Short Communications

A description of gametogenesis in the panga *Pterogymnus laniarius* (Pisces: Sparidae) with comments on changes in maturity patterns over the past two decades

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A description of gametogenesis in the panga *Pterogymnus laniarius*, a common endemic seabream species inhabiting the Agulhas Bank, South Africa, is presented. After sexual maturity, oogenesis and spermatogenesis continued throughout the year and were found to be similar to these processes in other seabream species and teleosts in general. Analysis of maturity data over the past two decades revealed a significant change in both age and size-at-maturity, a response to fishing pressure.

The panga *Pterogymnus laniarius* (Pisces: Sparidae) is an endemic seabream species inhabiting the Agulhas Bank, South Africa (Smith & Heemstra 1986). It is presently considered the most abundant commercial sparid species inhabiting the Agulhas Bank, where it forms an important bycatch component of the inshore and offshore trawlfisheries (Japp, Sims & Smale 1994) and as a targeted species in both the recreational and commercial offshore linefisheries (Smale & Buxton 1985; Hecht & Tilney 1989). Booth & Buxton (in press a), in an overview of the biology of this species, showed it to be a slow-growing, long-lived species with a late gonochoristic reproductive style (= rudimentary hermaphrodite, see Buxton & Garratt 1990) with all individuals passing through an immature, intersexual stage before sexually differentiating into either sex and later maturing and functioning as either male or female.

A complete description of gametogenesis in the panga is lacking as few comprehensive studies have been conducted in the past. One previous study conducted by Budnichenko & Dimitrova (1970) was superficial with material collected over a short period of time, whilst Hecht (1976) documented panga gametogenesis in his unpublished doctoral thesis. With a full description of gametogenesis, together with a validation of past macroscopical staging, past and future quantitative and qualitative studies concerning the reproductive biology of this species can be compared. In this communication, descriptions of oogenesis and spermatogenesis are given, together with preliminary evidence for changes in maturity patterns in relation to both age and length over the past two decades.

Data were collected during two time periods off the Eastern Cape coast from Plettenberg Bay to Port Alfred, between April 1974 to May 1975 and February 1994 to July 1995 using research and commercial demersal trawling gears. Each fish sampled was sexed using visual criteria (Table 1) and gonadal tissue was collected monthly during both sampling periods from a subsample of fish for histological examination of gametogenesis. Tissues were fixed in Bouin's solution for one week before being stored in 50% propanol. Tissues were later embedded in paraffin wax, sectioned to 3–7 μm and stained using Gill's haemotoxylin and Papanicoloau's eosin A.

Sexually mature female fish were noted if their ovaries contained vitellogenic oocytes which were characterised by the acidophilic nature of the stained material. Macroscopically the ovaries were swollen and orange-yellow in colour, often with clear hydrated oocytes visible under the tunica (Table 1). Male sexual maturity was not determined in this study as immature testes were often difficult to detect and on many occasions maturing testes were associated with functional ovaries, maturing directly after sexual differentiation from the juvenile intersexual gonad.

Length-at-maturity and age-at-maturity were determined only for female fish and estimated by fitting a logistic ogive

Table 1 Macroscopic appearance and equivalent histological characteristics of *Pterogymnus laniarius* gonads at various stages during gonadal recrudescence. After Booth & Buxton (in press a)

Stage	Macroscopic appearance	Histological appearance
1. Virgin and resting	Ovary long and thin, pink in colour with no visible eggs. Testis barely visible on the posterior edge of the ovitestis as a thin, clear ridge.	Oogonia and perinuclear oocytes in the ovary. Spermatogonia predominate in the testis.
2. Developing	Ovary increases in size, filling half or more of the visceral cavity, becoming a darker orange with grainy appearance due to visible eggs. Testis a small, white ridge on the posterior end of ovitestis.	Characterised by oocyte stages up to the cortical alveoli stage. Testis shows all stages of spermatogenesis with undeveloped seminiferous tubules and sperm ducts.
3. Active (mature)	Ovary swollen with orange-yellow and translucent eggs visible in the tissue and lumen. Testis triangular in cross-section and greyish-white in colour. Ovarian remnants visible on the testis as atrophied brown strips.	All stages of vitellogenesis present including final egg maturation. Testis shows all stages of spermatogenesis and the seminiferous tubules and sperm ducts are well developed and full of sperm.
4. Post-spawning (mature)	Ovary slightly flaccid with few translucent eggs visible. Brown spots are noticeable over most of the gonad. Testis becomes dirty-grey in colour and decreases in slightly in size.	All oocyte stages present in the ovary together with atretic follicles. Testis with all stages of spermatogenesis. Less sperm is visible in the sperm duct.

