A REVISION OF THE SUBFAMILY HAPLORCHINAE LOOSS, 1899 (TREMATODA: HETEROPHYIDAE)

II. GENUS *GALACTOSOMUM*†

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CONTENTS

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A taxonomic revision of the genus *Galactosomum* is proposed within the context of a revision of the subfamily Haplorchinae. The interpretation of the ventrogenital complex underlying the present revision is re-stated in phylogenetic terms in order to call attention to the differentiation of ventral sucker and gonotyl, and of genital sinus, genital sac, and ventrogenital sac. It is inferred from the multiplicity of structure in the terminal genitalia of digenetic trematodes in general, and heterophyids in particular, that they are cross fertilizing despite being hermaphroditic. It is also suggested that variations in terminal genitalia may constitute an important mechanical element in isolating mechanisms that separate closely related species. A general discussion is presented of the taxonomic significance of characters of the following; ventral sucker, gonotyl, lateral pocket, musculature of ventrogenital sac, seminal vesicle, prostatic ejaculatory duct, excretory bladder, vitellaria, body shape, egg size, shape of testes, pharynx, course of uterus, and gland cells. The materials of the revision comprise known specimens, published accounts of these, and new specimens collected in Australia and borrowed from overseas. Wherever possible, types were examined; thus, of 13 species redescribed, types were studied of 11 species, and other specimens of the remaining two. An attempt was made to verify published records by recourse to the specimens on which the records were based; although only partially successful, verification of a number of records has allowed more accurate assessment of host-specificity and geographic distribution of some species.

The genus *Galactosomum* Looss, 1899, is emended, the genera *Retevitellus* Cable, Connor & Balling, 1960, and *Galactosomoides* Cable, Connor & Balling, 1960, are reduced to synonymy, and the genera *Cercarioides* Witenberg, 1929, and *Knipowitschiatrema* Isaichikov, 1927, are removed from synonymy. The differentiation of *Galactosomum* from related genera is expressed in the form of a key. The following 19 species, of which five are new, are included. The genotype, *G. lacteum* Jägerskiöld, 1896, is redescribed from syntypes (metacercaria) and compared with adults from the type locality and from Great Britain. *G. angelae* sp.nov., from *Hydroprogne caspia* (type host), *Sterna bergi*, *Sula serrator*, *Eudyptula minor*, and *Larus novaehollandiae*, and as a metacercaria from *Hemirhamphus melanochir*, all from South Australia, is intermediate between *G. bearupi* with one group and *G. fregatae* with two groups of spines on the ventral sucker. *G. bearupi* sp.nov., from *Hydroprogne caspia* (type host), *Anous minutus*, *Sterna fuscata*, *S. bengalensis*, and *Larus novaehollandiae*, and as a metacercaria from *Hyporhamphus* sp., all from Queensland, differs from *G. angelae* in having a smaller, rounded ventral sucker armed with a uniform band of spines. *G. cochleare* (Rudolphi, 1819), orth. emend., is redescribed from three syntypes from *Sterna* sp. and compared with a specimen from Puerto Rico. *G. cochleariformum* (Rudolphi, 1819), orth. emend., is redescribed from one syntype from Brazil and five other specimens from the Caribbean. *G. darbyi* Price, 1934, is redescribed from specimens from *Pelecanus occidentalis* in Florida and compared with the type series. *G. dollfusi* sp.nov. (synonym *G. cochlear* Dollfus & Capron (not Diesing, 1850), 1958) from *Sterna hirundo* in Senegal, is singular in having a sinistral digitiform process on the gonotyl. *G. fregatae* Prudhoe, 1949 (synonyms *G. agrachanensis* Saidov, 1954; *G. canis* Yamaguti, 1954) is redescribed from syntypes, from specimens referred to *G. puffini* Yamaguti, 1941, by Caballero, Grocott & Zerecero (1954), Cable, Connor & Balling (1960), Lumsden & Zischke (1963), and Bravo-Hollis (1967) and to *Galactosomum* sp. by Hutton & Sogandares-Bernal (1960) and from specimens from the domestic dog in Ceylon. *G. humbargari* Park, 1936 (types untraceable) is redescribed from specimens from a variety of hosts, including the following new hosts: *Aechmophorus occidentalis*, *Podiceps grisegena* and *Phalacrocorax auritus*, from a new locality, British Columbia, Canada. *G. johnsoni* Price, 1934, is redescribed from the type series, together with other specimens. *G. phalacrocoracis* Yamaguti, 1939, is redescribed from the type series from Japan, is shown to be distinct from *G. lacteum*, and is recorded from North America for the first time from *Phalacrocorax* sp. in Washington State, U.S.A. *G. puffini* Yamaguti, 1941, is redescribed from the type series, and distinguished from *G. fregatae*. *G. renincola* sp.nov., from the renal ureter and *bursa Fabricii* of *Puffinus pacificus* (type host), *Sterna fuscata*, and *Anous minutus*, in Queensland, is singular in possessing a small, unarmed, asymmetric ventral sucker and a dorsal pit in the forebody. *G. sanaensis* Kobayasi, 1942, is based on a single specimen since lost; it is included tentatively since, as described and figured, it is distinct from those species seen at first hand. *G. sinuilactis* sp.nov. from the *bursa Fabricii* of *Phalacrocorax varius* (type host) in Queensland (type locality) and South Australia, and of *Phalacrocorax fuscescens* in South Australia, and as a metacercaria from *Haletta semifasciata* and *Platycephalus* sp. in South Australia, is closest to *G. renincola*, but has a submedian ventrogenital sac with sinistral pseudosucker, a one-chambered seminal vesicle, and a ventral pit in the forebody. *G. spinetum* (Braun 1901) (synonym *Retevitellus spinetus* (Braun) Cable, Connor & Balling, 1960) is redescribed from syntypes and compared with specimens from Puerto Rico and Florida; a brief description is given of the metacercaria. *G. timondavidi* Pearson & Prévot, 1971, is briefly referred to. *G. ussuriensis* Oshmarin, 1963 (types unobtainable) is redescribed from *Larus novaehollandiae*, *Hydroprogne caspia*, and *Sterna fuscata* in Queensland. *G. yehi* (Dissanaike) n.comb. (synonym *Heterophyopsis yehi* Dissanaike, 1961) is redescribed from the type and other specimens from the domestic dog in Ceylon. Species of *Galactosomum* are assigned to groups according to characters of ventral sucker, seminal vesicle and excretory bladder. Suggested inter-relationships among species and groups are expressed diagrammatically. A key to species is given. A hypothetical description of the mechanics of copulation is attempted on the basis of an interpretation of the functional morphology of the ventrogenital complex, particularly of the complex extrinsic musculature herein

described for the first time. It is suggested that opposition of the gonotyls allows mutual insemination to take place. In those species with non-eversible ventral sucker and without a lateral pocket, each gonotyl is supported by the ventral sucker of the partner; in those species with eversible, or protrusible, ventral sucker and with a lateral pocket, the ventral sucker of one partner is received in the lateral pocket of the other partner, and the gonotyls are opposed without direct support from the ventral suckers. In many species, locking of paired flukes is probably aided by one or more extrinsic hemisphincters. In a summary account of the life-cycle, cercarial types are discussed in *Galactosomum* and related genera, and in opisthorchioids in general. The metacercaria, now known for seven species, attains an advanced stage of development, and can be identified to species on characters of the ventrogenital complex. The host-range and site in the host of the adult is discussed briefly. All of the species are figured, and all but one of the 96 figures are new.

I. Introduction

As originally envisaged, paper II was planned to cover the proposed *Galactosomum* group, comprising the genera *Galactosomum*, *Cercarioides*, *Knipowitschiatrema*, *Stictodora*, *Neostictodora*, *Sobolephya*, *Parastictodora* and *Acanthotrema*. However, this has proved to be so much slower a task than hoped, that it seems expedient not to delay publication further, but to bring out sections as they are completed. Hence II deals solely with the genus *Galactosomum*. It is planned to cover *Cercarioides* and *Knipowitschiatrema* in III, *Stictodora* and *Neostictodora* in IV, and *Acanthotrema* in V.

In despite of clear statements by Cable, Connor & Balling (1960) and Pearson (1964) of their interpretation of the elements of the ventrogenital complex, there is still confusion and inconsistency in the naming of these elements. In part, this may reflect a difference in interpretation, but if so this has not been explicitly stated. One is left with the feeling that it is misinterpretation rather than re-interpretation. In view of this, it appears advisable to recapitulate briefly the interpretation agreed upon by Cable *et al.* (1960) and Pearson (1964). Perhaps the simplest way of doing so is in phylogenetic terms.

Originally, the ventral sucker was on the surface and the common genital pore opened immediately anterior to it (figure 1). Possibly following loss of the cirrus pouch and cirrus, either the ventral sucker or the body wall adjacent to the genital pore, or both, became associated with the genital pore as (accessory) copulatory structures. The muscular copulatory structure formed from the body wall adjacent to the genital pore is the gonotyl. At the same time the ventral surface about the genital pore invaginated, the invagination including the ventral sucker in some cases. If the invagination includes genital pore (and gonotyl) but not ventral sucker, it is termed a genital sac (figure 2). If it includes genital pore (gonotyl), and ventral sucker, it is termed ventrogenital sac (figure 3), and the whole assemblage, sac, pore, gonotyl, and sucker are referred to as the ventrogenital complex. Fusion of ventral sucker and gonotyl into a single organ does not occur in the subfamily Haplorchinae; hence there is no single or compound structure, the ventrogenital complex, combining ventral sucker and gonotyl, as is sometimes stated.

In those lines in which a deep ventrogenital sac was formed such that the ventral sucker could no longer function in attachment (haplorchines, cryptocotylines), the ventral sucker became more and more modified as a copulatory structure, acquiring spines and altering in orientation, shape, and internal structure, but retaining always its discrete muscular capsule and internal nuclei, by which it may always be recognized. In some forms in which the ventral sucker is highly modified, the gonotyl is lost (*Haplorchis*, *Cercarioides*, *Knipowitschiatrema*), but never, it seems, the ventral sucker. Thus, if a single armed structure with a distinct capsule is

found in the ventral invagination, sinistral to the genital pore, then it is the ventral sucker, and not the gonotyl.

Members of the genus *Galactosomum* exhibit a number of stages in the modification of the ventral sucker. A simple, unmodified, symmetric, unarmed ventral sucker is seen in *G. timon-davidi*; a symmetric, armed ventral sucker with dorso-ventral axis of symmetry in *G. bearupi*; progressive alteration in shape (loss of symmetry) and in inclination to left of axis of symmetry in *G. puffini*, *G. angelae*, *G. fregatae* and *G. ussuriensis*; and secondary loss of spines in *G. renincola* and *G. sinuilactis*.

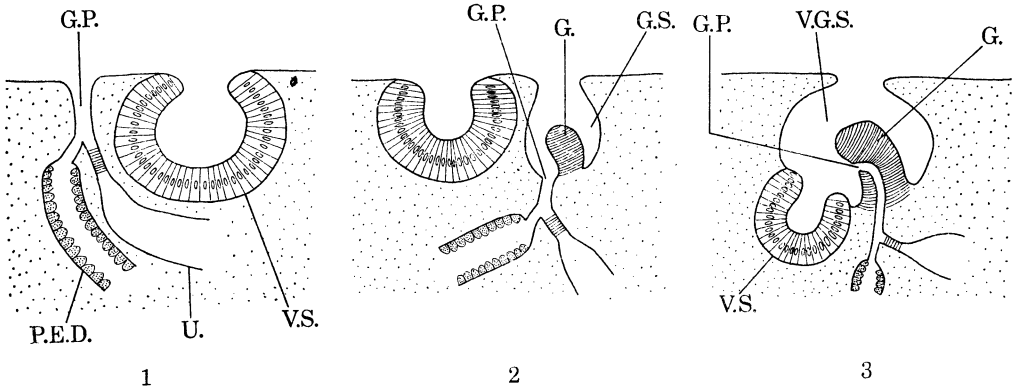


FIGURE 1. Sagittal section of hypothetical proto-heterophyid (anterior on left).

FIGURE 2. Transverse section of genital sac (worm's right on right).

FIGURE 3. Transverse section of ventrogenital sac.

1. Taxonomic characters

Among digeneans there is a multiplicity of structure in the terminal genitalia, especially in the male system. This in itself suggests that, although hermaphroditic, digeneans are cross-fertilizing. This inference is supported by occasional observations of worms *in copula* (Palombi 1932; Rausch 1947; Fernando, personal communication), by the pairing of didymozooids and of *Paragonimus* in cysts, by the clumping of *Alaria arisaemoides*, by permanent pairing in *Opisthovarium* described by Cable *et al.* (1960) and in *Tetracladium* described by Bykhovskaya-Pavlovskaya (1955) and seen by J. C. Pearson (unpublished), and especially by the elegant experimental demonstration of cross-fertilization in *Philophthalmus* by Nollen (1968).

Assuming, then, that haplorchine heterophyids are cross-fertilizing, variations in the form of the ventral sucker, and indeed in the whole of the ventrogenital complex, may well constitute an important mechanical element in isolating mechanisms that function to keep apart closely related species. With this in mind, particular attention is paid to the morphology of the ventrogenital complex of the various species. And as a corollary of this, differences in size, shape, proportions, and disposition of parts – features that vary widely depending on state at and nature of fixation, degree of flattening, etc. – are all considered secondary in importance to characters of the ventrogenital complex.

