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A Redescription of *Reighardia sternae* Diesing 1864 (Pentastomida: Cephalobaenida) with Some Observations on the Glandular Systems of Pentastomids

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Summary. Adult males and females of the pentastomid *Reighardia sternae* Diesing 1864 from the body cavity and air sacs of *Larus argentatus* are described. The species resembles other Cephalobaenid pentastomids closely, the main differences being the lack of abdominal annuli and the poorly developed hook-bearing podia.

Attention is paid to the secretory systems of this organism and these are compared to those described for other species. Possible functions are discussed.

A. Introduction

Reighardia sternae (Diesing, 1864) is the only member of the phylum Pentastomida which utilizes an avian definitive host. Bakke (1972), reviewing the literature on *R. sternae* provided a host list which comprised 13 species of gulls and terms (sub-order LARI). To this list can be added *Larus fuscus* (Riley, 1970), and the following auks (family Alcidae); the guillemot (*Uria aalge*) and the puffin (*Fratercula artica*) (Threlfall, 1971). The latter two hosts are the first records of *R. sternae* in hosts outside of the sub-order Lari.

R. sternae, belonging to the primitive order Cephalobaenida, is one of the most widely studied pentastomids. However, despite the extensive literature on this organism which includes developmental studies (Osche, 1959, 1963; Haffner and Rack, 1965), and various aspects of its structure (Haffner, 1967; Mill and Riley, 1972; Riley, 1972a, 1973) and life history (Bakke, 1972; Riley, 1972b), the adult has not been adequately described. Consequently this paper provides a description of the adults of *R. sternae* and draws particular attention to the glandular systems, these being an important, but neglected, diagnostic feature of the Pentastomida. A literature survey revealed differences between the glands of the Cephalobaenida and the advanced order Porocephalida. These are stressed, and possible functions are suggested.

B. Materials and Methods

Adult male and female specimens of the pentastomid *Reighardia sternae* Dies. 1864 were obtained from the air sacs and abdominal cavity of the herring gull *Larus argentatus* Pontopp.

Some specimens were fixed whole for 4 h in 10% buffered formalin, and subsequently cleared in lactophenol for whole mount observations, or alternatively were dissected for details of hook structure. Other specimens, after fixation, were cut up into pieces, dehydrated and cleared for wax embedding and sectioning at 8 μm, before staining in Mallory's trichrome solution.

For enzyme histochemistry specimens were fixed in ice-cold 10% formalin, buffered to pH 7.0. The azo-dye technique for acid-phosphatase (Burstone, 1958) was used.

Hook measurements were made on four adults of each sex, but the dimensions of entire worms are based on over 20 specimens of both males and females.

C. Observations

In both sexes living specimens appear white in colour with the prominent central black intestine showing clearly through the body wall. Mature females are more opaque due to the accumulation of eggs in the saccate uterus.

R. sternae exhibits a marked sex dimorphism: females are very much larger being 30–46 mm in length and up to 2.5 mm in diameter whereas mature males measure 6–8 mm in length and their maximum width is 0.8–1.0 mm. Both sexes show a dorso-ventral flattening of the head region but elsewhere are round in cross section. Males are claviform, being widest anteriorly in the region of the second hook pair, but then tapering gradually towards the caudal extremity (Fig. 1). Females are more uniformly thick and are bluntly rounded posteriorly but rather more gradually attenuated anteriorly.

The body of *R. sternae* does not show the false annulations characteristic of many pentastomids, especially the Porocephalida, although according to Haffner and Rack (1965) these do appear in the first 3 or 4 nymphal stages. The chitinous cuticle of the female is covered with stud-like projections which are most numerous on the ventral surface where they reach concentrations of 70 mm^2. These cuticular concretions are absent in immature females and males. This difference probably reflects directly the different behavioural patterns shown by the two sexes, as outlined by Riley (1972b): third stage larvae penetrate the wall of the intestine (Haffner and Rack, 1965) and feed and grow in the abdominal cavity until copulation occurs. Males then die and fertilized females migrate anteriorly, possibly via the bronchioles, into the interclavicular air sacs (Riley, 1972b). Thus the tegumental tubercles may have evolved to assist this migration, an aid to locomotion analogous to the chaetae of oligochaetes. Haffner *et al.* (1969) postulated a similar use for cuticular spines in certain Linguatulidae.