to the proportion of reproductively active fish (active and post-spawning, see Table 1) in total length centimetre size classes. For the purposes of this paper length-at-maturity will be defined as that size class at which half the fish are sexually mature. To ascertain whether any changes were due to a change in growth rate rather than a direct shift in length or age, both length-at-maturity and age-at-maturity were estimated using a logistic ogive based on age estimates from Sato (1977) and Booth & Buxton (in press a) for the two sample periods respectively. The two-parameter logistic ogive used is described by the equation

$$P(l) = \frac{1}{1 + \exp^{-(l - l_{50})/\delta}}$$

where $P(l)$ is the percentage of mature fish at length (or age) l, l_{50} the length-(or age)-at-maturity and δ the width of the ogive. Differences between the slopes and intercepts of both pairs of size and age-at-maturity ogives were determined using analysis of covariance. A linear regression model was used to approximate the linear mid-portion of the maturity ogive with the best fits ($r^2 > 0.9$) obtained by excluding the first and last data points.

Oogenesis

The classification of oocyte development was based on criteria used by Wallace & Selman (1981), Coetzee (1983) and Buxton (1990). Despite differences in the number of egg stages quoted by the various authors, two principal phases described by Buxton (1990) were identified, pre-vitellogenesis resulting from oogonia to the end of the perinuclear stage and vitellogenesis from the primary vesicle oocyte stage to final egg maturation.

Oogonia were most frequently observed at the periphery of the ovigerous lamellae embedded in the germinal epithelium. They are characterised by their small size, large nucleus to cytoplasm ratio and lightly basophilic cytoplasm. With the initiation of the first meiotic division and further growth, perinuclear oocytes appear (Figure 1a). They are strongly basophilic, have numerous nucleoli and a well defined thecal covering. Pre-perinuclear oocytes are polygonal in shape with an intensely basophilic cytoplasm and are found closest to the germinal epithelium, with the nucleus containing one or two large nucleoli and a number of smaller nucleoli. Early and late-perinuclear oocytes are larger, more ovoid in shape and are less basophilic with a proliferation of nucleoli in the nucleus. The formation of the zona granulosa occurred in late peri-nuclear oocytes. The formation of the zona radiata, a non-cellular membrane formed between the follicular layer (zona granulosa and theca) and the developing oocyte, marked the end of the primary growth phase and was followed by the appearance of primary yolk vesicles (cortical alveoli) in the cytoplasm (Figure 1b).

Vitellogenesis was initiated by the appearance of acidophilic 'secondary' yolk globules arising in the region of the cortical alveoli. Later this extravesicular yolk developed throughout the cytoplasm. Yolk accumulation continued until it obscured the cortical alveoli, entirely filling the cytoplasm in the tertiary yolk vesicle stage. During vitellogenesis the nucleus was well-defined with prominent lampbrush chromosomes, chromatin granules and peripheral nucleoli. The cortical alveoli surrounding the nucleus became enlarged, the zona radiata and zona granulosa increased in thickness and the zona radiata became striated. Towards the end of development, the nuclear membrane degenerated, yolk coalesced and a lipid drop formed displacing the nucleus to the oocyte periphery. Histological examination of mature eggs was unsatisfactory with oocytes collapsing during tissue dehydration (Figure 1c). With the ovulation of mature eggs, post-ovulatory follicles remained and these were only visible microscopically in mature ovaries, providing direct evidence for spawning (Figure 1c). Atresia associated with the termination of gonadal recrudescence was rare and most commonly occurred during ovarian regression associated with sexual differentiation (Figure 1d).