Features of the ventrogenital complex herein considered to be of taxonomic significance include: (i) form of ventral sucker, whether symmetric or asymmetric, with or without cavity; (ii) inclination of ventral sucker; (iii) spination of ventral sucker, (iv) form of gonotyl, and position of genital pore; (v) presence or absence of lateral pocket in sac; and (vi) musculature of mouth of ventrogenital sac. These features, together with the form of the seminal vesicle and

prostatic ejaculatory duct, the extent of the excretory bladder, distribution of vitellaria, and ratio of oral to ventral sucker, appear to be most specific and least variable, and hence best suited for the differential diagnosis of species.

(*a*) *Ventral sucker*

The ventral sucker may be so modified as to be unrecognizable as such and so misinterpreted as the gonotyl, or genital sucker. But no matter how modified, it may be identified by its discrete muscular capsule and nucleated medulla traversed by radial muscle-fibres (Cable *et al.* 1960; Pearson 1964).

Although the ventral sucker is in all species to some degree asymmetric, as a result of the presence of a laterally placed gonotyl, nevertheless, the degree of asymmetry exhibited beyond that induced by the gonotyl is a useful feature in separating species and in assigning them to groups.

Thus, assuming a radially symmetric ventral sucker of typical form as primitive, one can discern several lines of modification from it. The least modified condition is seen in *bearupi* (figure 18) in which the symmetric ventral sucker is armed with a uniform band of spines. Two different sorts of changes are seen in other members of the genus, namely modification of a part of the ventral sucker leading to an asymmetric condition, as in the *lacteum*-group, and modification of the whole of the sucker leading through bilateral symmetry to asymmetry in the *bearupi*-group.

The distinction between solidly muscular and parenchymatous with respect to the medullary portion is not clear-cut. Instead, there is a gradual increase in the amount of parenchymatous interstitial material with such modification of all or part of the ventral sucker as allows greater mobility, for example, eversion of cavity or protrusion of a modified portion of the rim.

The unmodified condition is seen in *bearupi*, with its symmetric ventral sucker. Slight modification is seen in *angelae*, *fregatae*, and *ussuriensis* in which a ventrally elevated portion of the rim has increased spaces between the radial fibres. The most extensive modification is seen in species such as *lacteum* and *phalacrocoracis* in which parenchymatous elements have increased greatly throughout to allow eversion of the cavity of the sucker.

But despite the gradation it is both convenient and useful for diagnostic purposes to describe the ventral sucker as being either solidly muscular or parenchymatous.

Modification of the ventral sucker allowing either, or both, eversion of the (spiny) cavity or protraction of the modified dextral lip, is accompanied in most cases by outpocketing of the ventrogenital sac sinistral to the gonotyl to form a lateral pocket. A functional interpretation of the relationship between the ventral sucker so modified and the lateral pocket is given below in § IV.

The ventral sucker attains its definitive condition in the metacercaria, and so is taxonomically useful from this stage in development.

(*b*) *Gonotyl*

The synonymous term, genital sucker, first used by Looss (1894) for *Distomum heterophyes* (*Heterophyes heterophyes*) is a doubly unfortunate choice, first because the structure so named is rarely sucker like, except in *Heterophyes* and *Heterophyopsis*, and secondly because its connotation frequently leads to its being applied to the ventral sucker, or even to the ventrogenital sac (Jägerskiöld (1899) for *Distomum lingua* (*Cryptocotyle lingua*)).

In all species examined, the gonotyl is muscular, unarmed, and without nuclei. In contrast, the ventral sucker, no matter how reduced, always contains nuclei. It should, perhaps, be pointed out that this distinction, although so far constant among haplorchines, breaks down in some heterophyids. There are nuclei in the gonotyl in *Heterophyes* (Looss 1894; J. C. Pearson, unpublished).

The bulk of the gonotyl consists of radial muscle-fibres, especially in those species in which the genital atrium enters the gonotyl, for example *angelae* (figure 14). Such an arrangement presumably allows the gonotyl to lengthen without reducing the lumen of the genital atrium.

In most species, the gonotyl is composed of closely packed muscle-fibres, but in one species, *timondavidi*, in which the gonotyl is distinctly bilobed, the muscle fibres are in part loosely packed and irregular.

The relationship of gonotyl and genital pore is variable between species and often difficult to ascertain without sectioning. The genital atrium pierces the muscular root of the gonotyl and may open separate from and dorsal to the gonotyl proper (*bearupi*, *timondavidi*); or on the dorsal (or dextral) face of the gonotyl (most species), often in a groove extending to the free tip (*fregatae*); or it may open ventrally on the tip (*sinuilactis*).

(*c*) *Lateral pocket*

In some species, there is an outpocketing of the wall of the ventrogenital sac sinistral to the gonotyl. It arises near the mouth of the sac and runs dorsad. Dorsally, its cavity is separate from that of the main part of the sac, and would so appear in horizontal section. It is separable, if only in degree, from the condition in such as *humbargari* in which the sinistral wall is folded and apparently expandable, but not separated from that part containing the gonotyl, and from *sinuilactis* in which the sinistral wall is a muscular cup (pseudosucker) but not an outpocketing separate from the sac proper. As pointed out below in § IV, it is thought that the lateral pocket receives the everted or protracted apex of the ventral sucker of the partner during copulation.

(*d*) *Musculature of ventrogenital sac*

In many species it could be seen that the ventrogenital sac possessed a specialized musculature. In favourable material, examination of wholemounts and sections revealed a complex array of bands and groups of fibres (§ III, *angelae*), and in less favourable material at least some of the more prominent elements could be distinguished. Such of the musculature as could be seen is described, as it manifested specific differences among the species.

In specimens of some species (*lacteum*, *puffini*, *darbyi*) no elements of the musculature could be seen, but in the others (except *sanaensis* which was not available) in which at least part of the musculature could be seen, a consistent element, present in all species except *phalacrocoracis*, *cochleare* and *ussuriensis*, is a band of fibres arising from or near the root of the gonotyl posteriorly and partly encircling the sac dextrally. This band, the dextral hemisphincter, so named from its supposed function (§ IV), may be so strongly developed that it appears superficially to be a part of the ventral sucker or gonotyl (*angelae*, figure 16).

(*e*) *Seminal vesicle*

Features of the seminal vesicle common to all of the species examined, include: (i) a muscular papilla projecting into the lumen about the common entrance of the two sperm ducts, and presumably acting as a valve to prevent sperm re-entering the sperm ducts during ejaculation;

(ii) a ring-like fold projecting into the lumen at the entrance into the prostatic ejaculatory duct; and (iii) a distinctly muscular wall fundamentally comprising inner circular and outer longitudinal fibres. In all of the species examined, the seminal vesicle, in whole or, if two-chambered, in part (at least the distal chamber), is an expulsor *sensu* Pearson (1964); it is never entirely thin walled as stated by Pearson (1964) for *humbargari*. In form, it may be undivided, or partly constricted into two parts, or clearly divided into two chambers joined by a discrete, narrow duct. If undivided or constricted, it presents a regular, often distinctive, shape; if two-chambered, at least one of the chambers has a regular shape and an obviously muscular wall (*cochleare*, *spinetum*). In conjunction with the change in form from undivided to constricted or two-chambered, there may be both a change in the relative development of the muscle layers in the two parts and the addition of an external diagonal layer over the posterior (proximal) part. For example, in species with undivided (except *sinuilactis*) or constricted (*bearupi*-group) seminal vesicle, the longer posterior part has an outer layer, often thick, of diagonal fibres, and the shorter anterior part has enlarged circular fibres. The undivided seminal vesicle in *sinuilactis* is unique in having a thick layer of circular fibres and no outer diagonal layer. Species with a two-chambered seminal vesicle fall into two categories, those with both chambers thick walled (*lacteum*, *phalacrocoracis*, *renincola*), and those with anterior chamber thick walled and posterior chamber thin walled (*humbargari*, *cochleare*, *cochleariformum*, *spinetum*).

Comparison of the metacercaria and/or early adult, in which the seminal vesicle is empty, with the mature adult, in which it is filled with sperm, has shown in each case (*lacteum*, *angelae*, *bearupi*, *fregatae*, *sinuilactis*, *spinetum*, *timondavidi* and *ussuriensis*) that the form of the seminal vesicle changes little from metacercaria to adult, although the relative thickness of the wall may change markedly. Thus, the form of the seminal vesicle is a taxonomic character useful for worms of all ages likely to be found in the definitive host.

(*f*) *Prostatic ejaculatory duct*

This, the *pars prostatica*, is typically elongate and tubular or cylindrical, with the outer longitudinal fibres larger and more prominent than the inner circular, and with the lumen lined, or indeed largely occluded by, an epithelioid layer formed by the inbulging, secretion-filled ends of the ducts of the prostatic-gland cells whose nucleated cell-bodies are external to the duct. The wall is exceptional, and so far unique, in *sinuilactis* in having a very thick layer of longitudinal fibres. The prostatic portion is separated from the seminal vesicle by a constriction, and opens into the genital atrium, typically dorsal to the uterus, through a muscular (? hence extensible) papilla that projects into the genital atrium. This papilla, whose function is speculated on in § IV, was described for *lacteum* by Jägerskiöld (1896), for *cochleariformum* and *spinetum* by Cable *et al.* (1960) and confirmed in the present study, in which it was found also in all of the species examined, except *humbargari*, *johnsoni*, *phalacrocoracis*, and *ussuriensis*. In *johnsoni* there is a ring-like projecting shelf at the entrance into the genital atrium which may represent a reduced papilla. In *ussuriensis* the papilla was clearly absent in sections. The absence of the papilla in *humbargari* and *phalacrocoracis* requires confirmation from sections.

A papilla at the end of the ejaculatory duct is apparently unique to the genus *Galactosomum*, although it must be added that few heterophyids have been looked at closely enough to determine the presence of such a structure. Among those that have, and in which a papilla is absent, are *Distomum heterophyes* (*Heterophyes heterophyes*) as described by Looss (1894), *Scaphanocephalus expansus* as described by Jägerskiöld (1904), *Distomum lingua* (*Cryptocotyle lingua*) as described by

Jägerskiöld (1899), and those members of the *Haplorchis* group studied in section by Pearson (1964).

Although apparently unique to *Galactosomum* among heterophyids, a similar papilla is described in the hemiurid, *Sterrhurus concavovesiculus*, by Reid, Coil & Kuntz (1965).

(*g*) *Excretory bladder*

The excretory bladder is tubular, rarely sac-like, and never Y-shaped. In most species, it does not exceed the posterior border of the posterior testis; in a few species (*lacteum*, *phalacrocoracis*, *sanaensis*, *renincola*, and *sinuilactis*) it extends to the anterior border of the anterior testis (*renincola*), to the posterior border of the ovary (*lacteum*, *phalacrocoracis*, *sanaensis*), or beyond the ovary to the level of the ventrogenital sac (*sinuilactis*).

In those species seen in both metacercarial and adult stages, it does not alter significantly in extent (*bearupi*, figures 17, 23; *timondavidi*; *sinuilactis*; *angelae* and *spinetum* figure 67); that is it is not inflated or larger in the metacercaria, as it is in many digeneans. According to Yamaguti (1941) the excretory bladder of *puffini* extends to the ovary, but this could not be confirmed in the type specimens. For reasons given below in the discussion of species groups (§ III 3), it is suggested that the bladder in *puffini* may be short, not exceeding the posterior testis.

The origin of the main (primary) collecting tubules varies, depending in part on the length of the bladder. Thus, it is nearly terminal (figure 23) in species with a short bladder, not exceeding the posterior testis; whereas, in species with a long bladder, the main collecting tubules may arise almost terminally (figure 53), or well behind the anterior end of the bladder. In the light of the phylogeny proposed in § III 3 it is suggested that the short bladder is primitive and the long bladder derived, an interpretation borne out by the difference in origin of the main collecting tubules.

According to Cable *et al.* (1960), the main collecting tubule in *cochleariformum*, *cochleare*, *johnsoni* and *spinetum* runs forward to the level of the pharynx, and in some cases turns posterad, before dividing; that is the system is stenostomate. While it is true that in wholemounts one can sometimes trace a prominent tubule forward to the level of the pharynx before it branches, in living specimens of *bearupi* and in wholemounts of *sinuilactis*, it was clearly seen that the prominent tubule so traced was the anterior collecting tubule and that the main collecting tubule divided, giving rise to anterior and posterior collecting tubules, at or behind the level of the ventrogenital sac; that is, the system is clearly mesostomate.