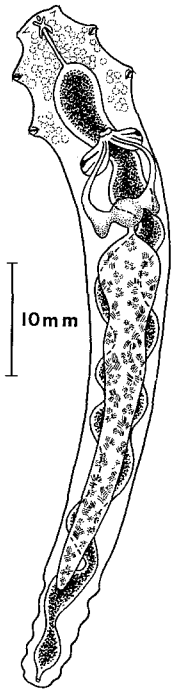


Fig. 1

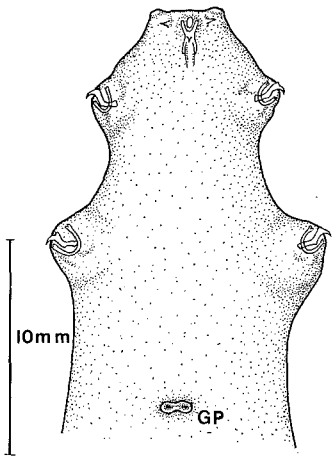


Fig. 2

Fig. 1. A semi-diagrammatic ventral view of an adult male *R. sternae* showing the disposition of the major organ systems. (The intestine has been omitted from certain regions where it obscures the reproductive system.) Note the anterior lateral and frontal papillae, the small hook-bearing podia with the hook glands, and the central mass of the frontal gland. Detail of the reproductive system is given in Fig. 5 but the large, single dorsal extending almost to the caudal extremity is easily seen in entire specimens

Fig. 2. Detail of the anterior region of an adult male from the ventral aspect. Note the lateral papilla flanking the mouth, and the rounded frontal papillae. The broadly elevated podia bearing simple hooks are characteristic of this species. *GP* genital pore

The stump-like legs or podia are especially prominent in the male where they appear as broadly conical elevations of the general body surface (Fig. 2). In both males and females the hooks are situated at the apex of the podia on exceedingly minute podial lobes which are flanked laterally by inconspicuous parapodial lobes. This arrangement is unique to *Reighardia*. Other Cephalobaenida have prominent podia and or strongly developed lobes. Hook measurements along the two axes indicated in Fig. 4 are given for females and males respectively: Anterior hooks A 87–100 μm, B 30–35 μm; posterior hooks A 92–106 μm, B 30 μm;

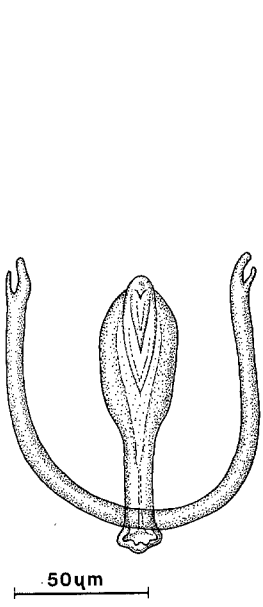


Fig. 3

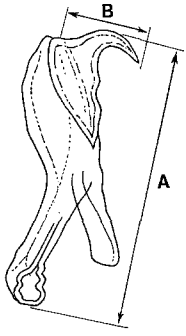


Fig. 4

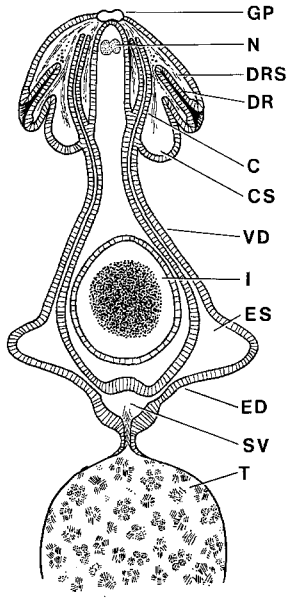


Fig. 5

Fig. 3. Detail of an anterior hook of a male *R. sternae* showing the horse-shoe shaped chitinous supporting rod

Fig. 4. A lateral view of an anterior hook. The hook is hollow and open at the book. Another opening, towards the front of the hook, is seen near the base

Fig. 5. A semi-diagrammatic representation of the male reproductive system. Note the testis (*T*) emptying into the seminal vesicle (*SV*) from which run paired ejaculatory ducts (*ED*). The latter expand to form ejaculatory sacs (*ES*) which encircle the intestine (*I*) and continue as paired vas deferens (*VD*) into the cirrus sac (*CS*). The cirri (*C*) terminate close to the genital pore (*GP*). The dilator rod (*DR*), carried in the dilator rod sac (*DRS*), is secretory, and droplets of secretion and mucus are associated with its distal end, *N* ventral nerve cord

Anterior hooks A 87–100 µm, B 23–28 µm; posterior hooks A 92–104 µm, B 28 µm. Each hook is located by a horseshoe shaped chitinous rod with forked termini (Fig. 3), on to which insert the muscle systems operating the hook. These simple hooks, devoid of a fulcrum, are also diagnostic of the order Cephalohaenida.

The mouth is an elliptical orifice supported internally by a Y-shaped chitinous mouthring. The anatomy of the buccal complex has been previously described (Riley, 1973).

