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PARAHEMIURUS BENNETTAE N.SP. (DIGENEA), A HEMIURID TREMATODE PROGENETIC IN SALINATOR FRAGILIS LAMARCK (GASTROPODA, AMPHIBOLIDAE)

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(With three Text-figures)

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SYNOPSIS

The adult of *Parahemiurus bennettae* n. sp. is described. This trematode attains sexual maturity and becomes gravid within rediae in the female gonad of *Salinator fragilis* Lamarck, an herbivorous, hermaphrodite, pulmonate snail occurring on estuarine mud flats at Botany Bay, New South Wales. No other host is known.

INTRODUCTION

The term progenesis was coined by Giard (1887) for precocious maturity in animals where this was associated with arrested development. In this sense it was synonymous with neoteny. Its use was extended by Dollfus (1924) to cover precocious sexual maturity of larval trematodes, particularly metacercariae, which occurs without inhibition of subsequent development. The occurrence of progenesis in molluscan hosts has escaped the attention of many zoologists and was denied by Baer (1951). He nevertheless pointed out that if progenetic metacercariae were to arise within the sporocyst, a direct life cycle would result which would require only a single host. The discovery of gravid appendiculate flukes, belonging to a new species, *Parahemiurus bennettae*, in rediae parasitizing the snail *Salinator fragilis* Lamarck is therefore of interest.

Application of the term progenesis to this hemiurid is not strictly appropriate as the only egg-bearing individuals observed were morphologically adults. Precocity is here manifested in attainment of the adult form in what, in the digenetic life cycle, is normally the first intermediate host and not in the premature onset of sexual reproduction. The same is true of several accounts of "progenesis" in the literature. Nevertheless, as it is not always possible to distinguish metacercariae (i.e. the immediate post-cercarial stage) from adults, the current broad use of progenesis to denote sexual maturity of trematodes, irrespective of their state of development, in non-definitive hosts, is best accepted.

The gravid individuals of *P. bennettae* are here regarded as true adults, in accordance with Buttner's interpretation (1955) of progenetic flukes with abbreviated developmental cycles. In the present communication only the adult is described. A further paper will be devoted to a discussion of this and other reported cases of progenesis in molluscan hosts.

Parahemiurus bennettae n. sp.

HOST AND HABITAT

The only known host of *Parahemiurus bennettae* n. sp. is *Salinator fragilis* Lamarck, an herbivorous, hermaphrodite pulmonate snail of the family Amphibolidae. The snails examined were from a population of many thousands on tidal mud flats by Cook's River a few hundred yards before its effluence into Botany Bay, N.S.W.; collector B. G. M. Jamieson, April, May, November, 1964, January, 1965. Except in periods of heavy rain, the outflow from the river is small and at high tide the snails must normally experience salinities near those of sea water. The snail is, nevertheless, absent from the neighbouring littoral zone.

MATERIAL EXAMINED

April, 1964: many snails, incidence of gravid flukes high. May 14, 1964: 80 snails, 31 (39%) harbouring several, sometimes 10 or more, rediae containing non-gravid flukes. November 8, 1964: 74 snails, 7 (9%) harbouring 7 to 10 or more rediae, some in each of five snails containing gravid flukes; those of two snails dead. November 14, 1964 (following reduction of snail population by pollution) : 20 snails, 1 (5%) infected, harbouring 15 rediae; gravid flukes in 3 of 5 rediae examined. January 4, 1965: 16 snails, 1 (6%) harbouring several rediae; gravid flukes present. Holotype and paratypes lodged in the British Museum (Natural History); paratypes in Queensland Museum.

Remarks. Total disappearance of gravid individuals between April and May indicates that egg-laying is completed by late autumn and an apparent reduction in incidence over this period that, having oviposited, the flukes die.

LOCATION IN HOST

Sporocysts and rediae were observed only in the female gonad. The rediae contained germ balls, cercariae and adults or only one, or two, of these stages.