Although I have been unable to confirm the observations of Cable *et al.* and have not myself seen a stenostomate species of *Galactosomum*, conditions intermediate between stenostomate and mesostomate are described for several heterophyids (e.g. *Cryptocotyle lingua* described by Stunkard (1930); *Rossicotrema donicum*, as described by Hsu (in Rothschild 1938*a*), among haplorchines (*Haplorchis sprenti*, as described by Pearson (1964); *H. parataichui*, *H. pumilio*, *Procerovum varium*, *P. batillans*, and *Stellantchasmus aspinosus*, observed by J. C. Pearson (unpublished)), and more particularly in *Galactosomum* itself (*G. lacteum* as described by Jägerskiöld 1896). Thus, it would appear that the condition of the excretory system may vary between stenostomate and mesostomate within the genus *Galactosomum*. It may be added, however, that there appear to be no heterophyids for which a figure and unequivocal description of the stenostomate condition exist.

(*h*) *Vitellaria*

In favourable material, such as metacercariae (figure 23) and immature or early mature adults (figure 57), in which the entire vitelline system can be traced, it is clearly seen that there is a single, median, typically ventral vitelline duct running posterad from the ootype, and giving off branches to right and left that end in one or more groups of follicles. This pattern was clearly seen in its entirety in *bearupi*, *renincola*, *phalacrocoracis*, *ussuriensis*, and *sinuilactis* and seen in part in *spinetum*, *timondavidi*, *angelae* and *humbargari*. It is, then, common and probably characteristic of the genus *Galactosomum*, and not singular to *spinetum* alone, which Cable *et al.* (1960) made the type of a new genus, *Retevitellus*, which name refers to the arrangement of vitelline ducts.

This pattern, which may be referred to as the I-type, differs from the H-type (occasionally U-type) so widespread among digeneans, and other heterophyid subfamilies (Cryptocotylinae, Heterophyinae) and may prove to be a characteristic of the whole of the subfamily Haplorchinae.

As pointed out by Dubois & Mahon (1959) in their key, in some species the follicles are in obvious rosettes, in others not. But the usefulness of this difference as a taxonomic character disappears when one compares metacercaria, young adult, and old adult, or even adults dead at fixation with those alive at fixation, for it is clear from such comparisons (compare figures 17 and 23) that the vitelline follicles form in rosettes, but that post-mortem changes and old age may so alter the sizes and arrangement of groups of cells that their fundamental disposition in rosettes is obscured.

Even in *humbargari*, in which the follicles are distributed among the coils of the uterus at all levels from dorsal to ventral surface, it can be seen that they are arranged in rosettes albeit highly distorted.

It seems likely that the vitellaria form in rosettes throughout the family, although the evidence is scattered and far from complete (consider *Haplorchis* and *Stellantchasmus* with one rosette (Pearson 1964, Figs. 14, 39); *Procerovum* with one rosette (J. C. Pearson, unpublished); *Heterophyes* with two rosettes (Looss 1894)).

(*i*) *Body shape*

Shape, particularly degree of division into expanded forebody and cylindrical hindbody, has been used by such as Witenberg (1929) as a taxonomic character. Cable *et al.* (1960), in rejecting Witenberg's genus *Cercarioides*, pointed out that among the species studied by them, there is a series of forms ranging from those, like *Cercarioides*, with expanded forebody to those with little or no differentiation between forebody and hindbody. Nevertheless, it does appear that shape is in some degree useful in characterizing species (cf. figures 77–81, 84, 85, 88, 90–93 of unflattened specimens), bearing in mind the mobility of the forebody and consequent variations in its form at death or fixation, and the gross widening of the thicker hindbody that may result from the unfortunate practice of flattening specimens.

When examined alive and *in situ*, the body, especially the forebody, is strongly flattened against the mucosa, but when fixed, it rounds up as the circular muscle-fibres contract more strongly than the dorso-ventral muscle-fibres. As Linton (1928) pointed out, the forebody appears to act as an additional organ of adhesion.

A peculiar feature of some species, best seen in unflattened specimens, is a pit, or depression,

in the forebody, produced by a group of better developed dorso-ventral muscle-fibres. Thus, in *G. renincola* there is a large dorsal pit, anterior to the level of the ventrogenital sac. In *G. sinuilactis*, there is a small ventral pit posterior to the bifurcation of the caeca. The differing positions of the pit in the two species makes an interpretation of function difficult, although it may be suggested that the ventral pit in *sinuilactis* may aid in attachment to the mucosa.

(*j*) *Egg size*

In a soft-bodied, variable, and easily distorted animal such as a digenean, any hard parts are seized upon for measurement, and their size used as a taxonomic character in discriminating between species. Although egg size is undoubtedly useful, caution must be applied unless the difference between two species is large. It is not enough to find that the averages differ, or even that the ranges do not overlap, unless all of the measurements were made by a single person, such is the variation possible between two workers (see *fregatae*).

(*k*) *Shape of testes*

Shape of testes, whether lobed or entire, has been employed taxonomically, but the difference is valid only for unflattened specimens. As in other digeneans, if a *Galactosomum* is flattened strongly, the testes may be squeezed between the scattered dorso-ventral muscle-fibres producing lobes artificially. In only one species, *spinetum*, are the testes distinctly lobed in unflattened specimens, and even here it would appear that the lobing, although natural, is produced in the same way. The body of *spinetum* is flattened throughout its length and related to this, has many more and better developed dorso-ventral fibres in the hindbody. Thus, when the small testes of the metacercaria enlarge in the developing adult, they are forced into lobes by the abundant dorso-ventral fibres, which in the adult can be seen in the indentations between lobes.

Conversely, lobed testes seen in flukes fixed alive may disappear in worms dead when fixed, presumably following relaxation of the dorso-ventral fibres.

(*l*) *Pharynx*

Among digeneans in general, and heterophyids in particular, the relative lengths of pharynx and prepharynx, have been used as specific characters, without inquiring into the functional relation between the two.

On examining numerous specimens of several species of *Galactosomum*, it was evident that the length of the prepharynx, and hence the relative lengths of prepharynx and pharynx, was affected not only by the degree of extension of the mobile forebody at death, but more importantly by the point reached in the act of ingestion. A series of conditions (figures 24*a–c*) were seen in *bearupi* which suggest that, contrary to the usual interpretation of the pharynx as a stationary pump, its method of functioning more nearly resembles that of the ancestral neorhabdocoel. In brief, from the condition at rest (figure 24*a*), the pharynx moves forward within the prepharynx (figure 24*b*), until it reaches (figure 24*c*) or even half enters the cavity of the oral sucker, and then returns to the resting position. That in the process, the pharynx engulfs material from the cavity of the oral sucker and carries it back and discharges it into the caeca has been observed *in vitro* by Howell (1970) in *Philophthalmus burrili*.

The morphology of pharynx and prepharynx that allow this are as follows. At its junction with the pharynx, the wall of the prepharynx is thrown into a fornix-like fold (the anterior

valves of Cable *et al.* (1960), which is, however, absent or incised ventrally (figure 53), so that on entering the oral sucker posterodorsally, the mouth of the pharynx opens antero-ventrally, directly into the cavity of the oral sucker. The pharynx is moved forward by protractor fibres that run from the oral sucker, about the entrance of the prepharynx, back external to the prepharynx to the pharynx itself, where they are inserted on the first part of the posterior half. In at least one species (*angelae*) the protractors exceed the pharynx and are inserted on the first part of the caeca dorsally and ventrally (figure 24*c*). Arising laterally, posterior to the protractors, are the retractors, which fan out posteriorly, passing dorsal to the caeca.

(*m*) *Course of uterus*

The uterus in *Galactosomum*, as in many heterophyids, forms a single posterior loop, comprising descending and ascending arms variously looped and coiled. Typically, both arms follow the same course in the region of the gonads, usually with the descending arm ventral to the ascending, between ovary and anterior testis, to right of anterior testis and to left of posterior testis. Behind the posterior testis, the descending arm is dextral and the ascending sinistral. Anteriorly, the ascending arm loops ventrally across the seminal vesicle before entering the genital atrium ventral to the male duct.

Variation within species, other than that induced by the number of eggs contained, affects principally the course of the arms past the testes. The descending arm may pass the posterior testis dextrally, and more rarely, the ascending arm may pass the anterior testis sinistrally.

There may also be variation between metacercaria and adult in the same species. This is suggested by the observation that in the metacercaria of *bearupi* the descending arm invariably passes dextral to the posterior testis, whereas in the adult, it invariably passes sinistral to the posterior testis. It would seem that as the uterus lengthens and fills with eggs, it is thrown around the posterior testis in a loop. If dorso-ventral muscle-fibres are abundant in the region, this loop may not be formed (consider *spinetum*, *q.v.*).

Variations between species, of minor taxonomic significance, include (i) more than one loop over the seminal vesicle (*angelae*, *cochleare*, *cochleariformum* and *humbargari*); (ii) tight, short loops in both arms post-testicularly so that the uterus is confined intercaecally (*ussuriensis*); (iii) wandering loops obscuring the caeca and largely filling the hindbody (*timondavidi*); (iv) extension anterior to the ventrogenital sac (*spinetum*); and (v) a pair of terminal masses formed by tight coils of the two arms (*cochleare*).

(*n*) *Gland cells*

A variety of gland cells has been described for various heterophyids, and although probably of minor taxonomic significance (except in odd cases, e.g. *renincola*) and not known for all species, it is perhaps worth commenting on these gland cells, both to call attention to their occurrence, and to forestall their use as taxonomic characters until they are better known in more species.

The various unicellular gland cells may be divided arbitrarily into those that open into the digestive tract, and those that open to the outside through the tegument. The former group comprises: (i) gland cells lateral to the prepharynx that open at the junction of prepharynx and oral sucker – the prepharyngeal glands; and (ii) gland cells lateral to the oesophagus that open at the pharyngo-oesophageal junction – the oesophageal glands. The latter group comprise (1) scattered, single gland cells that open through the tegument of the forebody,

especially ventrally – the tegumental, or skin, glands, and (2) one or more (paired) groups of gland cells with long ducts that open pre-orally in a transverse series in an invariably unspined apical area – the frontal glands.

Most, or all, of these gland-cell types are probably common to all heterophyids – indeed, to many groups of digeneans – and the paucity of references to them is probably a reflection of the interest of the investigator and their obscurity in badly fixed material.

Among heterophyids, prepharyngeal and oesophageal glands have not been described often (see Looss (1894) on *Distomum fraternum* (*Heterophyes fraternum*); *Galactosomum renincola*, this paper). On the other hand, frontal and especially tegumental glands, which are both larger and more conspicuous, have been described more frequently.

Frontal glands occur in many digeneans, especially among opisthorchoids and plagiorchoids. Casual observation of a number of species suggests that in both superfamilies the ducts form two bundles on each side, one lateral and one submedian.

In *Galactosomum*, frontal glands have been described in *G. lacteum* by Jägerskiöld (1896) in *G. timondavidi* by Pearson & Prévot (1971), and in *G. puffini* by Yamaguti (1941), who appears to have confused the ducts from these glands with the retractor fibres of the pharynx, and are described below in *G. angelae*, *G. bearupi*, *G. dollfusi*, *G. fregatae*, *G. humbargari*, *G. johnsoni*, *G. puffini*, *G. renincola* and *G. ussuriensis*. Of the other species examined, only in *G. sinuilactis* did it appear that frontal glands were absent, rather than inapparent.

In most species of *Galactosomum*, the cell-bodies form a single mass, largely intercaecal; in *G. renincola* they form four groups anterior to the caeca.

Although little is known of their function (Halton 1967) it would seem from their variable appearance in wholemounts that their activity may change with time. In this regard, it may be noted that in sections of an adult *ussuriensis*, it was observed that very few frontal-gland cells contained secretory granules.

II. Materials and methods

The methods employed did not differ from those described earlier (Pearson 1964).

As will be clear from the accounts of species given below, I am indebted to many sources for much of the material examined. Wherever possible recourse was had to types (holotypes, paratypes, or syntypes) and I have been indeed fortunate in having been able to study types of one sort or another of 10 of the 13 species redescribed herein.

In addition to redescribing known species and describing as new five species, I have attempted, with varying success, to verify all published records of the various species, in the first instance by examining the specimens in question, and failing this, by a comparison of description and figures with known specimens in hand. In the absence of specimens, or of adequate descriptions and figures, it is not possible to verify published records. Unverified citations in the following synonymies are marked with an asterisk.

In the lists of 'specimens examined', author's name and date in brackets refer to publication on the same specimens.

1. List of collections

Berlin	Zoologisches Museum, Humboldt Universität, Berlin, D.D.R.
B.M.(N.H.)	British Museum (Natural History), London, England
Coll. Cable	Professor R. M. Cable, Department of Biological Sciences, Purdue University, Lafayette, Indiana, U.S.A.