Spermatogenesis

The testes are paired structures, triangular in cross section, surrounded by a tunica albuginea of connective tissue and collagen fibres. They contain a number of seminiferous tubules leading into secondary sperm ducts which join posteriorly to form a main sperm duct. Spermatogenesis occurs within the seminiferous tubules and is initiated by the mitotic division of the lining spermatogonia which are characterised by their large size, prominent cytoplasm and lightly basophilic nuclear chromatin (Figure 1e). These later gave rise to primary spermatocytes with smaller nuclei. The first meiotic division produced secondary spermatocytes displacing the more advanced spermatocyte stages towards the lumen of the tubule. With the rupturing of the secondary spermatocyte cysts, spermatids were released into the tubule lumen to mature into spermatozoa. Spermatoza, characterised by their small size and intensely basophilic heads, accumulated in the tubules and moved towards and accumulated in the sperm ducts (Figure 1f). Spermatogenesis observed in the panga was similar to that observed in other teleosts (de Vlamming 1972; Coetzee 1983; Matsuura, Matsuura, Ouchi & Hidaka 1987; Buxton 1990).

Changes in maturity

Accurate determination of maturity patterns depends entirely on the method used. In many studies, estimations of maturity are restricted to macroscopical examination (West 1990) without any further histological investigation for validation. Microscopical examination is necessary if accurate results are to be obtained, particularly if these data are to be used for management purposes (Booth & Buxton, in press b; Booth & Punt, unpublished data). With the histological basis of the present study, data that was collected over the two sampling periods could be accurately compared thereby further reducing any associated error.

Maturation was initiated in the panga at 18 cm (1994/95) and 24 cm (1974/75) total length (TL) and proceeded rapidly with female fish attaining length-at-maturity at 23 cm (1994/95) and 29 cm (1974/75) TL and total maturity at 28 cm (1994/95) and 32 cm (1974/75) TL (Figure 2a; Table 2). A similar pattern was evident when maturity was observed as a function of age, with fish reaching maturity at 4.3 and 5.2 years for 1994/95 and 1974/75, respectively (Figure 2b). Although length-at-maturity ($F = 61.01$; 1,14 df; p-value <