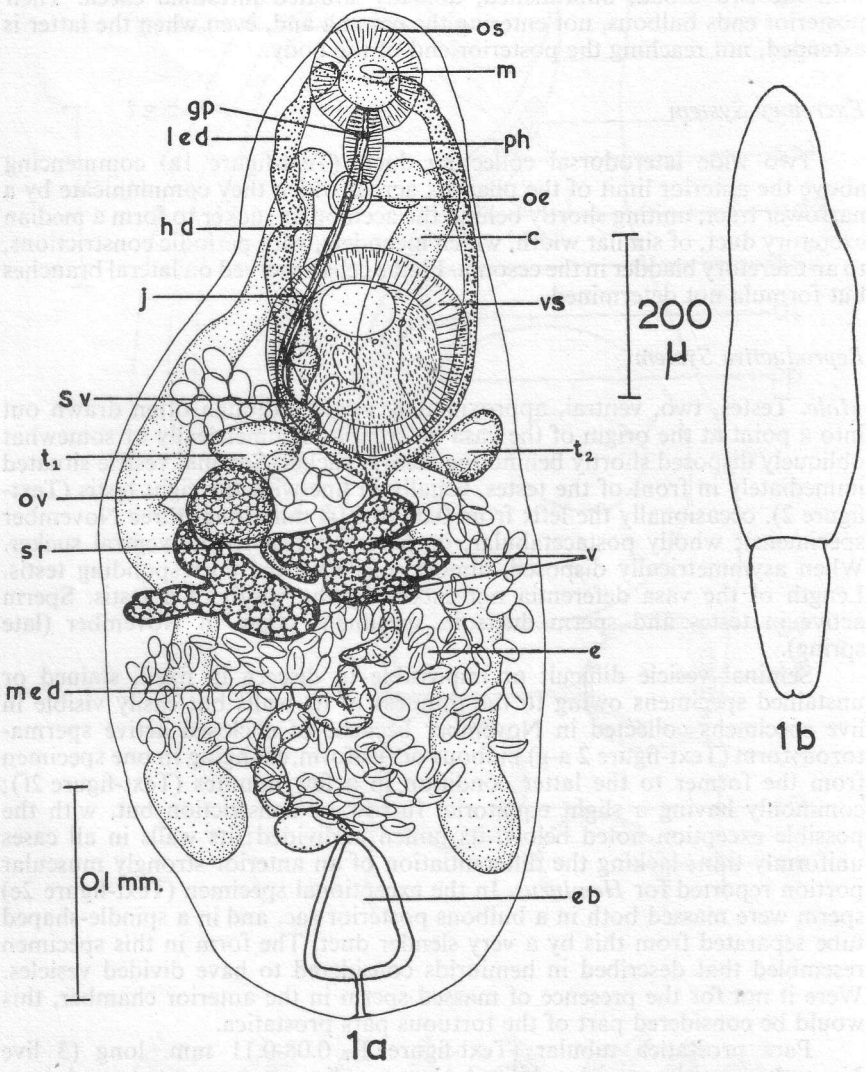
THE ADULT

External Features

Fifteen living specimens, removed from rediae and immobilized by light coverslip pressure, in dilute sea-water, had the following dimensions in millimeters (means in parentheses): length excluding ecsoma 0.79-1.26 (1.07); maximum width 0.30-0.37 (0.34); oral sucker 0.085-0.098 (0.092) in diameter; ventral sucker 0.139-0.200 (0.175) in diameter, situated 25-36% (31%) of body length (without ecsoma) from anterior end; ratio of oral to ventral sucker diameters 1 : 1.64-2.21 (1 : 1.91). Length of ecsoma (six specimens) 0.08-0.39; its usual extent about one fifth of the body length. Seasonal variation in size of gravid specimens suggested by range of body length in 12 specimens, fixed without pressure in 70% alcohol: from 0.44 in specimen collected in April to 1.35 for one taken in January.

Cuticle bearing narrow, transverse, minutely denticulate striations ventrally in the forebody. Small, rounded, wart-like papillae sometimes visible on the forebody; a large, transversely oval papilla seen in several specimens behind the genital pore which lies midventrally at the posterior

lip of the oral sucker. Striations and papillae rarely visible in euparal or balsam. Preacetabular pit absent. Oral sucker subterminal and, like the ventral sucker, circular with four or more equally spaced dome-shaped papillae on its rim.



Text-figure 1.—*Parahemiurus bennettae* n. sp.; a, ventral view of holotype collected in April; b, outline of a November specimen under slight pressure, showing fully extended ecsoma. Explanation of lettering: c, caecum of intestine; e, egg; eb, excretory bladder; gp, genital pore; hd, hermaphrodite duct; j, junction of pars prostatica and uterus; led, lateral excretory duct; m, mouth; med, median excretory duct; oe, oesophagus; os, oral sucker; ov, ovary; ph, pharynx; sr, seminal receptacle; sv, seminal vesicle; t 1 and t 2, testes; v, vitelline glands; vs, ventral (acetabular) sucker.