Coll. Ching	Dr H. L. Ching, Department of Zoology, University of British Columbia, Vancouver, Canada
Colombo	Department of Parasitology, University of Ceylon, Colombo, Ceylon
Coll. Dubois	Dr G. Dubois, Grand Rue 12, Neuchâtel, Switzerland
Coll. Jensen	Dr D. N. Jensen, Department of Biology, McMaster University, Hamilton, Canada
Coll. Johnston	T. H. Johnston Helminth Collection, Fisher Laboratories, University of Adelaide, Adelaide, S.A., Australia
Leningrad	Zoological Institute, Academy of Sciences, Leningrad, U.S.S.R.
Lille	Chaire de Zoologie et Parasitologie, Faculté de Medecine et de Pharmacie, Lille, France
Marseille	Faculté des Sciences, Marseille, France
Mexico	Instituto de Biologia, Universidad Nacional Autonoma de México, México
Moscow	Helminthological Laboratory, Academy of Sciences, Moscow, U.S.S.R.
M.P.M.	Meguro Parasitological Museum, Tokyo, Japan
Neuchâtel	Institut de Zoologie, Universite-Mail, Neuchâtel, Switzerland
Coll. Olson	Professor A. C. Olson, San Diego State College, San Diego, California, U.S.A.
Coll. Rao	Dr B. V. Rao, Indian Veterinary Research Institute, Izatnagar, U.P., India
Rice University	Department of Biology, Rice University, Houston, Texas, U.S.A.
S.A.M.	South Australian Museum, Adelaide, S.A., Australia
Coll. Sogandares-Bernal	Professor F. Sogandares-Bernal, Department of Zoology, University of Montana, Missoula, Montana 59801, U.S.A.
S.P.H.T.M.	School of Public Health and Tropical Medicine, University of Sydney, Sydney, Australia
Uppsala	Zoologiska Institutionen, Uppsala, Sweden
U.S.N.M.	United States National Museum Helminth Collection, U.S.D.A., Beltsville, Md., U.S.A.
Vienna	Naturhistorisches Museum, Wien, Austria
Coll. Williams	Dr I. C. Williams, Department of Zoology, The University, Hull, England

III. Taxonomy

1. The genus *Galactosomum*

(*a*) *Synonyms*

Galactosomum Looss, 1899 (t.o.d., *Monostomum lacteum* Jägerskiöld); Price, 1932 (*Stictodora* possibly a syn.); Yamaguti, 1939 (diagn. emend.); Price, 1940 (*Stictodora* valid); Prudhoe, 1949 (diagn. emend.; syn.; descr. spp.; key); Morozov, 1952 (descr. spp.; key); Witenberg, 1953 (syn.; key); Dubois & Mahon, 1959 (key); Cable, Connor & Balling, 1960 (diagn. emend.).

Microlistrum Braun, 1901 (t.o.d., *Distoma cochleariforme* Rudolphi); Odhner, 1910 (possible syn. of *Galactosomum*); Witenberg, 1929 (validity upheld); Price, 1940 (syn. of *Galactosomum*); Witenberg, 1953 (invalid).

Retevitellus Cable, Connor & Balling, 1960 (t.o.d., *Microlistrum spinetum* Braun) new syn.

Galactosomoides Cable, Connor & Balling, 1960 (t.o.d., *G. johnsoni* Price) new syn.

non Cercarioides Witenberg, 1929.

non Tubanguia Srivastava, 1935.

non Knipowitschiatrema Isaichikov, 1927.

As Price (1932) has pointed out, Pratt (1911) in effect synonymized *Microlistrum* with *Galactosomum* when he transferred *cochleariforme*, the type of *Microlistrum*, to *Galactosomum*; but Price (1932) appears to be the first to have formally proposed the synonymy. The type, *cochleariforme*, of *Microlistrum* agrees in all points with the diagnosis of *Galactosomum* given below.

Of the features listed by Cable *et al.* (1960) wherein *Retevitellus* differs from *Galactosomum*, the most significant are the conspicuous network of vitelline ducts and the extension of seminal vesicle and uterus anterior to the ventrogenital sac. The first of these is not valid, as has been pointed out in the section on specific characters above. The second character loses its significance in the light of *G. renincola* (*q.v.*) in which the seminal vesicle, although not the uterus, overlaps the ventrogenital sac. With these two characters invalidated, those remaining, namely shape, posterior extent of vitellaria, and lobed testes, are not together enough to warrant a separate genus.

Although Cable *et al.* (1960) reduce *Knipowitchetrema* (*sic*!) to synonymy with *Galactosomum* and are apparently the first to consider the two genera comparatively, they do not advance any argument for so doing. In his original diagnosis, Isaichikov (1927) did not compare his new genus *Knipowitschiatrema* specifically with any other, nor did he suggest its affinities; indeed, he simply stated that it differed from all known genera of heterophyids in a number of features, which he listed. Price (1940) was apparently the first to place the genus, although in assigning it to the subfamily Heterophyinae, he quotes Yamaguti (1939), who, however, did not so assign it except by implication in comparing his new genus *Pseudoheterophyes* with it and with *Heterophyes*. Morozov (1950) assigned *Knipowitschiatrema* to his new family, the Galactosomatidae, an assemblage roughly equivalent to the present *Galactosomum* group; but he put it in a separate subfamily, the Knipowitschiatrematinae, erected on supposed differences in the ventrogenital complex.

Timon-David (1955) described a second species, *echinatum*, but examination of some of his specimens, and comparison of these with Isaichikov's description of *nicolai* suggests that the two are synonymous. While admitting to the uncertainty inherent in a decision made without reference to the type specimens, and neither these nor other specimens of *nicolai* were obtainable from Russia, Timon-David's *echinatum* agrees closely with Isaichikov's full, if in part inaccurate, description. On the assumption that *echinatum* is *nicolai*, the genus *Knipowitschiatrema* is considered valid as *echinatum* lacks a gonotyl, thus differing significantly from *Galactosomum*.

The genus *Cercarioides*, proposed by Witenberg (1929) for his new species, *aharonii*, based on a single specimen, and added to by Gohar (1930), who described *baylisi* from a single specimen, was early considered to be a synonym of *Galactosomum* by Price (1932), and later by Prudhoe (1949). Subsequently, Morozov (1952) and Witenberg (1953) revived it and the latter added *G. cochleariforme* as a third species, but later authors (Yamaguti 1958; Dubois & Mahon 1959; Cable *et al.* 1960) suppressed it as a synonym of *Galactosomum*. Deblock (1966) assigned a new species, *gonacanthodes*, based on four specimens, to the genus *Cercarioides*, at the same time point-

ing out the uncertainty surrounding the validity of the genus. Study of well-fixed specimens, collected in Australia, of a species close to *aharonii*, has revealed that a gonotyl is lacking, and that the ventral sucker differs distinctly in its spination from all species of *Galactosomum*. These characters, together with others to be discussed in a future paper, are here considered to be of generic importance.

Price (1940), Prudhoe (1949), and Witenberg (1953) list *Tubanguia* Srivastava, 1935, as a synonym of *Galactosomum*, but as the single type specimen of *anguillarum*, the sole species, has been destroyed (C. C. Velasquez, personal communication) and Tubangui's (1933) description is incomplete, the position of the genus cannot be decided.

(*b*) *Diagnosis*

Galactosomum Looss, emended

Body elongate or oval, divided or not by constriction, forebody expanded or not; armed with scales (becoming spines posteriorly) or spines to or almost to posterior end. Oral sucker variable in size; prepharynx variable; oesophagus short, caeca straight or sinuous. Ventrogenital sac median or submedian, a variable distance behind caecal bifurcation; with or without lateral pocket; contains ventral sucker on right and gonotyl on left. Ventral sucker variable in size, smaller or larger than oral sucker; armed with numerous minute (< 12 μm) spines or unarmed; symmetric and sucker like, or asymmetric. Gonotyl simple, lobed or divided; unarmed, without nuclei; separate from or attached (in part) to ventral sucker. Genital atrium short; opens at base of gonotyl, or on dorsal or ventral face of gonotyl. Prostatic ejaculatory duct variable in length and thickness of wall; lumen lined by conspicuous or inconspicuous ends of prostatic-gland cells; opens into genital atrium directly or via a papilla. Seminal vesicle muscular, one- or two-chambered. Testes entire or lobed; diagonal or tandem. Seminal receptacle posterior or anterior to ovary. Uterus with one primary loop comprising descending and ascending arms. Eggs symmetric or asymmetric. Excretory bladder tubular; long (exceeds anterior testis or ovary) or short(extends to, or almost to, posterior testis).

GENOTYPE. *Monostomum lacteum* Jägerskiöld, 1896.

SPECIES INCLUDED. Those listed in §III 2.

The essential differences between this diagnosis and that given recently by Cable *et al.* (1960) are: (i) the shape of the body is more variable; (ii) the prepharynx is more variable and may be longer or shorter than the pharynx; (iii) the ventrogenital sac may be either median or submedian; (iv) the ventral sucker may be unarmed; (v) the lateral pocket ('pouch-like folds' of Cable *et al.*) may be absent; (vi) the seminal receptacle may be either posterior or anterior to the ovary; (vii) both seminal vesicle and uterus may extend anterior to ventrogenital sac; and (viii) the eggs may be symmetric or asymmetric.

Perhaps the simplest way to point out the differences between *Galactosomum* and other genera in the group is by means of a key. A disadvantage of this method, but possibly a minor one, is that it anticipates decisions on several genera which are not to be dealt with in detail until a future paper.

(*c*) *Key to genera*

(1) Gonotyl present. 4
Gonotyl absent. 2

(2) Genital atrium long; oesophagus ≈ prepharynx *Neostictodora*
Genital atrium short; oesophagus ≪ prepharynx. 3

(3) Ventral sucker unarmed; lip of ventrogenital sac thickened; body not divided; seminal vesicle one-chambered; excretory bladder extends to posterior testis. *Knipowitschiatrema*

Ventral sucker armed with three spined knobs; lip of sac unmodified; body divided into wide forebody overlapping ventrally narrow hindbody; seminal vesicle two-chambered; excretory bladder very short, post-caecal. *Cercarioides*

(4) Ventral sucker armed with more than 200 minute spines (< 12 μm), or unarmed; seminal vesicle one- or two-chambered, of which one or both are muscular; excretory bladder tubular. *Galactosomum*

Ventral sucker armed with less than 150 large spines (> 12 μm) or with sclerotizations; seminal vesicle two- or three-chambered, always thin walled; excretory bladder Y, V, or sac shaped. 5

(5) Ventral sucker armed with fewer than 12 spines or sclerotizations; seminal vesicle two-chambered; prostatic bulb absent. *Acanthotrema*

Ventral sucker armed with more than 12 spines; seminal vesicle three-chambered; prostatic bulb present. *Stictodora*

New observations and interpretations alluded to above necessitate the following emendations (1–3) and additions (4, 5) to the diagnosis of the subfamily Haplorchinae given by Pearson (1964):

(1) The ventral sucker may be unarmed also in *Galactosomum.*
(2) Either or both gonotyl and lateral pocket may be absent.
(3) The excretory bladder may extend anterior to the ovary.
(4) A circumoral row of enlarged spines is absent.
(5) The wall of the ventrogenital sac may be armed or unarmed.

(i) *Species indeterminata*

Galactosomum sp. (Gvozdev)

Syn. *Stictodora sawakinensis* Gvozdev (not Looss, 1899), 1962, Fig. 5, p. 98 (*Sterna hirundo* L.; Kazakhstan, U.S.S.R.; no descr.).

It is clear from Gvozdev's figure that this species is not in *Stictodora* but in *Galactosomum*; further, from the form of the seminal vesicle and the relative sizes of oral and ventral suckers, it appears to be close to *fregatae.*

Galactosomum sp. (Bykhovskaya–Pavlovskaya)

Syn. *Stictodora sowakinensis* (*sic*!) Bykhovskaya–Pavlovskaya, 1954, Fig. 16 (ex *Sterna hirundo* L.; western Siberia; descr.).

It would appear from the figure, which shows a thick-walled seminal vesicle and outstretched gonads, that this form belongs in *Galactosomum.*

(ii) *Species excluded from* Galactosomum

Galactosomum tuvensis Sergeeva & Krasnolobova, 1963, Fig. 1 (*Sterna hirundo* L.; Tuva, U.S.S.R.; descr.).

It is clear from the figure, which shows an H-shaped gut, posterior gonads, and pre-ovarian uterus, that this form belongs in or near the genus *Tetracladium* Kulachkova, 1954. Sudarikov (personal communication) says Sergeeva and Krasnolobova have told him that this species does not belong to the family Heterophyidae, but to my knowledge this opinion has not been published.

(iii) *Taxonomic status of specific names in* Galactosomum

Galactosomum sp. Bykhovskaya–Pavlovskaya, 1955.

Cf. *ussuriensis* Oshmarin, 1963 (*q.v.*).

Galactosomum sp. Hutton & Sogandares-Bernal, 1960.

Syn. of *fregatae* Prudhoe, 1949 (*q.v.*).

agrachanensis Saidov, 1954.
Syn. of *fregatae* Prudhoe, 1949 (*q.v.*).
aharonii (Witenberg, 1929) Price, 1932.
Syn. of *Cercarioides aharonii* Witenberg, 1929.
anguillarum (Tubangui, 1933) Tubangui & Africa, 1939. (*spec. indet.*)
baylisi (Gohar, 1930) Price, 1932.
Syn. of *Cercarioides baylisi* Gohar, 1930.
canis Yamaguti, 1954.
Syn. of *fregatae* Prudhoe, 1949 (*q.v.*).
cochlear (Diesing, 1850) Travassos, 1929 (valid).
cochleariforme (Rudolphi, 1819, *sensu* Diesing, 1850) Pratt, 1911 (valid).
darbyi Price, 1934 (valid).
erinaceum (Poirier, 1886) Bittner & Sprehn, 1928 (*spec. indet.*).
fregatae Prudhoe, 1949 (valid).
humbargari Park, 1936 (valid).
johnsoni Price, 1934 (valid).
lacteum (Jägerskiöld, 1896) Looss, 1899 (valid).
phalacrocoracis Yamaguti, 1939 (valid).
puffini Yamaguti, 1941 (valid).
sanaensis Kobayasi, 1941 (*nomen dubium*).
semifuscum (Olsson, 1876) Price, 1934 (*spec. indet.*).
spinetum (Braun, 1901) Travassos, 1929 (valid).
tuvensis Sergeeva & Krasnolobova, 1963 in or near *Tetracladium* Kulachkova, 1954.
ussuriensis Oshmarin, 1963 (valid).