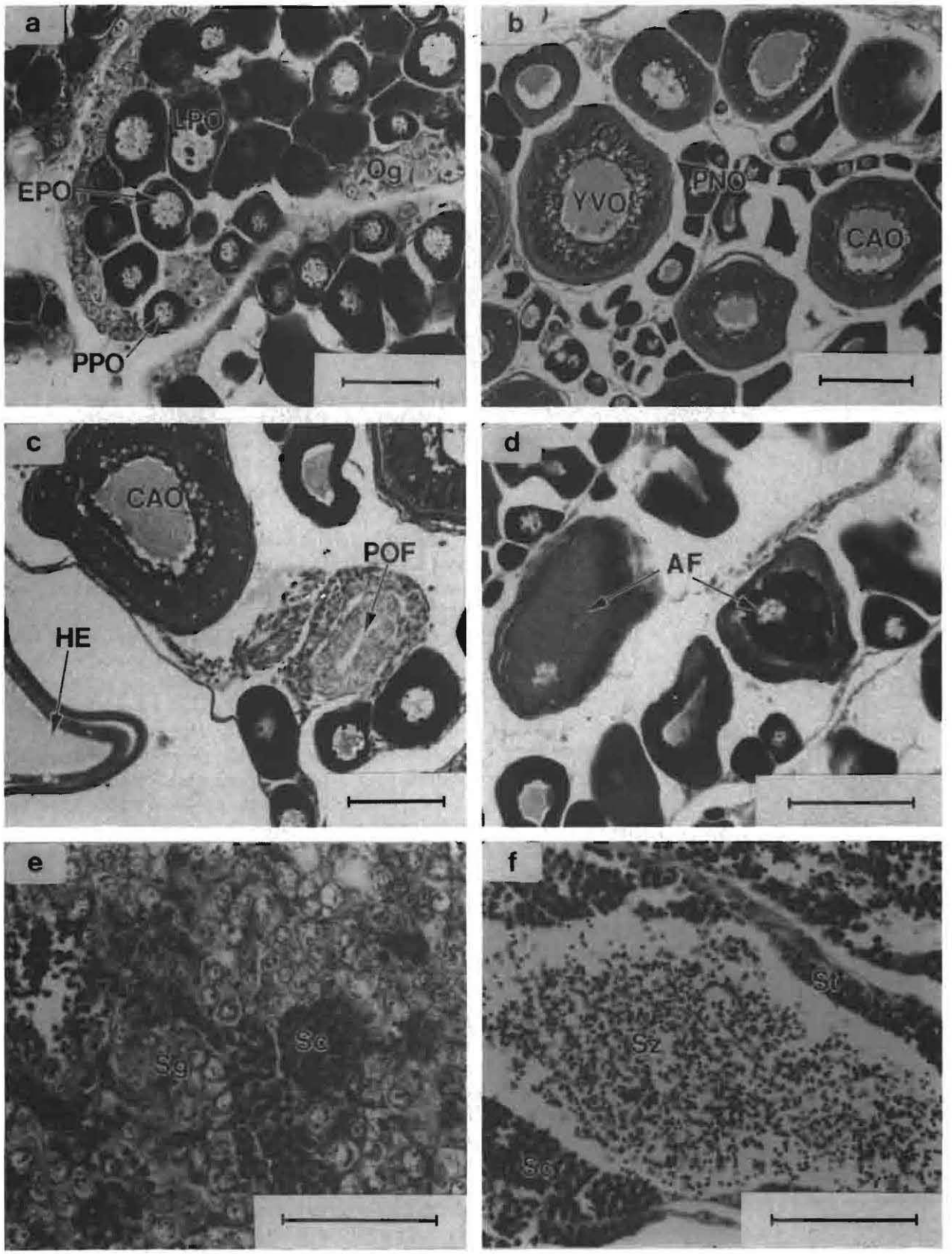

Figure 1 Transverse sections through gonads of *Pterogymnus laniarius* illustrating gametogenesis. (a) Immature ovary containing oogonia (Og), pre (PPO), early (EPO) and late perinuclear oocytes (LPO). (b) The onset of maturation begins with the appearance of primary vesicle oocytes (CAO) with cortical alveoli forming in the periphery of the cytoplasm. Perinuclear oocytes (PNO) and a yolk vesicle oocyte (YVO) are also visible. Secondary yolk vesicle oocytes (YVO) appear with the sequestration of vitellogenic yolk. (c) Hydrated oocytes (HE) and post-ovulatory follicles (POF) were noticeable in the ovaries of spawning fish. (d) Zoning of the cytoplasm was clearly evident in atretic primary vesicle oocytes (AF). (e) Immature testis containing predominantly spermatogonia (Sg) and spermatocytes (Sc). (f) During the breeding season spermatozoa (Sz) fill the lumen. St = spermatids. All scale bars = 200 µm. Stained using Gill's haematoxylin and Papanicoloau's eosin A.