The alimentary tract is of the normal type described for pentastomids (Heymons, 1935) and consists of a chitinous pharynx, a long narrow oesophagus, a long, slightly convoluted intestine, and short rectum

communicating with the anus which is ventral and slightly subterminal (Fig. 1). On either side of the mouth, at the extreme anterior tip of the animal, are located the sensory lateral papillae (Fig. 1) which although much reduced in this species, reveal a difference in structure between males and females and this historically has considerable significance. Each papilla in the former consists of a small sensory spike, whereas in the females the lateral papillae are small raised areas apparently devoid of projections. The spike, first observed by Faust (1927), and subsequently commented upon by Osche (1963, 1965) and Haffner and Rack (1965) was termed by Faust the first limb pair, which would mean *R. sternae* has a six-limbed embryo, a feature which has been used to argue arthropod affinities (Sambon, 1922). However from my observations, both in whole mounts and sectioned material, there is no doubt that the spike is sensory and in no way a locomotory aid, Papillae of the type have been described in another Cephalobaenid, *Raillietiella boulengeri* (Fain, 1961). The paired frontal papillae lie outside of the latter at the anterior-margin of the head (Fig. 2), and are present in both sexes.

The male genital apparatus consists of a single large dorsal testis which can extend almost to the caudal extremity (Fig. 1). Anteriorly this enters a thick walled, spherical seminal vesicle via a short duct. Paired ejaculatory ducts pass forward from the seminal vesicle and expand into muscularised ejaculatory sacs. Long extensions of the latter, the vasa deferentia, encircle the gut and enter on the ventral side the paired cirrus sacs. The continuation of the vasa deferentia inside the cirrus sac is the penis which measures approximately 240 μm long × 10 μm wide (Fig. 5). This organ is protrusible, and in certain fixed specimens the terminal portion projected through the genital pore. Lateral compartments off the cirrus sacs are the dilator rod sacs, each containing a dilator rod. This is a uniformly thick, bluntly rounded spicule 180 μm long and 10μm wide, and in stained sections the core is fibrillar with the distal end associated with a mucous sheath and acidophilic droplets of secretion. In this species therefore, the dilator rod may have a secretory function, its length and position precluding its use as a mechanical copulatory aid as suggested for other Cephalobaenida (Fain, 1961).

The female genital apparatus (Fig. 6) consists of an elongate, tubular ovary, lying between the dorsal body wall and the intestine and extending almost the whole length of the animal. Anteriorly the ovary passes on the right side of the gut where it joins the oviduct in the mid-ventral line. At this junction enter connections from the paired receptacula semini which lie on either side of the oviduct and contain stored sperm. Also entering the system at the base of the ovary are the individual ductules from paired glandular masses which extend anteriorly under the midgut (Fig. 6). This gland will be referred to in greater detail later. The uterus

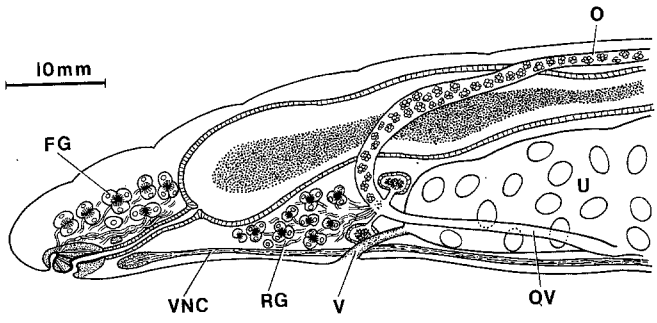


Fig. 6. A semi-diagrammatic lateral view of the head of an adult female showing the general disposition of the major organs. The buccal cavity is shown receiving the efferent ductules of the frontal gland (*FG*). From the pharynx the intestine communicates with the intestine via an oesophageal intestinal valve. The oesophagus is encircled by commisures of two ganglia and from these run the paired ventral nerve cords (*VNC*). The reproductive system consists of an ovary (*O*), leading to an oviduct (*OV*) which joins the uterus (*U*) ventrally. A thick-walled vagina (*V*) opens from the uterus in the mid-ventral line. At the junction between the ovary and the oviduct enter the paired receptacule semini and the different ductules of the reproductive gland (*RG*)

is a capacious, thin-walled sac which occupies most of the ventral haemocoel posterior to the genital pore. In fully mature gravid females the uterus is full of thin-walled, oval, embryonated eggs which measure on average 275 × 165 μm. Each egg is invested by a mucous capsule, up to 350 μm in diameter which is secreted by the dorsal-organ of the embryo (Osche, 1963). The detailed structure of the embryonated egg and the subsequent four larval developmental stages are given by Haffner and Rack (1965).

D. The Secretory Systems of *R. sternae*

The remainder of this paper deals with the glandular systems of *Reighardia sternae* and compares them with those described in other Cephalobaenida. Later, the secretory systems of this primitive group are compared to those found in the advanced order Porocephalida.