2. Description of species

(*a*) *Galactosomum lacteum*

Synonyms

Monostomum lacteum Jägerskiöld, 1896, Text-fig., Pl. 9, Figs 1–9. (*Cottus scorpius* Bloch; Kristineberg, Sweden; metacercaria, syntypes Zoological Institute, Uppsala, Sweden).

Galactosomum lacteum (Jägerskiöld) Looss, 1899; Jägerskiöld, 1908 (*Phalacrocorax carbo* (L.); Sweden; descr. adult); *Nicoll, 1915 (*Cottus bubalis* Euphrasen; Scotland; metacercaria); *Westblad, 1922 (*Cottus scorpius* Bloch; Sweden; metacercaria); *Lewis, 1927 (*Phalacrocorax carbo* (L.); Wales); *Vlasenko, 1931, Fig. 26 (*Smaris chriselis, Onos tricirrhata, Blennius* sp.; Black Sea, U.S.S.R.; descr.; metacercaria); Baylis, 1939 (*Ardea cineria* L., *Phalacrocorax aristotelis* (L.); Great Britain); *Chulkova, 1939 (*Gadus merlangus, Acipenser sturio, Bothus maeoticus, Trachinus draco, Trachurus trachurus, Uranoscopus scaber*; Batum, U.S.S.R.; metacercaria, muscle); *Osmanov, 1940 (*Bothus maeoticus, Uranoscopus scaber, Onos tricirrata, Smaris chriselis, Scorpena porcus; metacercaria*); Prudhoe, 1949, Figs. 1, 2 (redescr. of Jägerskiöld's (1908) specimens from *Phalacrocorax carbo*, and Baylis's (1939) specimens from *Phalacrocorax aristotelis*); Dollfus, 1951, Figs. 23, 24 (*Phalacrocorax carbo maroccanus*; Morocco; descr.); *Shul'man, 1954 (*Acipenser sturio*, U.S.S.R.; metacercaria); *Pogorel'tseva, 1957 (*Trachurus trachurus*; U.S.S.R.; metacercaria); *Leonov, 1958 (*Sterna hirundo* L., *Hydroprogne tschegrava*; Black Sea, U.S.S.R.); *Leonov, 1960 (*Ardea cineria* L.; U.S.S.R.);

*Kostina, 1961, Fig. 1 (*Spicara smaris* (L.); Black Sea, U.S.S.R.; descr.); Smogorzhevskaya, 1961, Fig. 3 (*Phalacrocorax aristotelis* (L.); Caspian Sea, U.S.S.R.; descr.); Williams, 1961 (*Phalacrocorax aristotelis* (L.), *Phalacrocorax carbo* (L.); Great Britain); *Nikolaeva, 1963 (*Spicara smaris* (L.); Black Sea, U.S.S.R.).

As can be seen below in the list of material examined, only a few of the many references to *lacteum* could be verified by recourse to the actual specimens. In some cases neither description nor figure is given, and even in those references with description or figure, except that of Dollfus (1951), it is not possible to decide what species was found, particularly in the case of metacercariae.

A further difficulty concerns the site of the metacercaria in the fish host. Jägerskiöld (1896) found the metacercaria on the brain of *Cottus scorpius*, as did Westblad (1922) later. Similarly, Nicoll (1915) found it on the brain of *C. bubalis*. On the other hand, Vlasenko (1931) records it from the muscle of the branchial chamber in *Smaris chriselis*, and from the peritoneum in *Onos tricirrhata* and *Blennius* sp., and Chulkova (1939) records it from the muscles of six species of fish. Although the extent of variation in location within the fish host is not known for any species of *Galactosomum*, it would appear unlikely that a single species would localize on the brain in one genus of host, but in the muscles or on the peritoneum in other genera.

This is to suggest that records, especially of metacercariae, cannot be verified, in the absence of specimens, unless the ventrogenital complex is described in considerable detail.

Description (*figures* 4, 5, 75)

Jägerskiöld's (1896) description of the metacercaria is both accurate, as far as can be judged from fixed material, and full, particularly in regard to the excretory and reproductive systems; however, his terminology of the ventrogenital complex is confusing. The original description was based on living material, wholemounts, and sections, but the drawings (Text-fig., p. 11, and Fig. 4, pl. 9) were apparently made from living and flattened specimens. Also, the type material now in existence comprises unmounted metacercariae, labelled cotypes. For these reasons, types (lectotype and five paralectotypes) have been selected and are described and figured below. The lectotype selected (figure 1), although lacking the anterior end and oral sucker, shows most clearly, of the six syntypes available, the diagnostic features of the ventrogenital complex. The range in measurements is given of the types.

With the characters of the genus. Body elongate, of even width; 1600–1740 μm long and 314–450 μm wide; forebody concave ventrally, covered in scales anteriorly becoming spines about level of ventrogenital sac, and extending to posterior end. Numerous cell bodies of frontal glands between level of bifurcation of gut and just anterior to ventrogenital sac; most numerous intercaecally, but extend laterally both dorsal and ventral to the caeca; ducts and openings not seen.

Oral sucker, subterminal, large; 121–185 μm long and 153–169 μm wide. Prepharynx 130 μm long. Pharynx 82–113 μm long and 32–60 μm wide. Oesophagus short or absent. Caeca inflated, extend almost to posterior end.

Ventrogenital sac small, 320–380 μm behind bifurcation of gut, and a little in front of middle of body; largely filled by apex of ventral sucker and gonotyl; with sinistral lateral pocket arising ventral to gonotyl; opens in mid-line by inconspicuous pore; musculature obscure, but includes dextral hemisphincter and group of fibres from base of gonotyl to posterior margin of mouth. Ventral sucker parenchymatous with axis inclined to left; 101–115 μm long and 65–83 μm wide; markedly smaller than oral sucker, ratio o.s./v.s. (widths) 1.8–2.4 in paralecto-

types; cavity reduced to a ventral groove, lined with spines, overhung by enlarged, dextral, solidly muscular lip bearing spines ventrally and medially, continuous with spines lining cavity; spines in cavity 4.5–5 μm long, in adult (Williams), longer than spines on lip. Gonotyl unarmed, solidly muscular, ellipsoidal, 33–50 μm long and 50–63 μm wide; arises postero-dextrally; base pierced by genital atrium, genital pore opens medially at base of dorsal groove. Genital atrium short, formed by union of short ejaculatory duct and terminal muscular portion of uterus; terminal papilla on ejaculatory duct not seen.

Testes slightly diagonal, with anterior sinistral and posterior dextral; anterior 161–250 μm long and 97–110 μm wide, posterior 177–270 μm long and 121–185 μm wide; seminal vesicle two-chambered, equally thick-walled, both with outer layer of diagonal fibres, formed by union of separate sperm ducts; proximal part 65–79 μm long and 29–36 μm wide, smaller than distal part 76–130 μm long and 29–50 μm wide; prostatic ejaculatory duct short.

Ovary submedian, on right, immediately behind seminal vesicle; 89–145 μm long and 89–121 μm wide. Seminal receptacle small and empty, postero-dorsal to ovary. Vitellaria in rosettes; extend anteriorly to or just beyond posterior border of ovary, posteriorly exceed caeca; lateral anterior to posterior border of posterior testis, but posterior to this extend to or almost to mid-line both dorsally and ventrally.

Excretory bladder tubular, extends forward between testes to posterior border of ovary.

Host. *Cottus scorpius* Bloch.

Location. Encysted on surface of brain.

Locality. Kristineberg, Sweden.

Types. U.S.N.M. lectotype 72068, paralectotype 72069; B.M.(N.H.) paralectotype no. 1972.1.24.9.10; Uppsala, cotypes in spirit.

Remarks. The course of the uterus, which cannot be made out with certainty in the lectotypes, is included below from Jägerskiöld's (1896) account.

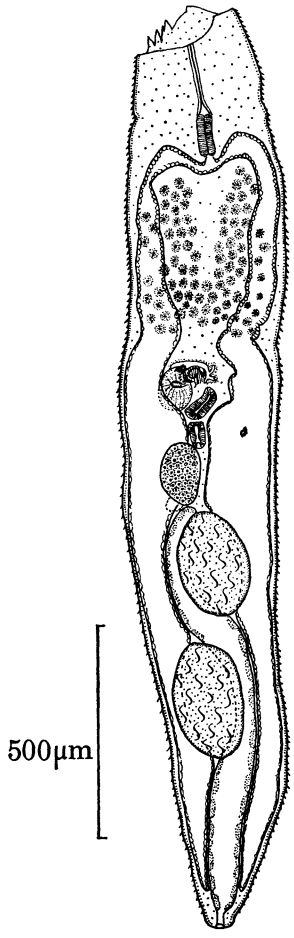
Uterus with descending and ascending limbs; descending limb passes anterior testis dextrally, crosses between testes, and passes posterior testis sinistrally, crosses to and descends on right side to posterior end, crosses to left side to become ascending limb; runs froward on left side, crosses between testes to right side, and then between ovary and anterior testis to left side, loops across mid-line ventral to seminal vesicle and unites with ejaculatory duct to form genital atrium.

Jägerskiöld (1896) describes and figures (Fig. 7, Pl. 9) a small papilla projecting into the genital atrium and bearing the opening of the ejaculatory duct. Although this could not be seen in either the lectotypes or in Jägerskiöld's sectioned adult, its presence cannot be discounted as such a papilla is present in several species of *Galactosomum*.

Jägerskiöld (1896) gave the size as 2–3 mm long and 500–800 μm wide, whereas the five paralectotypes ranged from 1.6 to 1.7 mm long and from 300 to 450 μm wide. Presumably Jägerskiöld measured flattened specimens.

Adult (*figure 6*). As the material available of adults is not good enough for re-description, a brief account is given of the similarities and differences of adult and metacercaria.

The ventrogenital complex of the adult does not differ from that of the metacercaria and so it is omitted from the following description, although its eversibility is discussed below. The main differences are seen in (i) widened forebody, (ii) the size and form of the seminal vesicle, now distended with sperm. Whereas in the metacercaria the seminal vesicle is relatively small and has a very thick wall, in the adult, the wall is relatively thinner.



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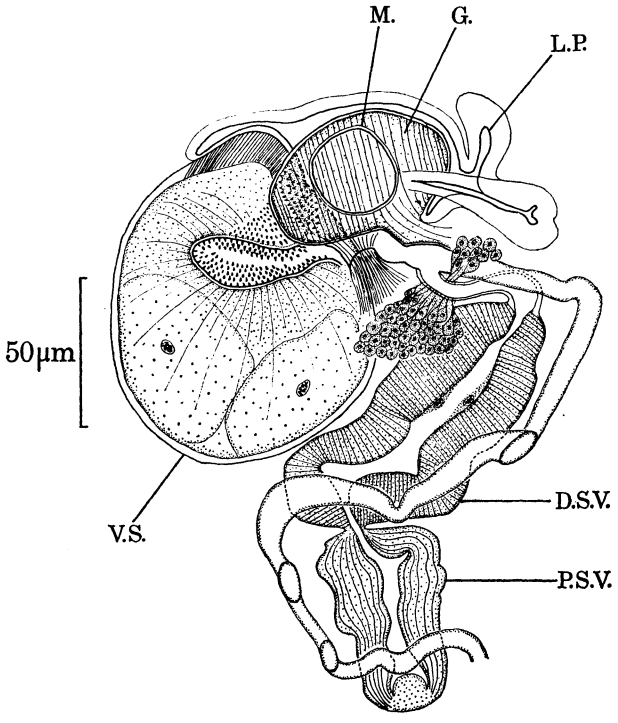

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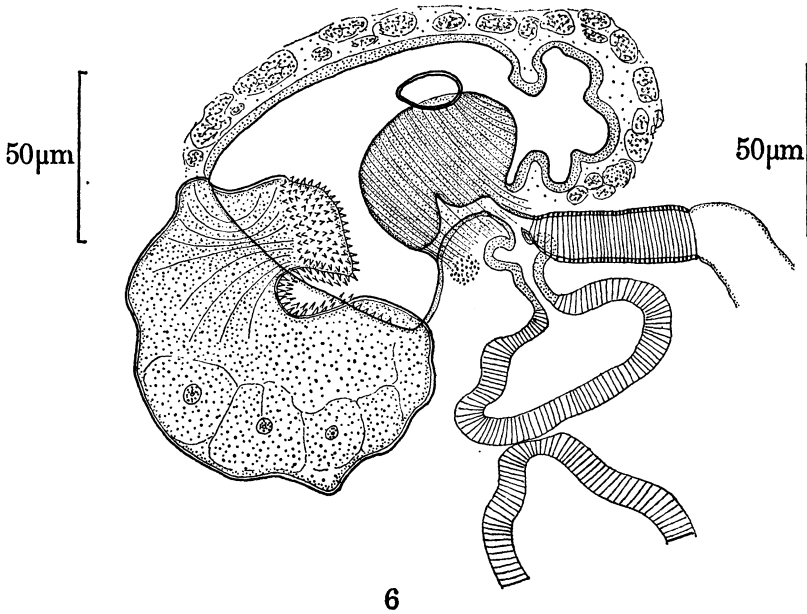

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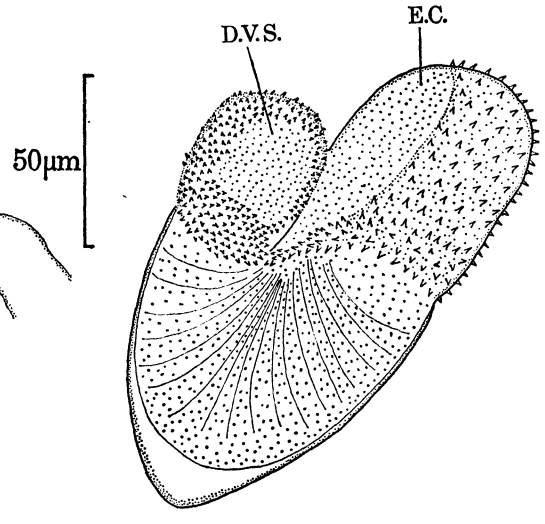

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FIGURE 4. *G. lacteum.* Lectotype, metacercaria (ventral).