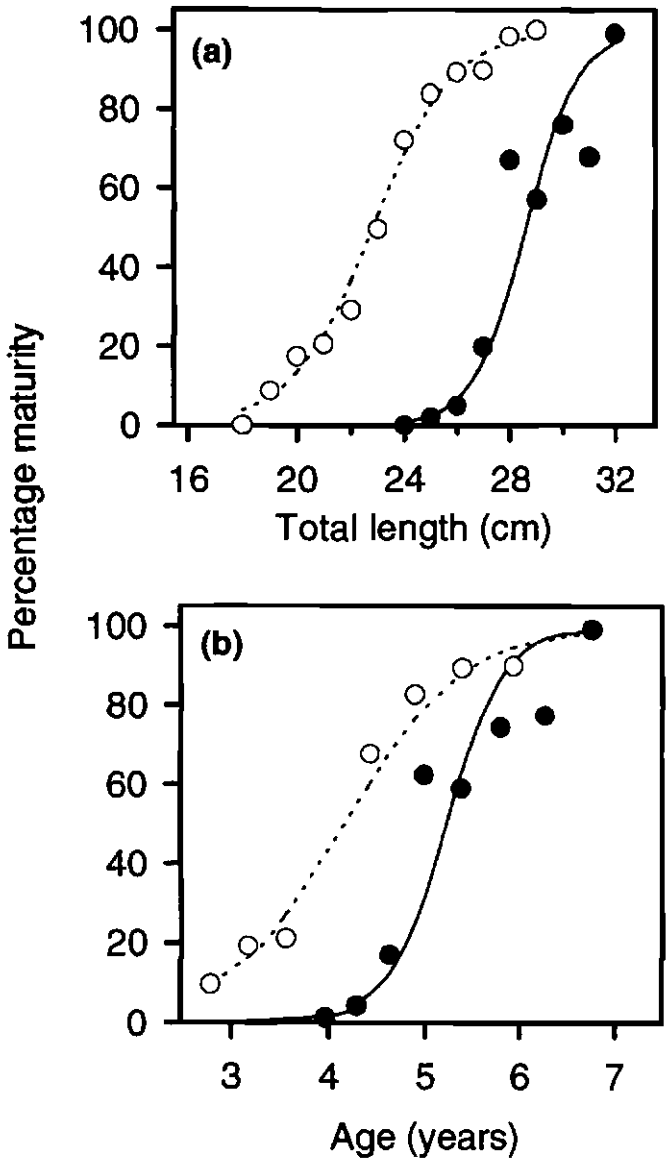

Figure 2 Maturity patterns of *Pterogymnus laniarius* as a function of both (a) length and (b) age from samples collected in 1974/75 (●) and 1994/95 (○). The lines were fitted using a two-parameter logistic ogive.

Table 2 Length-at-maturity, age-at-maturity and mean length of *Pterogymnus laniarius* sampled during the two sampling periods

	1974/1975	1994/1995
Length-at-maturity	28.6 cm TL	23.0 cm TL
Age-at-maturity	5.2 years	4.3 years
Mean length	33.9 cm TL	30.6 cm TL

0.05) and age-at-maturity (F = 18.12; 1,12 *df*; p-value < 0.05) estimates were found to be significantly different between 1974/5 and 1994/95, no significant difference was found between the rates of attaining maturity as both functions of size (F = 0.75; 1,13 *df*; p-value > 0.05) and age (F = 0.84; 1,11 *df*; p-value > 0.05), respectively. There have been changes in mean size of fish over the two sampling periods with fish sampled between 1994/5 being significantly smaller

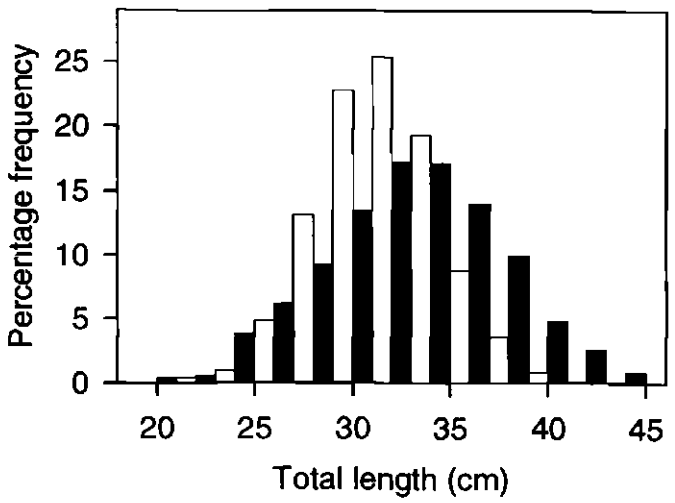

Figure 3 Length frequency histograms of *Pterogymnus laniarius* sampled between 1974/75 (■) and 1994/1995 (□) from Port Elizabeth.

than fish sampled between 1974/75 (t-test; p-value < 0.05) (Figure 3; Table 2).

Inherent natural heterogeneity results in animal populations consisting of a mixture of early- and late-maturing individuals. This is particularly evident in long-lived fish species which mature for the first time over a variety of ages, such as the Northeast Atlantic cod *Gadus morhua* which matures between the ages of 7 and 14 years (Jørgensen 1990). Owing to the size-selective nature of the fishing gear utilised, if there were genotypic differences in growth and/or maturity, intense exploitation would therefore be expected to have a dramatic effect by decreasing genotypic variability. Removal of late-maturing individuals from the population would probably shift the genetic composition towards a higher proportion of earlier maturing individuals (Pollock 1995).