1. The Cuticular-Glands

R. sternae resembles all other pentastomids described to date in that the cuticle is permeated by pores, previously termed stigmata (the "hautdrüsen" or "stigmendrüsen" of German authors) because of their superficial resemblance of leaf pores. These communicate with specialised epidermal cells called cuticular glands. When live animals are fixed in hot

70% alcohol the epicuticle becomes detached from the endocuticle except in the region of these gland pores.

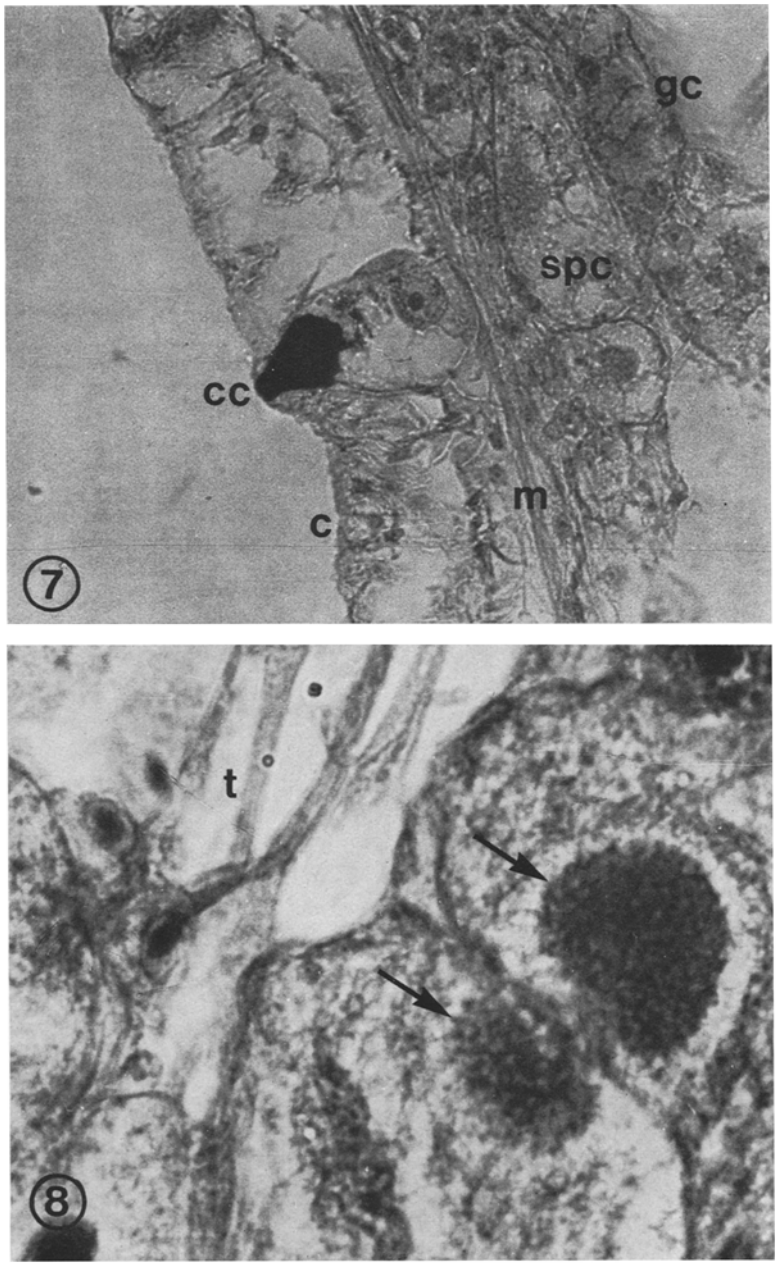
Cuticular gland cells are pyriform, with an oval body measuring 50–75 μm wide and up to 100 μm long, narrowing to a prominent neck which distally constitutes the pore of the gland. The latter is an amorphous plug of material supported by a chitinous collar, which, when viewed from above, appears oval and measures 18–20 × 15 μm. The central pyriform cell is overlapped by smaller cells which invest it like the scales of an anion. A deeply staining mass of fibrils extend into the vacuolated basal cytoplasm of the central cell and these converge on to the pore plug (Fig. 7). Concentrations of 10–15 gland pores/mm² have been counted on the exised cuticle of adult females. Cuticular glands gradually disappear in the posterior half of the animal, but anteriorly are distributed annularly.

In the head region, groups of cuticular cells erupt near to the sensory papillae and on the parapodial lobes, but these do not resemble the cells of Bovien mentioned by Heymons (1935) in other species of Cephalobaenida (*Raillietiella* sp., *Cephalobaena tetrapoda*).

The remaining glandular systems lie free in the haemocoel, and according to Doucet (1965) are mesodermal in origin. They show a singular uniformity in structure despite their undoubted functional specialisation.