Alimentary System

Funnel-shaped buccal aperture of the oral sucker opening directly into an approximately spherical, thick-walled muscular pharynx, 0.048 to 0.058 (0.050) long (7 live specimens). Pharynx leading into a globular thin-walled oesophagus (Text-figure 1a) of similar dimensions which communicates with the two broad, unbranched, dorsally situated intestinal caeca. Their posterior ends bulbous, not entering the ecsoma and, even when the latter is extended, not reaching the posterior end of the body.

Excretory System

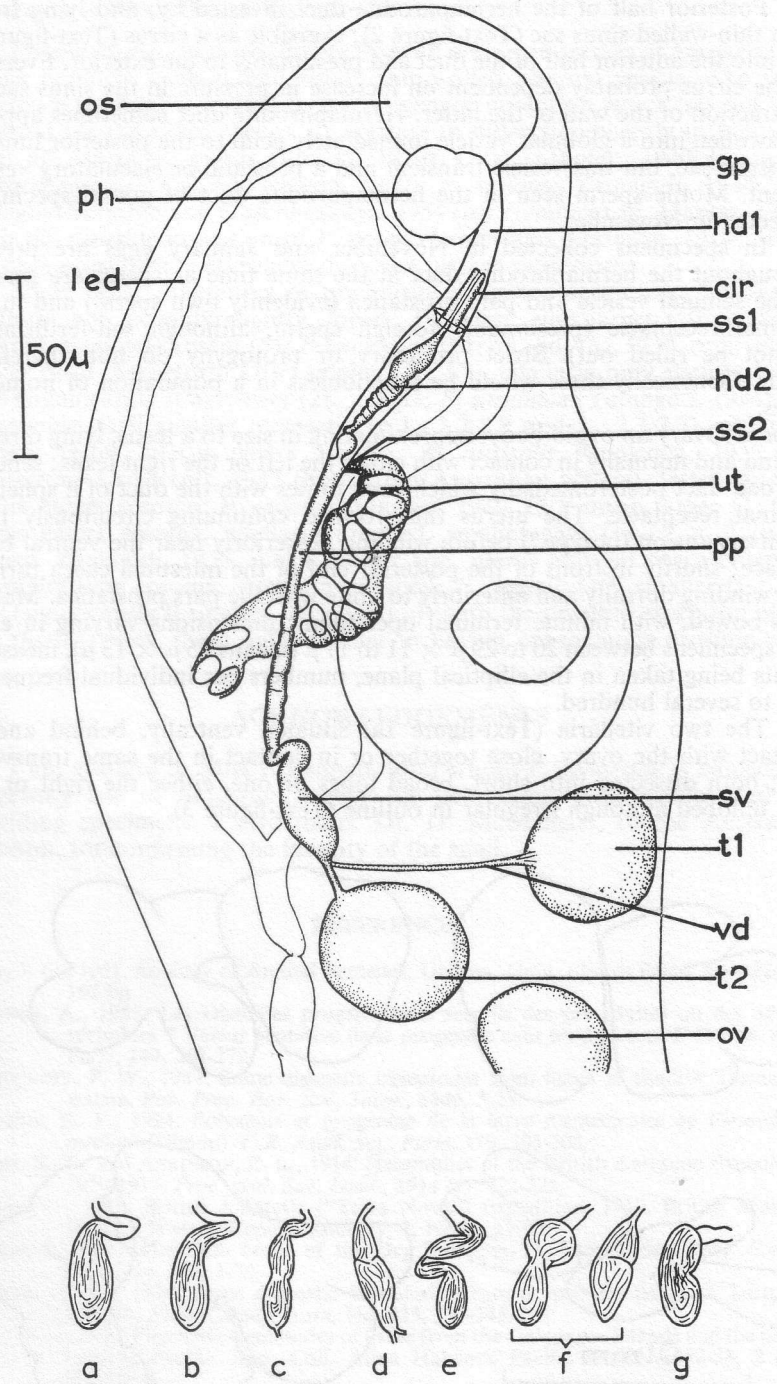
Two wide laterodorsal collecting ducts (Text-figure 1a) commencing above the anterior limit of the pharynx across which they communicate by a narrower tract, uniting shortly behind the acetabular sucker to form a median excretory duct, of similar width, which meanders, with periodic constrictions, to an excretory bladder in the ecsoma. Flame cells observed on lateral branches but formula not determined.