FIGURE 5. *G. lacteum.* Lectotype, ventrogenital complex.

FIGURE 6. *G. lacteum.* Adult, ventrogenital complex (B.M.(N.H.) 1927.3.9.10–19, det. Jägerskiöld).

FIGURE 7. *G. lacteum.* Adult, ventral sucker everted.

Eggs (15, uterine) measure 22–26 × 10–14 μm.

The metacercaria is well advanced toward the adult condition; the reproductive system is fully formed and lacks only sperm and eggs, and the body is as long (1.60–1.74 mm) as the smaller adults (1.3–3.0 mm) measured by Prudhoe (1949).

Specimens examined

Sweden	ex *Phalacrocorax carbo* L. Coll. by Jägerskiöld (Jägerskiöld 1908), B.M.(N.H.), 1927.3.9.10–19	4 (2 wholemounts, 2 sectioned)
Great Britain	ex *Phalacrocorax aristotelis* (L.) Coll. by Baylis, 27. ix. 35. Weymouth (Baylis 1939, Prudhoe 1949), B.M.(N.H.) Tr. 1935.12.30.60–75	6 wholemounts
	ex *Ardea cinerea* Coll. by Baylis, 25. i. 36, Scotland (Baylis 1939, Prudhoe 1949), B.M.(N.H.) 1936.8.5.91–110	4 wholemounts
	ex *Phalacrocorax aristotelis* (L.) Coll. by I. C. Williams, 16. xi. 53, 6. xii. 54 (Williams 1961). coll. Williams.	17 wholemounts

Remarks

Jägerskiöld's (1896) 'sphäroiden Körper' and 'stacheliger Körper' together comprise the ventral sucker, as is suggested in his Fig. 6, Pl. 9, and as can be clearly seen in his sections of adults. The reduced but conspicuous spiny cavity of the oral sucker, a feature here considered to be of taxonomic significance, was briefly described by Jägerskiöld (1896), as a spiny fold. That this spiny cavity is eversible is suggested by Baylis's (1939) and Williams's (1961) wholemounts. In the former, intermediate stages in eversion of the cavity are seen, and in the latter (figure 7) the cavity is fully everted, forming a finger-like process, and the spiny knob is rotated dorsally so that the spines are on the dorsal face rather than the ventral.

The spines that Jägerskiöld (1896) said lined the ventrogenital sac and lateral pocket could not be seen in wholemounts of the metacercaria or in Jägerskiöld's sections of the adult.

Diagnosis

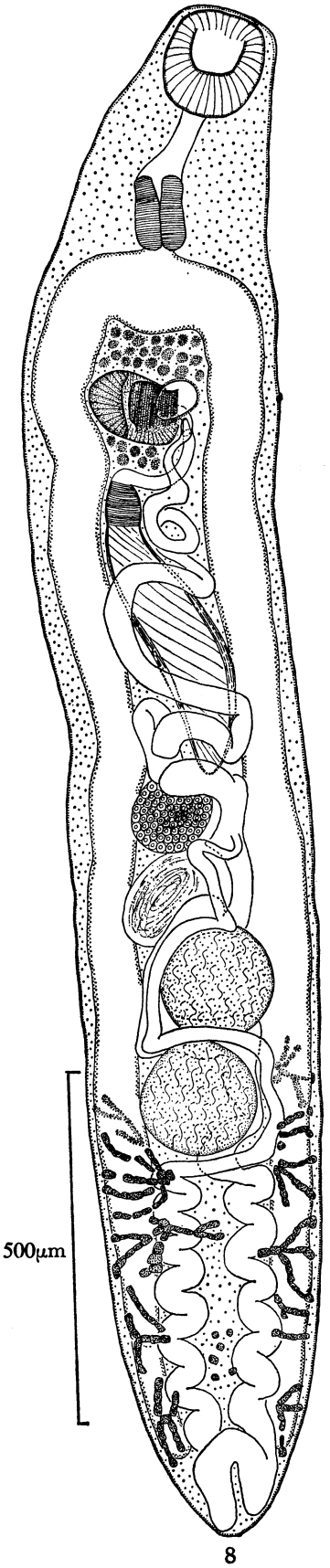
Body divided into flattened forebody and narrower hindbody. Prepharynx longer than pharynx. Ventrogenital sac with lateral pocket, well behind caecal bifurcation; ventral sucker parenchymatous, with spiny dextral knob overhanging reduced spiny cavity, ratio o.s./v.s. (widths) (in metacercaria) 1.8–2.4; gonotyl simple, not pierced by genital atrium. Seminal vesicle two-chambered, both with thick layer of outer diagonal fibres, distal chamber larger than proximal. Vitellaria do not exceed anterior testis, extend beyond ends of caeca posteriorly. Eggs 22–26 × 10–14 μm. Excretory bladder extends to posterior border of ovary.

(*b*) *Galactosomum angelae* sp.nov.

Among a large South Australian collection of heterophyids from fish-eating birds, generously donated by Miss L. Madeline Angel, were adults and metacercariae of a species of *Galactosomum* distinct from other members of the genus.

Description (*figures* 8–15, 77)

A description is given of the holotype and 10 paratypes, together with notes on 64 wholemounts and sections of three specimens from other hosts and a brief description of the metacercaria. Measurements (average and range) are given of the 11 types.



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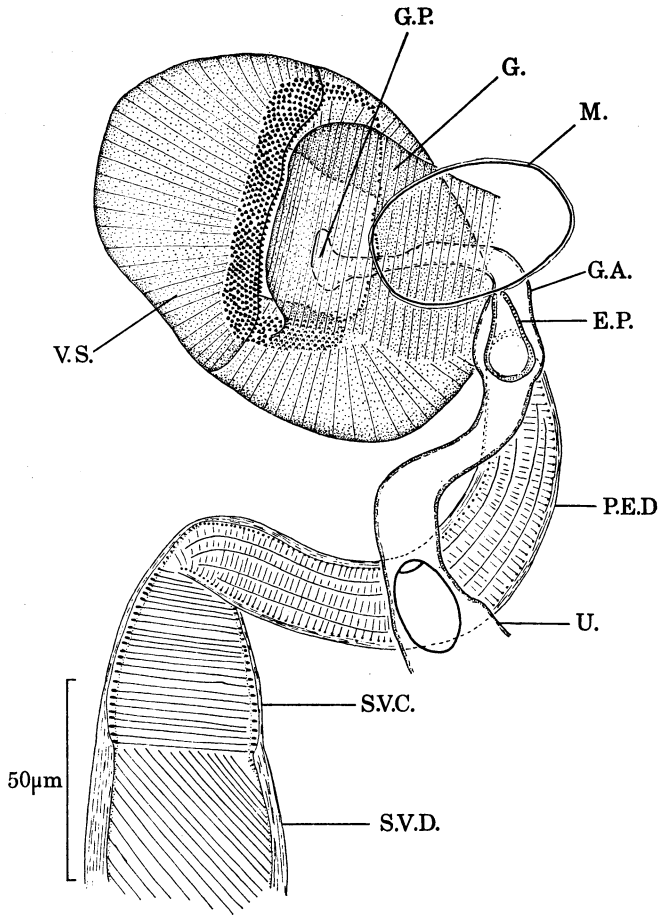

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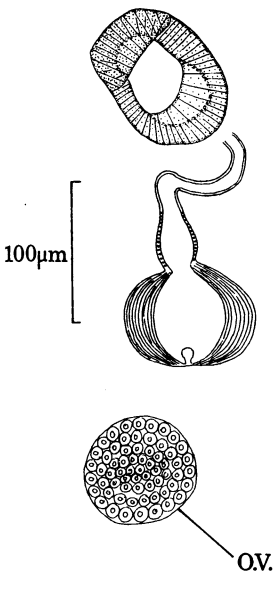

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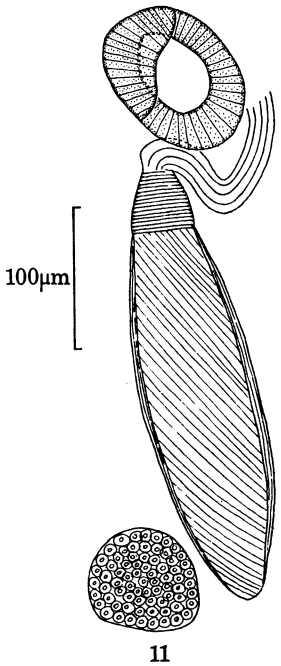

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FIGURE 8. *G. angelae.* Holotype (ventral).

FIGURE 9. *G. angelae.* Holotype, ventrogenital complex.

FIGURE 10. *G. angelae.* Seminal vesicle empty.

FIGURE 11. *G. angelae.* Seminal vesicle distended with sperm.

With the characters of the genus. Body strap-shaped, slightly flattened dorso-ventrally, 1.48 (1.39–1.74) mm long, tapering anterior to ventrogenital sac, constricted slightly immediately behind ventrogenital sac, posterior end bluntly rounded; width at ventrogenital sac 282 (242–322) μm, greatest width of hindbody 290 (234–314) μm; forebody without pit, either dorsal or ventral, and without specialized dorso-ventral musculature.

Tegumental armature comprises large, closely set scales on forebody, smaller and narrower posteriorly becoming spines at level of posterior testis, and extending to posterior end. Anterior tip unarmed, with three rows of scales across anterior margin of oral sucker. Scales absent near mouth of ventrogenital sac.

Frontal-gland cells numerous in space bounded by caeca and ventrogenital sac; open in two staggered rows in anterior unarmed region.

Oral sucker subterminal; 107 (104–130) × 110 (94–126) μm. Prepharynx about as long as and forming ventrally incised fornix at junction with pharynx. Pharynx 77 (68–91) × 50 (39–58) μm. Caeca large, curve inward behind ventrogenital sac, extend almost to posterior end.

Ventrogenital sac large, median, nearly symmetric, unarmed, without lateral pocket; 27–30/100ths from anterior end, and close to bifurcation of gut; musculature well developed, especially dextral hemisphincter (see below); mouth usually slightly submedian and on left. Ventral sucker large, wider than long, 80 (75–94) × 113 (100–120) μm, long axis oblique with respect to the mid-line, occupies 2/3 of intercaecal space; ratio o.s./v.s. (widths) 1.05 (0.94–1.4) μm; solidly muscular, sucker like, with well-developed cavity; lip dextrally enlarged ventrally; armed with complete circle of minute 2.0–2.5 μm spines, 10 rows wide on raised dextral lip and adjacent portion of lip posteriorly, narrowing to as few as 2–3 rows on lip anteriorly and sinistrally. Gonotyl solidly muscular, unarmed, axis transverse; 53 (39–68) × 47 (42–55) μm; arises sinistrally and posteriorly, overlies ventral sucker ventrally, with free tip directed dextro-dorsally or dorsally into cavity of ventral sucker; traversed by genital atrium genital pore a subterminal transverse slit. Genital atrium begins sinistral to ventral sucker and externo-dorsal to gonotyl.

Testes diagonal, rounded, contiguous, occupy most of intercaecal space; anterior testis 123 (110–133) × 120 (84–130) μm, posterior testis 136 (130–143) × 126 (97–143) μm; sperm ducts unite at seminal vesicle. Seminal vesicle fusiform, one-chambered, unconstricted, or with slight constriction; 262 (195–324) × 86 (78–100) μm; with thick outer layer of diagonal fibres, except at distal end where strongly developed circular fibres describe the incipient distal portion. Prostatic ejaculatory duct elongate, not inflated; with conspicuous outer longitudinal muscle-fibres; opens into genital atrium dorsal to uterus via an elongate muscular papilla with prominent circular fibres; surrounded by prostatic gland-cell bodies.