2. The Frontal Gland

The most prominent and compact of the secretory systems is the cephalic or frontal gland which occupies most of the available haemocoel anterior to intestine. In the female the gland is oval measuring 750 × 550 μm and the constituent oval cells of the gland can attain maximum dimensions of 130 × 210 μm. The gland in the male is smaller and the component cells are correspondingly about half the size of those of the adult female. Histologically the cytoplasm of these cells is strongly basophilic, suggesting intense secretory activity, and protein stains (bromophenol-blue) reveal numerous cytoplasmic granules which are presumably secretory. Cells are grouped into bi- or tricellular secretory units and from the central point of each lobule emerges a tiny thick-walled ductule (Fig. 8). These ductules do not unite to form a common collecting duct but rather traverse the mass of the cephalic gland and aggregate into two groups above the pharynx to eventually discharge singly into the buccal capsule (Riley, 1973). Elongate, pyriform ductule secretory cells lie along the length of these efferent canals. The latter measure 4–6 μm across, with a lumen about 3 μm in diameter, and in extreme cases are continuous for at least 650 μm. At the point of emergence of the ductule from the individual secretory lobules, rays of intensely staining material radiate out into the contiguous cytoplasm of the cells; these processes presum-



Figs. 7 and 8

ably chanelling secretory products into the ductule (Fig. 8). Large acidophilic droplets of secretory material up to 2 μm in diameter, can be observed in the lumen of these efferent canals, and very infrequently in the lumen of the buccal capsule.

3. The Hook Glands

Many authors have described these glands, but only in the Porocephalida are they clearly delimited (Hett, 1924; Heymons, 1935). In the Cephalobaenida the glands closely flank the frontal gland and the precise limits of each system are difficult to define.

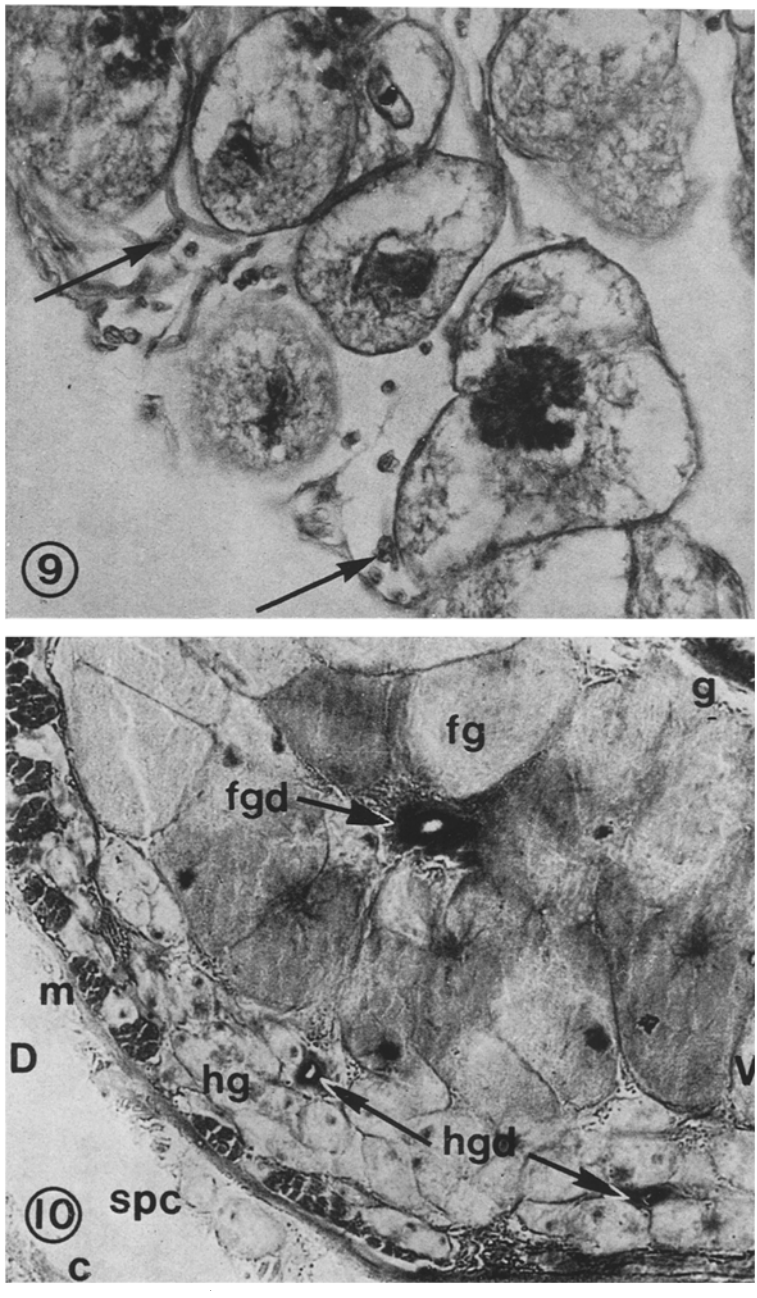
In *R. sternae* the glands are represented by small cells which surround the head gland, and in the male extend posteriorly as far as the genital apparatus. Again cells are associated in groups of two or three, each unit discharging through a single efferent ductule. Some of the latter appear to erupt in the general area of the hook bay, but others apparently penetrate the cuticle in the antero-ventral region of the head (in the general area of the sensory papillae). It was not possible to ascertain whether two distinct secretory systems were involved because the cells were scattered and intimately associated with the peripheral cells of the frontal gland. A further complication was introduced by sheets of small oval cells, 6 μm long, which appear to support and locate the above gland cells in the haemocoel.