Reproductive System

Male. Testes, two, ventral, approximately ovoid although often drawn out into a point at the origin of the vasa deferentia; symmetrically or somewhat obliquely disposed shortly behind the ventral sucker. Seminal vesicle situated immediately in front of the testes, usually in line with the right testis (Text-figure 2), occasionally the left; from 0.04 to 0.08 mm. long (three November specimens); wholly postacetabular, or posterodorsal to the ventral sucker. When asymmetrically disposed, almost sessile on the corresponding testis. Length of the vasa deferentia not exceeding the width of a testis. Sperm active in testes and sperm ducts in specimens taken in November (late spring).

Seminal vesicle difficult or impossible to discern in fixed, stained or unstained specimens owing to the thinness of its walls but easily visible in live specimens collected in November because of enclosed active spermatozoa; form (Text-figure 2 a-g) bulbous or fusiform, changing in one specimen from the former to the latter condition in a few minutes (Text-figure 2f); commonly having a slight equatorial furrow or constriction but, with the possible exception noted below, its lumen undivided; its walls in all cases uniformly thin; lacking the differentiation of an anterior strongly muscular portion reported for *Hemiurus*. In the exceptional specimen (Text-figure 2e) sperm were massed both in a bulbous posterior sac, and in a spindle-shaped tube separated from this by a very slender duct. The form in this specimen resembled that described in hemiurids considered to have divided vesicles. Were it not for the presence of massed sperm in the anterior chamber, this would be considered part of the tortuous pars prostatica.

Pars prostatica tubular (Text-figure 2), 0.08-0.11 mm. long (3 live November specimens immobilized by coverslip pressure), measured in a straight line from the seminal vesicle to its termination which varies from mid-acetabulum to a short distance anterior to that sucker; coiled, sinuous or straight depending on extension of the forebody, joining the uterus to form a long, narrow hermaphrodite duct leading to the genital pore (Text-figure 2). Prostatic cells not visible but, under phase contrast, width of the pars prostatica appears to be approximately doubled by an investing sheath, presumably of prostatic tissue. Sections stained with Azan show only a few nuclei associated with the duct.



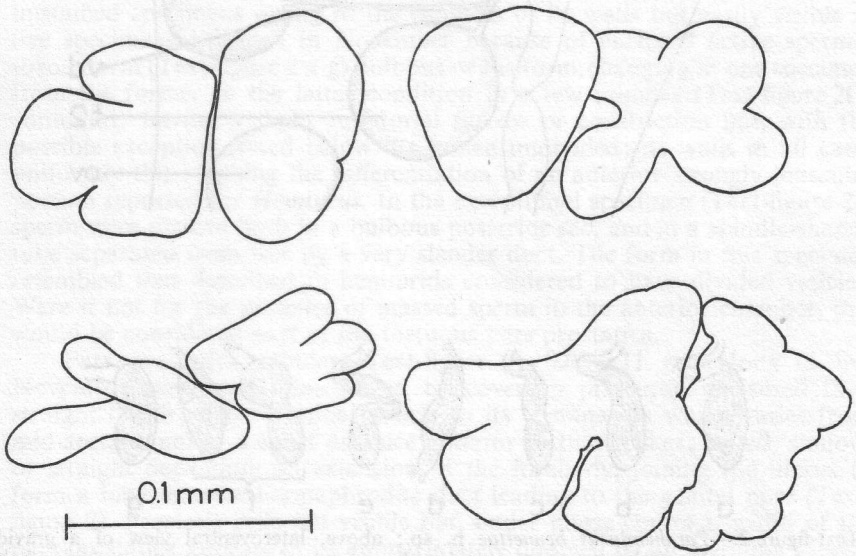
Text-figure 2.—*Parahemiurus bennettae* n. sp.; above, lateroventral view of a gravid November specimen showing the reproductive organs; the posterior half of the hermaphrodite duct is evaginated into the anterior half as a cirrus (from a photograph of a living fluke); a-g, different forms of seminal vesicles, containing sperm, from November specimens. Lettering: cir, cirrus; hd1, hd2, anterior and posterior regions respectively of hermaphrodite duct; pp, pars prostatica; ss1 and ss2, anterior and posterior limits of sinus sac; ut, uterus; vd, vas deferens; other lettering as for Text-figure 1.