Ovary rounded, dextral, 76 (65–84) × 82 (68–91) μm; ootype postero-medial to ovary; seminal receptacle rounded, contiguous with ovary and anterior testis, 87 (71–114) × 95 (71–113) μm. Course of uterus typical, except that ascending arm loops twice across seminal vesicle. Vitellaria in rosettes; extend anteriorly to between middle of posterior testis and posterior border of ovary, posteriorly almost to, occasionally beyond, ends of caeca; extend irregularly over whole of dorsal and ventral faces behind posterior testis, lateral elsewhere; rosettes apparently arise from single median vitelline duct that follows same course as uterus in region of testes. Eggs (10, uterine) 28.6 (28.0–29.8) × 13.5 (12.7–13.6) μm, with small anopercular knob.

Excretory pore terminal; excretory bladder tubular, does not exceed posterior border of

posterior testis; bladder arms apparently extend to level of pharynx before dividing into anterior and posterior collecting tubules.

TYPE HOST. *Hydroprogne caspia* (Pallas).

LOCATION. Small intestine.

TYPE LOCALITY. Port River, South Australia.

OTHER HOSTS AND LOCALITIES. *Sterna bergi* Lichtenstein, Normanville and St Vincent Gulf, South Australia; *Sula serrator* (Banks), Seacliff, South Australia; *Eudyptula minor* (Forster), Kangaroo Island, South Australia; *Larus novaehollandiae* Stephens, St Kilda and West Island South Australia.

DISPOSITION. U.S.N.M. holotype 72041 and two paratypes 72042.

OTHER SPECIMENS. S.A.M. paratype E.888; B.M.(N.H.) paratype 1972.1.24.1; M.P.M. paratype 19023; author's colln.

Remarks

The caeca are inflated in all of the type specimens, which appear to have been fixed after death as they have lost most of the body spines. In other, better preserved specimens from other hosts, the caeca are narrow. The latter appears to be the normal condition and the former the result of post-mortem changes.

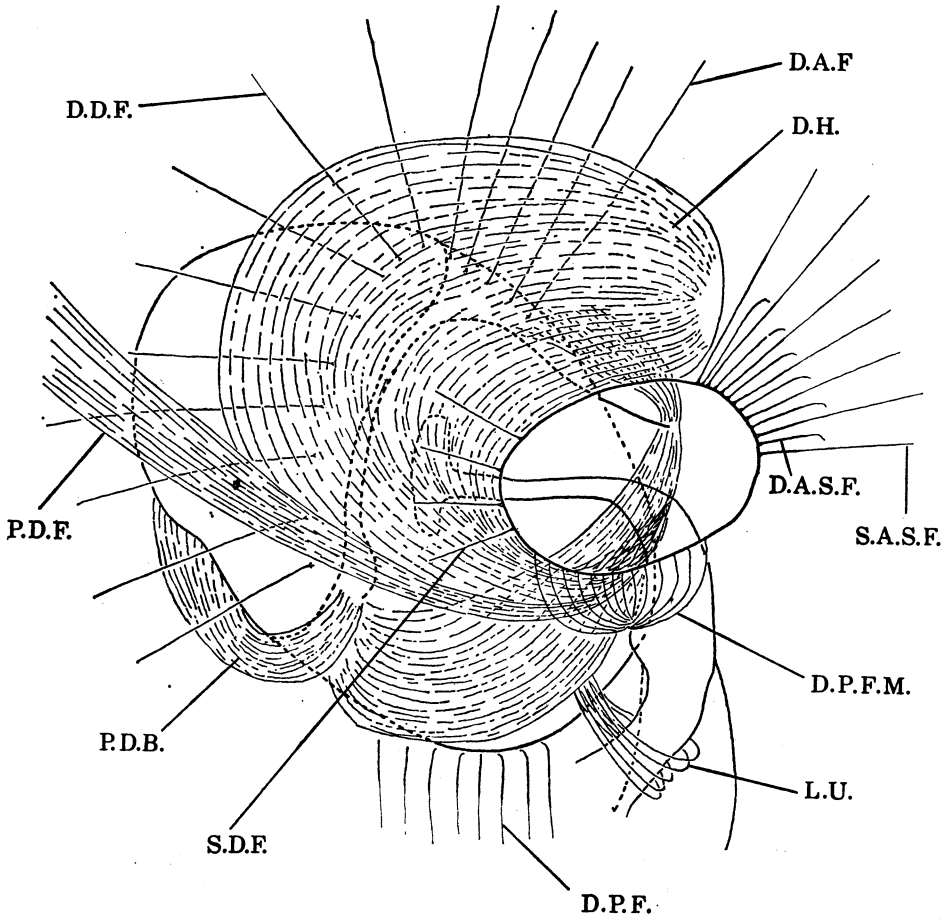
The seminal vesicle varies both in shape and in relative thickness of the wall, depending on the volume of sperm contained. When empty (figure 10), it is short, rounded, thick walled, and clearly constricted. When full (figure 11), it is elongate, fusiform, thinner walled, and not clearly constricted.

Study of transverse (figure 14) and sagittal (figure 15) sections confirmed certain features seen in wholemounts, namely relation of genital atrium to gonotyl, papilla at end of ejaculatory duct, absence of both pits and specialized dorso-ventral fibres in the forebody, and absence of lateral pocket on ventrogenital sac. Additionally, Laurer's canal was seen in sections to open in the mid-line medial to the ovary.

The dextral hemisphincter is so large and thick that it may be displaced in flattened specimens (figure 16) and appear as a discrete organ.

Diagnosis

Body strap shaped, slightly constricted behind ventrogenital sac. Prepharynx and pharynx of equal length. Ventrogenital sac without lateral pocket, 27–30/100ths from anterior end, dextral hemisphincter well developed; ventral sucker diagonally elongate, as wide as oral sucker, with raised dextral lip, armed with uninterrupted band of minute spines 10 rows wide dextrally and two to three rows wide sinistrally; gonotyl elongate, tip bearing slit-like genital pore directed into cavity of ventral sucker; seminal vesicle slightly constricted, with anterior part small and poorly differentiated. Vitellaria extend anteriorly to between middle of posterior testis and posterior border of ovary, posteriorly to about ends of caeca, scattered over dorsal and ventral faces of body behind posterior testis. Eggs 28.6 (28.0–29.8) × 13.5 (12.7–13.6) μm, with small anopercular knob. Excretory bladder extends to or almost to posterior border of posterior testis.



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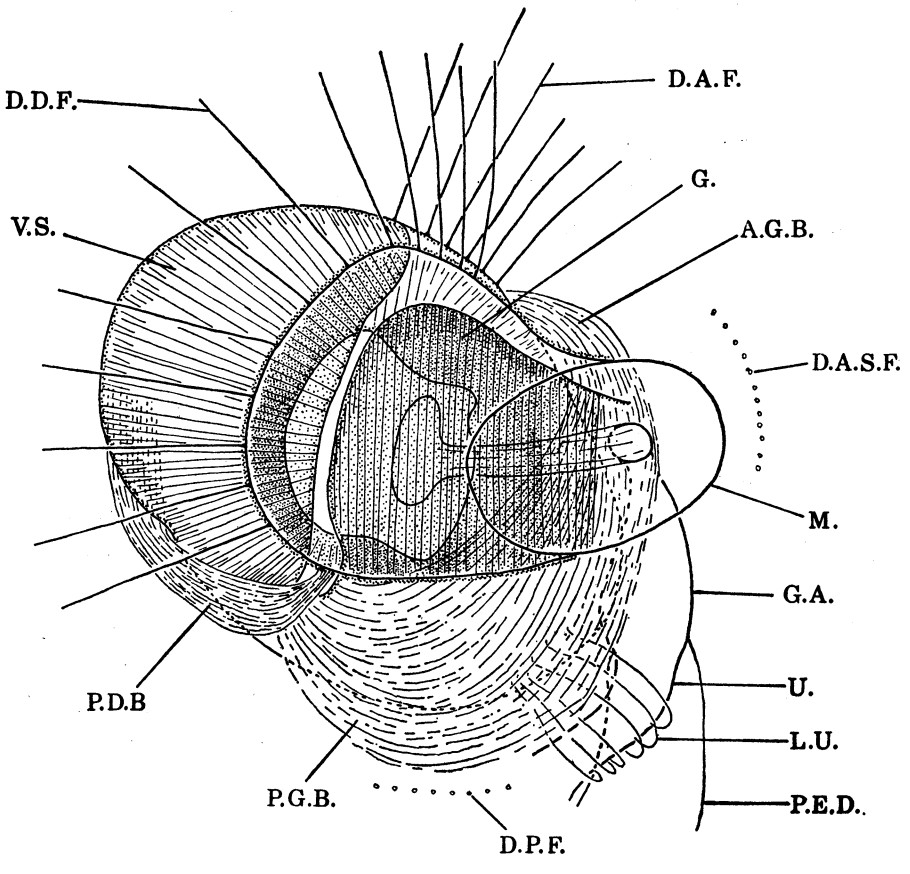

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FIGURE 12. *G. angelae.* Superficial musculature of ventrogenital sac (free-hand).

FIGURE 13. *G. angelae.* Deep musculature of ventrogenital sac (free-hand).

Comparison

In characters of the ventral sucker, *angelae*, with transversely elongate sucker armed with uninterrupted band of spines, which is, however, narrower sinistrally, is intermediate between *bearupi*, with rounded sucker armed with uniform band of spines, and both *puffini* and *fregatae* in which the spines are clearly divided into a dextral U-shaped band and a sinistral patch.

A further difference between *angelae* and *fregatae* is seen in the relative position of the ventral sucker and gonotyl. In both species, the ventral sucker is elongated and its long axis is oblique to the long axis of the body, but in *angelae* the sucker axis runs postero-sinistrad, whereas in *fregatae* it runs postero-dextrad. It is as if the ventral sucker but not the gonotyl in *angelae* were rotated through 90° from the condition in *fregatae*, which condition is common to most of the species in *Galactosomum*. A further difference is seen in the gonotyl, which in *angelae* is simple, but in *fregatae* has a dextral digitiform projection.

The seminal vesicle in *angelae*, as in *bearupi*, is superficially undivided, thus clearly differentiating it from *fregatae* and *puffini* which have a distinctly constricted seminal vesicle.

Metacercaria (*figure* 16)

The following brief description is based on three specimens dissected from their cysts and flattened in fixing. Measurements are given of the largest specimen.

Body elongate, with roughly parallel sides, slightly tapered at both ends; 1590 × 240 μm. Oral sucker 114 × 117 μm; ventral sucker 71 × 110 μm; ratio o.s./v.s. (widths) 1.06. Ventrogenital sac 25/100ths from anterior end; ventral sucker and gonotyl as in adult; seminal vesicle small, clearly divided into large, fusiform posterior portion with thick layer of diagonal fibres and small narrow, tubular anterior portion with prominent circular fibres. Gonads well developed, tandem and separated; uterus and vitelline ducts present, but difficult to trace.

Host. *Hemirhamphus melanochir* C. & Val.

Location. Gills.

Locality. St Vincent Gulf, South Australia.

Date. June 1937.

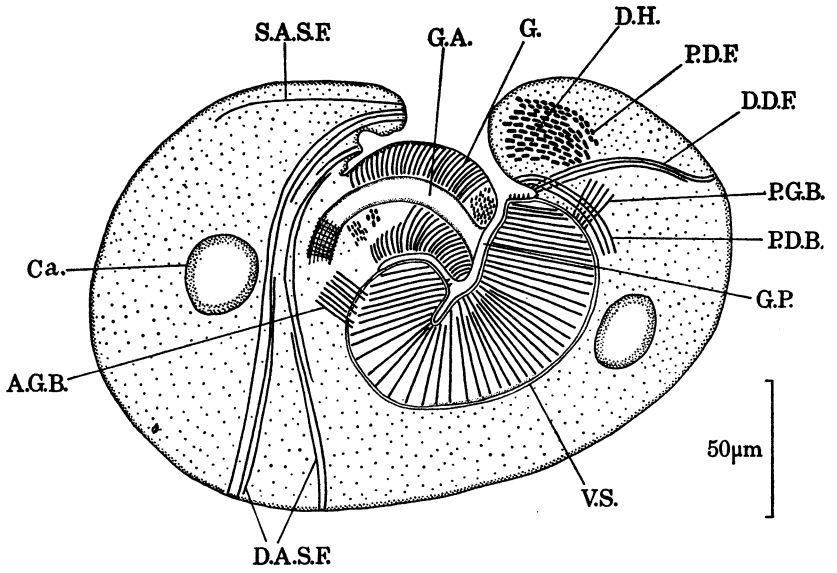
Disposition. U.S.N.M. no. 72043; author's colln.

The largest of the three metacercariae is longer (1.59 mm) than the average length of the adult (1.48 mm) and exhibits a fully developed ventrogenital complex and a well-developed reproductive system. As in the metacercariae of other species of *Galactosomum*, the parenchyma is not as dense as in the adult.

Musculature of the ventrogenital sac (*figures* 12–15)

The greatest contribution of serial sections was towards elucidating the complex musculature associated with the ventrogenital complex. The elements of this musculature are of two intergrading types, discrete bands of contiguous fibres, and groups of separated fibres.