Fishery-induced reductions in both length and age-at-maturity are well documented for several fish stocks which have been subjected to intense fishing pressure in the past (Beacham 1983; Agnault 1989; Armstrong, Roel & Prosch 1989, Jørgensen 1990). At the time of the termination of directed fishing, the panga stock was considered over-exploited (Sato 1980) with spawner biomass at its lowest levels, at 20% of pristine levels (Booth & Punt, unpublished data). The intensive selection on late-maturing individuals as a result of fish being selected at lengths smaller than the length-at-maturity could have provided a mechanism to decrease the length-at-maturity over the 20 years between sampling periods. Although it is not possible to separate the changes in length-at-maturity from changes in age-at-maturity owing to the dependence and interaction between them, these results suggest that the observed changes in length-at-maturity are possibly a synergistic combination of both a slower growth rate and a decreased age-at-maturity.

The need for long-term biological monitoring (including the time consuming and expensive histological preparation of reproductive material) of commercial fish stocks in order to understand possible life-history changes cannot be stressed enough, as this information is critical for stock assessment models and other management-related issues such as the setting of minimum mesh sizes for trawling vessels or minimum

size limits for hook and line fishers.

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A new record of a deep-sea echiuran (Phylum: Echiura) from the east coast of southern Africa

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The echiuran *Thalassema elapsum* was originally described from the North Atlantic by Sluiter (1912). The discovery of this species from the east coast of southern Africa is a new record and considerably extends its range of distribution. The species is redescribed and some of the taxonomic characters are reviewed.

Although the echiuran fauna of southern Africa is fairly well documented there is still scope for further research. Some of the earlier reports on this group in southern Africa are those of Wesenberg-Lund (1959, 1963) and Stephen & Cutler (1969). This is the fifth in a series of papers by the present author dealing with the systematics and distribution of the echurians of Africa south of 20°S (Biseswar 1983, 1984, 1985, 1988a and 1988b). Biseswar (1985) provided a list of the genera and species of echurians from southern Africa and analysed their distribution, partly from the literature and partly from surveys undertaken along the coast.

The echiuran fauna of southern Africa is currently confined to five genera: *Listriolobus*, *Thalassema*, *Ochetostoma*, *Echiurus* and *Anelassorhynchus*. Since the paper by Biseswar (1985) several new species have been added to the list (see Biseswar 1988a and 1988b). Five species of *Thalassema* are currently known from the southern African region, namely: *T. diaphanes* Sluiter, 1888, *T. philostracum* Fisher, 1947, *T. thalassemum* (Pallas, 1766), *T. neptuni* Gaertner, 1774 and *T. jenniferae* Biseswar, 1988b. The taxonomic status of two species of *Thalassema* from the UCT collection remains to be resolved as the internal organs were macerated owing to poor preservation (Biseswar 1988b). The present report on the occurrence of *T. elapsum* from the Kwa Zulu-Natal coast is a new record and marks an extension of its geographical range.

The descriptions of several species in the genus *Tha-*

lassema by earlier authors are very brief and lack critical information on several characters which can be used to separate them. Furthermore, some of the authors made no mention of the gonostomal lips, with the result that it is uncertain whether the species belong to *Thalassema* or *Anelassorhynchus*. The distinction between the two is based on the structure of the gonostomes which in the genus *Anelassorhynchus* are elongate and spirally coiled and in *Thalassema* are funnel-like. In their monograph, Stephen & Edmonds (1972) were unable to construct a key to the species of *Thalassema*, especially those possessing a single pair of gonoducts.

It is thus apparent that some of the species listed in the genus need re-examination and redescription. The present report is a further contribution and sheds light on some of the important taxonomic characters.

Systematic account

Genus *Thalassema* Lamarck

Generic diagnosis

Longitudinal and inner oblique muscle layers continuous and not grouped into bands or fasicles. Proboscis well developed and without bifurcation. Gonoducts from one to three pairs; gonostomal lips not elongate and not spirally coiled. No sexual dimorphism.

Thalassema elapsum Sluiter, 1912

Figures 1, 2

Type locality: Atlantic Ocean; 15°14'N, 23°03'45"W; depth 628 m.

