opens into the stomach about halfway down its dorsal surface. The rectum is a thick, cylindrical tube which extends posteriorly from the right side of the stomach to the atrial cavity.

There is a male and female gonad on each side of the body. Each female gonad is a short ovarian tube extending dorsally around the posterior end of the stomach, separated from it by the atrial cavity on each side. The male gonad consists of a single unbranched male follicle with a fairly short duct that opens into the atrial cavity about halfway along the ovary. Individuals appear to mature rapidly, reaching sexual maturity at 1.5 mm long.

REMARKS

The species resembles *O. unigonas* in its simplified branchial arms, few stigmata and small body. However in *O. unigonas* the stomach occupies only half of the body and the oesophagus the other half. In the present species the oesophagus is relatively short and the stomach occupies most of the body. The undivided male follicles in the present species are unique, as are the unbranched pointed branchial arms and pointed tubercles in the extrudible siphon lining.

The course of the branchial tubules through the thickness of the pharyngeal wall has not been described, nor have ciliated stigmata been detected in this species. Despite this, Monniot *et al.* (1975) regard the branchial apparatus as similar to that of *Oligotrema lyra*, differing only in the reduced number of tubules in the present species.

Oligotrema unigonas (Monniot and Monniot, 1974)

Sorbera unigonus Monniot and Monniot, 1974, p. 777.
Monniot and Monniot, 1984a, p. 209; 1985a, p. 35;
1985b, p. 307.

DISTRIBUTION

Atlantic (N. central to E. Atlantic — 4100–4452 m, Monniot, C. and F. 1974; 3338–4465 m, Monniot C. and F. 1985a. Tropical E. Atlantic — 3138–4019 m, Monniot, C. and F. 1974. S.E. Atlantic — 4600 m, Monniot C. and F. 1984a, 1985a). Indian Ocean (Tropical to S.W. Indian Ocean — 2608–5043 m, Monniot, C. and F. 1984a).

DESCRIPTION (after Monniot and Monniot 1974 including Fig. 23A,B; Monniot *et al.* 1975)

Individuals are known up to 9 mm in length, narrowing to the small atrial aperture at the postero-dorsal end of the body. The cylindrical branchial siphon is at the anterior end of the body with 6 large papillated branchial lobes around its rim. These are not pinnate as they are in other species of the Hexacroblyidae. The test is covered with fine hair-like extensions to which foramini-

fers are attached. The buccal cavity is partially eversible.

The body wall is delicate and transparent. It has yellowish-green granules embedded in its outer layer (as described for *O. psammites* Bourne, 1903). The longitudinal muscles radiate from the branchial siphon to the vicinity of the stomach, and transverse muscles are present over the length of the body.

The neural gland is dorsal and to the right of the ganglion. A small black particle, referred to by Monniot and Monniot (1974) and Monniot *et al.* (1975) as an otolith, is present in the neural gland. There are only 4 to 8 minute branchial tentacles reported. Behind these, the prepharyngeal band forms a deep, narrow V behind the small dorsal tubercle, and in the mid-ventral line it forms a short ciliated groove that may be the homologue of the endostyle.

The pharynx of this species is clearly seen through the body wall. It is cone-shaped. Anteriorly it has longitudinal folds (possibly the result of contraction: Monniot *et al.* 1975) Posteriorly (the base of the cone) the wall of the pharynx is slightly convex, pierced by the oval oesophagus in its mid-dorsal radius, and by 3 to 8 irregular ciliated stigmata per side. The stigmata open into the anterior horns of the atrial cavity which extends anteriorly around each side of the oesophagus to terminate just behind the posterior wall of the pharynx. The stigmata are said to open directly into the cloacal cavity.

There is a relatively narrow oesophagus opening into a large almost spherical stomach (in the postero-ventral part of the body) about halfway along its dorsal border. The short cylindrical rectum curves either to the left or the right and posteriorly from the anterior part of the stomach. The kidney is on the right side of the body anterior to the stomach.

A tubular ovary is present only on the right side of the body, curving dorsally and posteriorly to open into the atrial cavity near the atrial aperture. A single large branched male follicle is also present on the right side of the body spreading over the stomach wall at the proximal end of the ovarian tube. There is a smaller male follicle on the left between the stomach and the rectum. There is no ovarian tube on the left.

REMARKS

The species is distinguished from others by the absence of regular pinnate branches on the branchial arms, the limited number of ciliated stigmata in the posterior rather than anterior part

of the pharynx, and the unpaired ovary on the right side of the body. Although the oesophagus is longer than in *Oligotrema lyra* and *O. sandersi*, the stomach is also relatively large — a character which helps to distinguish the species from *O. psammotodes*. The pharyngeal pouches that are present in *O. psammotodes* and *O. lyra* have not been observed in the present species, in which the pharyngeal perforations are said to open directly into the atrial cavity.

ACKNOWLEDGEMENTS

I thank Dr Robin Millar of the Dunstaffnage Marine Research Laboratory, Oban, whose contribution of ideas and observations on these organisms have significantly advanced my own understanding of them. I am also grateful to Dr A. Pierrot Bults of the Zoological Museum, University of Amsterdam, for the loan of the type specimen of *Hexacrobylus psammotodes* Sluiter, 1905; and to Linda Cole of the US National Museum for the loan of *Oligotrema psammites*: Kott 1969.

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