4. The Sub-Parietal Glands

Sub-parietal glands are suspended in the haemocoel by mesenteries which position them below the two muscle layers associated with the body wall. This system consists of paired cells, histologically identical to the cells of the frontal-gland, dispersed throughout the body, but never displaying the composite arrangement typical of the other haemocoelic glands. Individual cells measure between 120–185 μm by 100–150 μm, and as before they are united in pairs with each of these units giving rise to an efferent ductule. Unfortunately it was not possible to determine the path of the ductules not their point of discharge, but the

Fig. 7. A light micrograph of a single cuticular cell (*cc*) showing phosphatase activity in the neck region. The cuticle (*c*), underlying muscle systems (*m*), paired sub-parietal cells (*spc*) and gastro-intestinal cells (*gc*) are also visible. Azo-dye technique, neutral red. × 450

Fig. 8. A pair of frontal gland cells showing the inter-cellular junction from which arises the efferent ductule. Rays of densely staining material (arrows) radiate our from this region. Individual ductules (*t*) are also shown. Note the granular cytoplasm. Mallory, × 540



Figs. 9 and 10

granular nature of the secretory cell cytoplasm, and the secretion droplets in the lumen of the ductules, indicate active secretion.

5. Reproductive Gland

Glands associated with the reproductive system were found only in the females of *R. sternae*. Paired glandular masses, up to 450 μm long, lie ventrally on either side of the intestine and fill the available haemocoel anterior to the commencement of the saccate uterus (Fig. 6). Histologically the cells are distinct from the cells of the other haemocoelic glands being notably less basophilic. Again the structure of this secretory system is remarkably similar to the cephalic, hook, and parietal glands and consists of bi- and tricellular secretory units composed of oval cells measuring 30–70 μm × 70–100 μm, each unit giving rise to a simple efferent ductule. The relatively diffuse nature of this gland is apparent from Fig. 9 which shows clearly the individual ductules meandering through the mass of the gland. The ductules eventually discharge into the oviduct at a point slightly anterior to the insertion of the paired receptacula semini (Fig. 6). Numerous secretory droplets are evident, both in the lumen of the ductules and in the adjacent oviduct lumen.

E. Discussion

The abundance of secretory systems, most composed of large cells suspended in the haemocoel has long been recognised as one of the principal characteristics of the Pentastomida. However the nomenclature associated with the various components of the system is confused mainly because certain major differences in the disposition of some gland systems between the Porocephalida and the Cephalobaenida have been largely unappreciated.

Spencer (1893) from his work on the anatomy of *Waddycephalus teretiusculus* divided the glands into two classes, a scheme later elaborated

Fig. 9. A light micrograph of a transverse section through part of the reproductive gland. Note the bi- and tri-cellular secretory units, the central rays of densely staining material, and the efferent ductules meandering through the mass of the gland. Secretory droplets (arrows) can be observed in the lumen of two of the ductules. Mallory, × 126

Fig. 10. A section through the body of a Porocephalid pentastomid (*Kiricephalus* sp. ?) taken from the mid-region of the body. *D-V* indicates the dorso-ventral axis. Note the cuticle (*c*) and the gut (*g*) and the muscle systems (*m*) associated with the body wall. The mass of the frontal gland (*fg*) with its duct (*fgd*) are plainly visible. Flanking this is the hook gland (*hg*) with paired ducts (*hgd*). Sub-parietal cells (*spc*) are associated with the body wall. Mallory, × 180

by Hett (1924). Basically the glandular systems were divided naturally into two groups depending upon their origin from embryonic germ layers, viz: 1. Epidermal or cuticular glands of ectodermal origin and 2. Haemocoelic glands of mesodermal origin. Hett noted that mesodermal glands had been previously classified according to their position of their ducts, which varied from group to group. Accordingly Hett distinguished the following mesodermal glands on the basis of their position in the body: 1. Head glands, 2. lateral glands and 3. parietal glands.