Present records: Four specimens, three sexually mature, Zululand coast, vicinity of Port Durnford; loaned by Natal Museum; dredged by *R.V. Meiring Naude*, 13-6-1988. Locality coordinates: 28°58.7'S, 32°08.0'E, depth 52 m (one specimen); 29° 00.0' S, 32°11.4' E, depth 105 m (three specimens).

Habitat: All the specimens occurred in coarse sand.

Description: Colour of preserved specimens is creamy white. Trunk pear-shaped in one sexually mature specimen (Figure 1A), but cylindrical or sausage-shaped in the others. Length of trunk ranges from 31–36 mm, proboscis lacking in all four specimens. Longitudinal and inner oblique muscle layers continuous without any tendency of aggregating into bands. Integument opaque. Papillae minute, round, closely packed, distributed over entire surface of integument. Papillae slightly larger and more closely arranged at extremities of trunk and aligned roughly in transverse rows at posterior end. Genital pores one pair, located posterior to ventral setae.

Ventral setae (Figure 1B) one pair, minute (0,86 mm in length), located a few millimetres away from anterior tip of trunk. Setae not visible externally. Each seta consisting of a cylindrical shaft with a slightly curved terminal end tapering in a sharp point. Curved terminal part golden-yellow in colour, rest of shaft dark brown. Fine concentric markings around middle region of shaft. Narrow interbasal muscle between the setae present. Internally, bases of setae located in setal sacs supported by thin radiating muscle strands.

Internal anatomy: Alimentary canal extremely long and intricately coiled, fragmented in several places owing to poor preservation. Foregut terminates at intestinal ring vessel. Fine mesenteric strands fasten alimentary canal to body wall at several points. Intestine extremely thin-walled with a narrow intestinal siphon. Contents of gut moulded into small, sausage-shaped faecal pellets. No caecum was found on the rectum, but this may be due to poor preservation.

Gonoducts one pair, elongate, tubular, about half length of trunk. In one specimen without sexual cells, gonoducts cylindrical and more or less of uniform diameter (Figure 2A). In the other three specimens gonoducts with a few constricted and dilated portions owing to different degrees of inflation caused

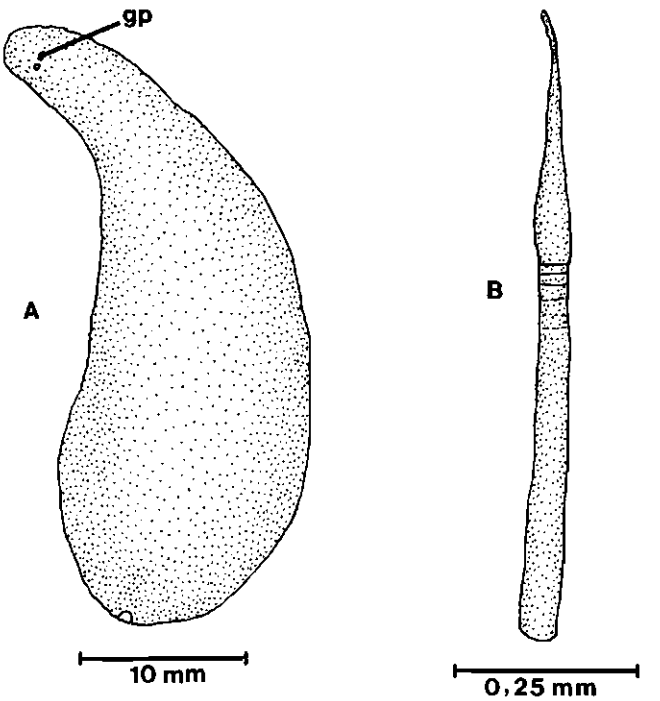

Figure 1 (**A**) Ventral aspect of *Thalassema elapsum*. (**B**) Right functional seta of *Thalassema elapsum*. gp = gonopore.