Posterior half of the hermaphrodite duct invested by, and lying freely in, a thin-walled sinus sac (Text-figure 2); eversible as a cirrus (Text-figure 2, cir) into the anterior half of the duct and presumably to the exterior. Eversion of the cirrus probably dependent on increase in pressure in the sinus sac by contraction of the wall of the latter. Hermaphrodite duct sometimes appearing swollen into a globular vesicle immediately ectal to the posterior limit of the sinus sac, but this vesicle transient and a prostatic or ejaculatory vesicle absent. Motile sperm seen in the hermaphrodite duct of gravid specimens collected in November.

In specimens collected in November and January eggs are present throughout the hermaphrodite duct at the same time as sperm are present in the seminal vesicle and pars prostatica (evidently own sperm) and in the seminal receptacle (presumably foreign sperm, although self-fertilization cannot be ruled out). Strict protandry or protogyny do not, therefore, occur. Genetically these would be functionless in a population of homozygotes.

Female. Ovary an ovoid body, approximating in size to a testis, lying directly behind and normally in contact with either the left or the right testis; sending a broad duct posteromedially which soon unites with the duct of a spherical seminal receptacle. The uterus thus formed continuing circuitously to a slight expansion (ootype?) before winding posteriorly near the ventral body surface; shortly in front of the posterior end of the intestinal caeca turning and winding dorsally and anteriorly to unite with the pars prostatica. Mature eggs bowed, with minute terminal operculum; dimensions varying in eight live specimens between 20 to 29 $\mu \times 11$ to 17 μ (means 25 $\mu \times 13$ μ), measurements being taken in the elliptical plane, numbers per individual frequently one to several hundred.

The two vitellaria (Text-figure 1a) situated ventrally, behind and in contact with the ovary, close together or in contact in the same transverse line; both dissected into short, broad lobes or one, either the right or the left, unlobed although irregular in outline (Text-figure 3).



Text-figure 3.—*Parahemiurus bennettae* n. sp.; different forms of vitelline glands from April and November specimens.

Comparison With Other Species

Parahemiurus bennettae differs from all described species of *Parahemiurus* in the papillate suckers and small, thin-walled seminal vesicle. The latter difference is possibly related to the progenetic condition which has not been reported for the other species. It appears to differ significantly in body-size from all except *P. merus* (Linton, 1910) s. lat. Manter, 1940 (including *P. parahemiurus* Vaz and Pereira, 1930), *P. seriolae* Yamaguti, 1934, and *P. dogieli* Skrjabin and Guschanskaya, 1954 (for *Hemiurus* sp. Manter, 1934). With the possible exception of *P. oatesi* (Leiper and Atkinson, 1914; 1915), the pars prostatica is elsewhere disposed further posteriorly.

Some other differences of previously described species are: *P. merus*, vitellaria not, or only slightly, lobed; *P. oatesi*, eggs larger (50 × 30 μ), seminal receptacle absent (?); *P. anchoviae* Pereira and Vaz, 1930, oral/ventral sucker ratio (henceforth O/V) smaller (1 : 2.3), vitellaria only slightly lobed, eggs (significantly?) narrower (28 × 8 μ); *P. sardiniae* (Yamaguti, 1934) and *P. seriolae*, O/V smaller (respectively 1 : 2.2-2.9 and 1 : 2.3-2.7), obliquely tandem testes, uterus enters ecsoma; *P. australis* Woolcock, 1935 and *P. lovettiae* Crowcroft, 1947 (both from Australian waters), testes tandem, uterus enters ecsoma; *P. ecuadori* Manter, 1940, O/V much larger (1: 0.8), uterus enters ecsoma, vitellaria unlobed, smaller eggs (14-15 × 7 μ); *P. clupeae* Yamaguti, 1953, much greater size, uterus and gut caeca enter the unusually long ecsoma, vitellaria unlobed; *P. dogieli*, O/V smaller (1 : 2.7), eggs (significantly?) smaller 18 × 9-10 μ); with the possible exception of the first three species, these differ further in having conspicuous prostate cells.

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