However, Heymons (1935) formulated what is very nearly the modern scheme of pentastomid classification, and subsequently commented upon differences in gland disposition in the two major pentastomid orders. In the comparatively advanced Porocephalida, Heymons observed two constant and distinct mesodermal glands which discharged either at, or in the immediate vicinity of the frontal papillae, or into the 4 hook pits. He therefore proposed the names frontal and hook glands respectively, [compared to the Hett (1924) scheme: Lateral glands = frontal glands, Head glands = hook glands]. Heymons nomenclature is adopted in this account, for the Porocephalida at least, because in some species glands discharging at the frontal papillae and hooks can both be lateral in position. According to Heymons, the Cephalobaenida did not conveniently fit into this scheme because the individual gland ducts were too small to be traced.

Since then, only Doucet (1965) has made a significant contribution to out understanding of pentastomid gland systems, in particular the sub-parietal (= parietal) cells which he showed were connected to the cuticle by a tenuous efferent canal in 3 pentastomid species (2 Porocephalida and 1 Cephalobaenida).

With respect to the anterior coelomic glands, the frontal and hook glands, the Porocephalida appear to be a fairly uniform group. In *Armillifer armillatus* hook glands are compact and situated anteriorly, whereas frontal glands, with ducts discharging at the frontal papillae, extend laterally down the intestine (von Haffner, 1924; Doucet, 1965). This is also the situation in *Porocephalus clavatus* (Stiles, 1891), *Waddycephalus teretiusculus* (Spencer, 1893) and *Kirricephalus coarctatus* (von Haffner, 1926). In *Linguatula serrata* (Leuckart, 1860), *Sebekia* (Heymons, 1935) and *Alofia ginae* (Gigloli, 1922) both frontal and hook glands flank the intestine for most of its length, but always the frontal glands, containing single, centrally located collecting ducts occupy the more median position (Fig. 10). In the Porocephalida then, these two haemocoelic glands are a constant feature and discharge in the same position in all species.

In the Cephalobaenida, the frontal and hook glands do not conform to this pattern, Firstly, in *Raillietiella mediterranea* and *Cephalobaena tetrapoda* (Heymons, 1935), in *R. boulengeri* Doucet (1965), and in *R.*

sternae it appears that the glands are concentrated anteriorly and rarely make any appreciable lateral extension along the intestine. Secondly, common collecting ducts are unknown in frontal glands, each secretory unit gives rise to an efferent duct which travels singly to the point of discharge. Finally the central part of anterior coelomic gland, the frontal gland, discharges into the buccal capsule in *R. boulengeri* Doucet (1965), and in *R. sternae,* the only two species in which this has been fully investigated. Hook glands invest this gland laterally and probably in all Cephalobaenida pour secretions into the hook pits or hook sacs. Certainly Heymons (1935) observed this in *R. meditteranea* and *Cephalobaena tetrapoda.* According to Doucet (1965), 4 large collecting ducts erupt into the hook bays in *R. meditteranea,* but as far as I can tell these large ducts are absent in *R. sternae* where ductules discharge singly. The primitive condition of the frontal and hook glands, is therefore clearly exemplified by the Cephalobaenida.

Unfortunately there is little indication as to the function of these glands. Lohrmann (1889) suggested a digestive role, whereas Spencer (1893) thought the secretions acted as an anticogulant. However Heymons (1935), and Doucet (1965) observed that in the Porocephalida the frontal glands are exceedingly well developed in nymphal forms but regress significantly in the adults. The obvious inference from this is that frontal gland function is more important in the developmental stages. External secretions could play an important role in nymphs (in contrast to adults) in only two ways: assisting in tissue migration by producing histolytic secretion, in other words developing as a penetration gland, or, alternatively by assisting in moderating or attenuating the host tissue response; these two functions being unique to the nymph which has a more intimate association with the hosts tissue and would therefore provide a much greater antigenic stimulus. Two additional indirect lines of evidence supporting the latter hypothesis came from Doucet (1965), who described acid-mucopolysaccharide and protein in the secretory cell cytoplasm near to the collecting ducts, and from Self and Kuntz (1967) and Self (1972) who noted that nymphal pentastomids elicit remarkably little host tissue response in initial infections, irrespective if their position in the host body. Acid mucopolysaccharide production and parasite antigenicity are related. Antigenic mucopolysaccharide has been extracted from the cyst membranes of *Echinoccocus granulosus*, and this is identical to certain P blood group human antigens (Smyth, 1969). These polysaccharides are a component of cyst membranes and therefore presumably shield the parasite against the immunological responses of the host. A similar function is suggested for the frontal gland secretion in larval pentastomids, which acting externally could "protect" the parasite during the phase of intimate contact with host tissue and later con-

tribute to the formation of cyst membranes. Respiratory cavity-inhabiting adult pentastomes would presumably elicit comparatively little immunogenic host response as only the head and hooks are in permanent physical contact with the host tissue. Hook gland secretions may supplement this activity.