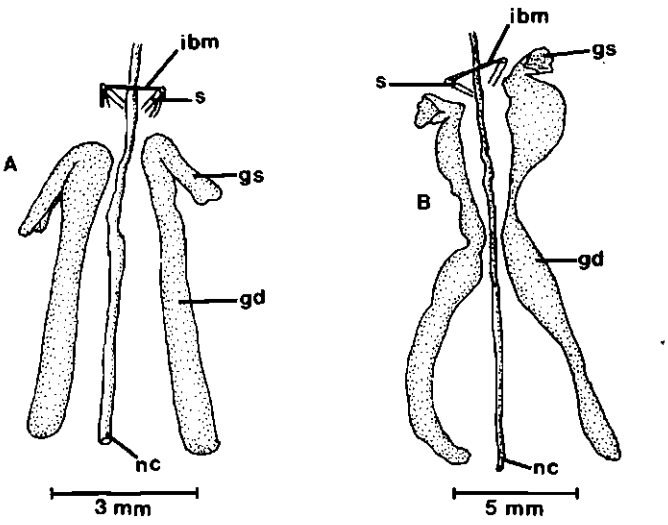

Figure 2 (**A**) Anterior end of trunk cavity illustrating the gonoducts of a specimen without sexual cells. (**B**) Anterior end of trunk cavity showing the gonoducts of sexually mature specimens, gd = gonoduct; gs = gonostome; ibm = interbasal muscle; nc = nerve cord; s = seta.

by the storing of sexual cells within them (Figure 2B). Gonostomes basal in position not located on stalks. Gonostomal lips prolonged into flap-like structures which are folded (Figures 2A and B).

Anal vesicles thin walled, transparent tubular sacs, less than one-quarter trunk length. Both vesicles open into posterior end of rectum. Ciliated funnels minute, located on short stalks, sparsely distributed over surface of both vesicles.

Intestinal ring sinus located around posterior end of foregut. Ventral vessel runs alongside nerve cord. Dorsal and neuro-intestinal vessels damaged owing to poor preservation.

Remarks

The species *Thalassema elapsum* is originally described by Sluiter (1912) from 10 specimens in all of which the proboscis was missing. As the proboscis is also lacking in the specimens from the Natal coast, it is probable that it is highly deciduous. Datta Gupta (1981) recorded and briefly redescribed this species from a single specimen collected from the North Atlantic at a depth of 4 228 m. The discovery of this species from the east coast of southern Africa is a first record of its occurrence in the West Indian Ocean and extends its range of distribution considerably.

The present specimens approach the description provided by Sluiter (1912) in possessing a single pair of postsetal gonoducts, in the shape and arrangement of the dermal papillae and the size of the specimens. The structure of the gonostomal lips is basically similar. Sluiter describes the gonostomal lips as 'merely folded or crumpled'.

The interbasal muscle is an important taxonomic character in echiurans. Unfortunately, Sluiter makes no mention of this muscle in his description. The specimens on hand differ from the description provided by Datta Gupta in possessing a narrow interbasal muscle between the setae. Differences are also apparent in the structure of the setae. In the specimens from the Natal coast, the setae are minute, averaging less than one millimetre in length and the terminal ends are only slightly curved. From the description and illustration given by Datta Gupta (1981) the setae are prominent structures with the distal ends sharply curved and hook-like in appearance. On the bases of the differences in the shape and size of the setae and the interbasal muscle it seems likely that the present specimens represent an undescribed species. Unfortunately, it is not possible to provide a more detailed description as some of the internal organs, such as the alimentary and blood systems are damaged owing to poor preservation. A closer study of additional material from that region in the future will confirm its true identity.

The species that is most nearly related to *T. elapsum* seems to be *Thalassema diaphanes*, described originally from a single specimen from Indonesia by Sluiter (1888). This species was later recorded and redescribed from several other localities in the Indo-West-Pacific and East Atlantic Oceans. Along the southern African coast *T. diaphanes* has been recorded from the vicinity of Cape Town and from the Natal coast by the UCT ecological survey (1964). *Thalassema diaphanes* differs from *T. elapsum* in the nature of the integument and the structure of the gonostomes. According to Sluiter's description (1888), the integument is thin and transparent. The description provided by Biseswar (1988b) states that the gonostomes are oval with smooth margins which unite to form a funnel-shaped structure. In view of the above differences, it is probably best to consider the two species separate.

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