In the Cephalobaenida, frontal gland secretion may perform a different function, but earlier observations on *R. sternae* (Riley, 1972) would indicate that this is probably not concerned with digestion, despite the fact that frontal gland secretions are discharged into the buccal capsule.

Parietal cell function is even more obscure. Doucet (1965) showed that the efferent canals emerging from each parietal cell lobule followed a direct path towards the cuticle to emerge at the neck of cuticular glands in *Armillifer armillatus* and *Raillietiella boulengeri* and at the apices of small conical elevations of the cuticle in *Sebekia wedli*. In *Porocephalus sublifer* the ducts could not be traced, this latter situation being encountered in *R. sternae*. There is the distinct possibility that they could contribute to structural precursors for some epicuticular membrane component, especially if they are considered homologous with the dermal glands of insects. In those species with no external parietal gland cell duct (i.e. *P. sublifer* and *R. sternae*), this suggested function is still a possibility, for they could be regarded as oenocytes and function in the manner described by Wigglesworth (1970), in the blood-sucking bug *Rhodnius*.

Most attention has been focussed on the cuticular glands but again there is little evidence as to their function. That they are secretory in some species is well established; Doucet (1965) demonstrated mucopolysaccharide in the neck of cuticular cells of *A. armillatus*, and Haffner (1924) observed secretory product actually issuing from the gland cells of this species, as did Hett (1924) in several other pentastomids. Apparently then, the secretory product, containing at least mucopolysaccharide may attenuate the host immune response and be involved in cyst wall formation in the intermediate host as suggested by Hoyle (1883), or may perhaps be bacteriostatic. For example, Doucet (1965) observed that the epicuticle of *Sebekia wedli* was ensheathed in a thin layer of mucus which contained numerous bacteria. Cuticular cells in *R. sternae* however, fail to stain positively with P. A. S. or Alcian blue techniques.

Heymons (1935) favoured the notion that cuticular cells regulated the water content of the body cavity by controlling turgor pressure. Doucet (1965), performed simple experiments to test this hypothesis, by plunging living specimens of *R. boulengeri* into 1% neutral red in physiological saline. He found that abdominal cuticular cells and parietal cells stained vitally, but that the anterior specialised cuticular cells, the so-called Cells of Bovien (which incidentally are absent in *R. sternae*), did not. From these observations he concluded that cuticular cells were not in-

volved in maintaining turgescense, but that the Cells of Bovien possibly fulfilled this role. Considering the constant isosmotic environment of the parasite the need for such an extensive system of thus specialised tegumental cells is difficult to imagine. However our ultrastructural observations on the cuticle of *R. sternae* (Riley and Banaja, in prep.) reveal it to be almost identical to insect cuticle in all respects including the moulting process. Furthermore pentastomids can increase in size between 3 and 10 times between each moult [figures computed from the data of Esslinger (1962)]. As the cuticular cells and intestinal epithelium represent the only breaches in anotherwise impermeable cuticle which invests the organisms, the former may well contribute very significantly to the influx of salts and water necessary for the substantial intermoult expansions.

A corollary to another study on this pentastomid (Riley, 1972a) was the presence of broad-spectrum phosphatase activity (activity manifest between pH 5–11) in the neck of these cuticular glands in the region of the fibrils (Fig. 7). Read (1966) noted that there is a correlation between absorption and phosphatase distribution in the epithelia of certain parasites. It appears therefore that cuticular cells may have a cycle of activity, being both secretory and absorptive.

The extensive paired glandular masses pouring secretions into the distal oviduct in *R. sternae* are apparently unique to this species, but again the nature and function of the secretion is unknown. Other pentastomids have small secretory cells associated with the female reproductive system but these are aggregated around the ducts of the receptacula semini (Leuckart, 1860; Spencer, 1893), and are therefore probably concerned with the maintainence of stored spermatozoa. The secretions of the reproductive gland of *R. sternae* possibly from a component of the egg shell as embryos appear well developed in the lower oviduct, but according to Osche (1963) the egg shell is secreted by the blastoderm and the outer mucous capsule by the embryonic dorsal organ.

Clearly, at the present time there are very considerable gaps in our knowledge of pentastomid physiology. If pentastomids are derived from mandibulate arthropods, and more specifically the Myriapoda, as Osche (1963) very convincingly argues, then it should be possible to homologise the secretory systems of the two groups, once the precise functions of the components of pentastomid system are established. Additionally pentastomids have utilized a simple, unique secretory cell type in at least 4 different ways, another feature of this obscure group which merits renewed attention.

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