The groups of separated fibres comprise: (1) a small group (S.D.F.) arising from the wall of the ventrogenital sac just inside the mouth dextrally and fanning out dextrad near the ventral surface; (2) a large group (S.A.S.F.) arising from the wall of the sac just inside the mouth antero-sinistrally and fanning out antero-laterad near the ventral surface; (3) a second antero-sinistral group (D.A.S.F.) arising near and slightly dorsal to group (2) running firstly antero-laterad, then turning dorsad and running to the dorsal surface of the body; (4) a group of fibres (D.D.F.) arising from the point of attachment of the sac to the ventral sucker anteriorly



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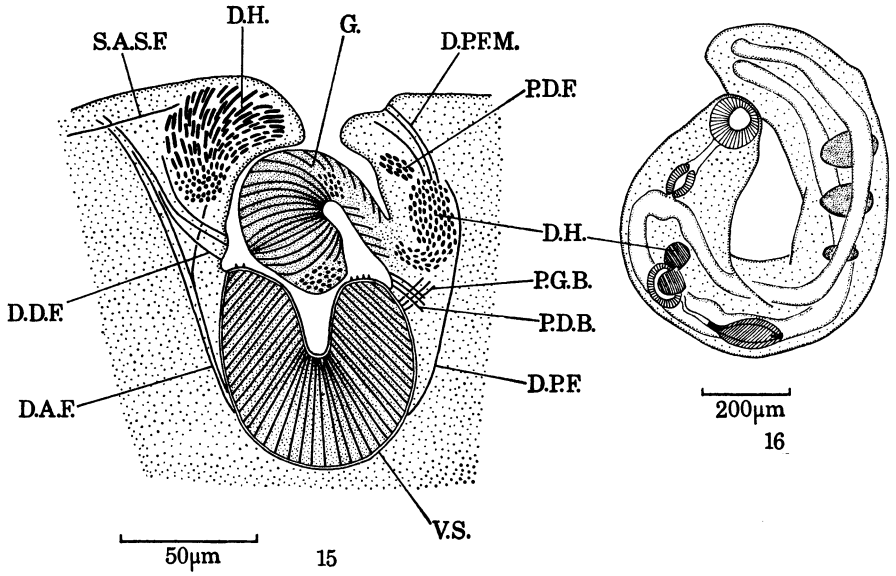

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FIGURE 14. *G. angelae.* Transverse section of ventrogenital complex.
FIGURE 15. *G. angelae.* Sagittal section of ventrogenital complex.
FIGURE 16. *G. angelae.* Metacercaria.

and dextrally, and radiating out and ventrad to the ventro-lateral surface of the body; (5) a group (D.A.F.) arising from the anterior face of the ventral sucker dorsally, and running antero-ventrad to the ventral surface of the body; and (6) a similar group (D.P.F.) arising from the posterior face of the ventral sucker and running postero-ventrad to the ventral surface.

The bundles of contiguous fibres comprise: (7) a large muscle, the dextral hemisphincter (D.H.), the largest and most conspicuous element in the complex, arising from a slender root medial to the first part of the genital atrium, running clockwise first over the postero-sinistral corner of the ventral sucker, then, rising toward the ventral surface, increasing in size, encircling the dextral and anterior faces of the ventrogenital sac and ending abruptly; (8) a band (P.D.F.)

arising in common with and externo-ventral to (7) and running antero-dextrad close to the ventral surface of the body; (9) a curved, fan-shaped band (D.P.F.M.) arising in common with (7) and curving ventrad and anterad, widening as it approaches the ventral surface, its fibres separating as they approach their insertion on the posterior lip of the mouth of the ventrogenital sac; (10) a band (A.G.B.) arising at the root of the gonotyl at the point where the genital atrium enters, and running antero-dorsally to its attachment on the antero-sinistral face of the ventral sucker; (11) a band (P.G.B.) arising in common with (10) and running postero-dextrad, dorsal to the gonotyl, to its attachment on the posterior face of the ventral sucker; (12) a small band (L.U.) arising from (11) and encircling the uterus near its entrance into the genital atrium; and (13) a band (P.D.B.) arising from the wall of the sac in the angle between the raised dextral lip and the posterior lip of the ventral sucker, and curving postero-dextrad and then anterad against and attached to the dextral face of the ventral sucker.

(*c*) *Galactosomum bearupi* sp.nov.

Among material from gulls and terns collected at Townsville by Mr A. J. Bearup, School of Public Health and Tropical Medicine, University of Sydney, was a species of *Galactosomum* distinct from other members of the genus. Additional material was collected from terns at Townsville, at Heron Island, and at Caloundra, Queensland.

Description (*figures* 17–22, 78)

A description is given of the holotype and 11 paratypes, together with notes on 13 specimens from other hosts and a description of the metacercaria.

With the characters of the genus. Body 1.72 (1.39–1.90) mm long, and 280 (218–348) μm wide, not divided by constriction into forebody and hindbody, not tapering at ends; forebody roughly cylindrical, 244 (202–322) μm wide, slightly narrower than hindbody, not concave ventrally, and without dorsal or ventral pit or specialized dorso-ventral musculature.

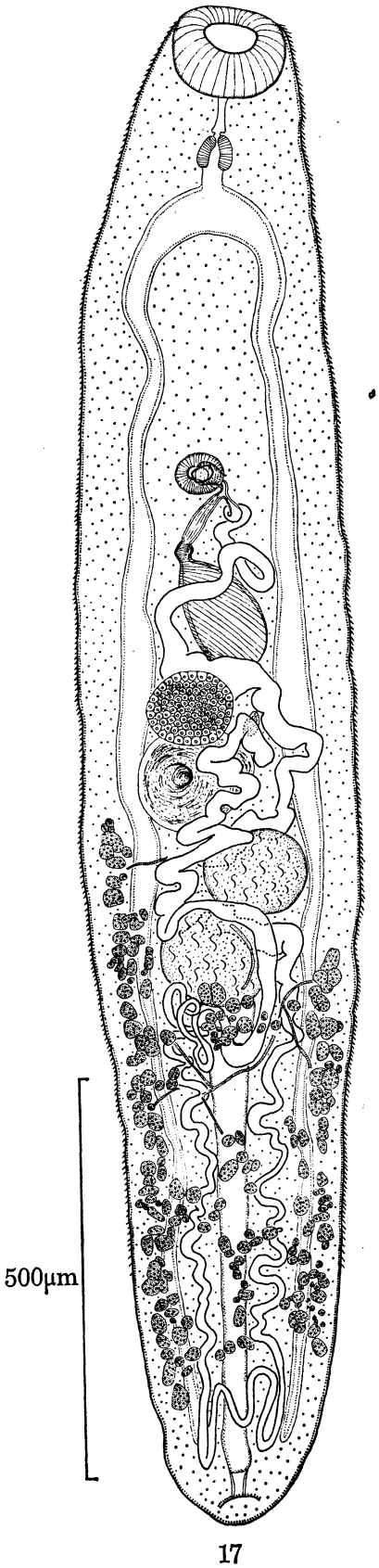
Body closely covered with scales, larger anteriorly and dorsally, becoming spines about level of posterior testis that continue at least half way from posterior testis to posterior end; absent about mouth of ventrogenital sac; band of scales across dorsal lip of oral sucker absent.

Pigment granules scattered in parenchyma about pharynx and between caeca anterior to ventrogenital sac.

Frontal-gland cells numerous, especially between caeca anterior to ventrogenital sac; extend anteriorly to level of pharynx and posteriorly to level of ventrogenital sac; ducts from inter-caecal gland-cells pass forward dorsal and ventral to caeca, and mostly lateral to oral sucker, and open in pre-oral spineless area by numerous duct mouths disposed in several transverse rows. Tegumental glands small, scattered, most numerous anteriorly and ventrally. Prepharyngeal-gland cells not seen. Oesophageal-gland cells form cuff about oesophagus.

Oral sucker subterminal, large, 117 (109–126) × 146 (130–155) μm. Prepharynx present, about as long as pharynx, variable in length, forms ventrally incised fornix posteriorly. Pharynx 51 (45–60) × 43 (37–52) μm. Oesophagus short, 22 (12–29) μm long; bifurcation of caeca 258 (242–274) μm from anterior end. Caeca simple, straight, slender, extend to within 117 (97–165) μm of posterior end, with right caecum longer than left.

Ventrogenital sac (figure 18) small, median, 26–33/100ths from anterior end; mouth (figure 19) symmetric, variable in size, with outer circular (C.F.) and inner radial (S.R.F.) muscle-fibres, circular fibres about mouth lie between circular and longitudinal fibres of body wall,



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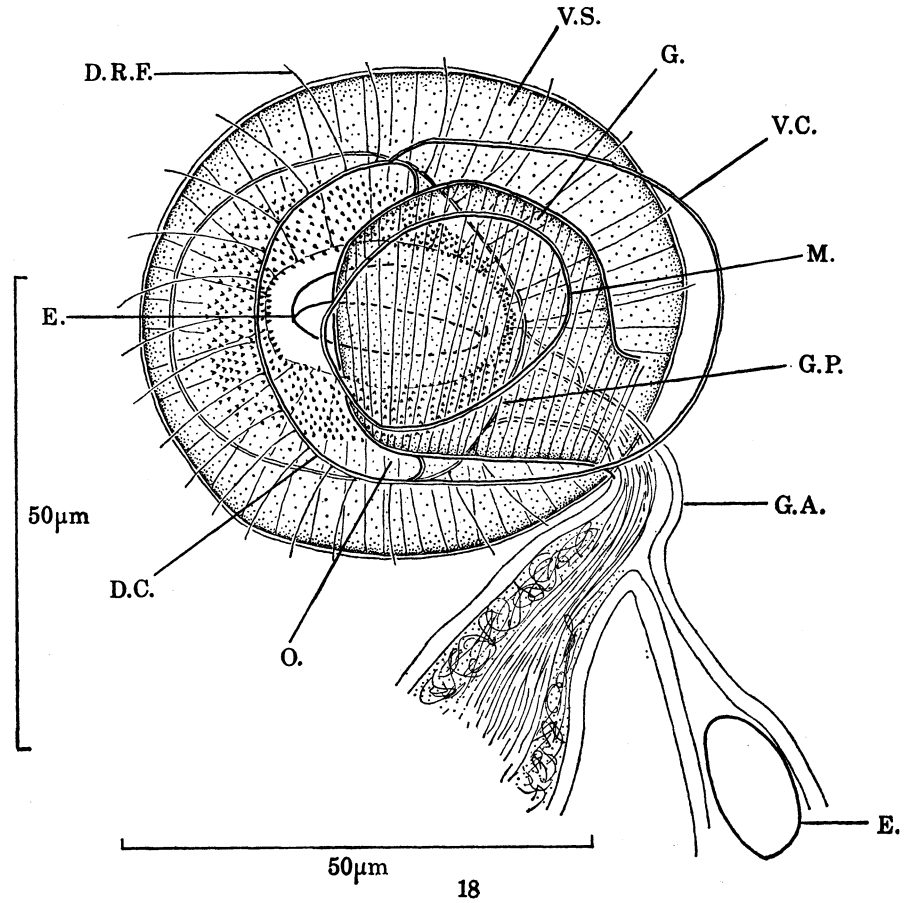

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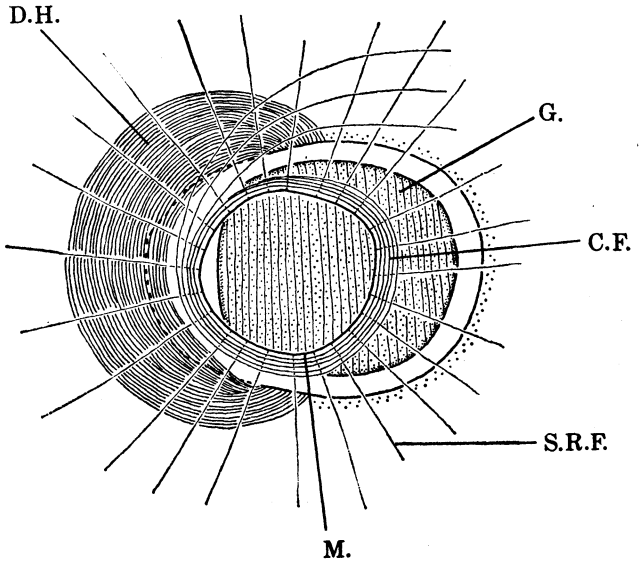

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FIGURE 17. *G. bearupi*. Holotype (ventral).

FIGURE 18. *G. bearupi*. Holotype, ventrogenital complex.

FIGURE 19. *G. bearupi*. Musculature of ventrogenital sac (free-hand).

outermost fibres on right arch away sinistrad from mouth anteriorly and merge with circular fibres of body wall; dextral hemisphincter (D.H.) inserted on wall of upper chamber of ventrogenital sac anteriorly and posteriorly half encircles ventrogenital sac on right side, deep to radial fibres of mouth; sac divided into two chambers (figure 20*a*, *b*), a ventral (V.C.), ventral and sinistral to gonotyl, and a dorsal (D.C.) over mouth of ventral sucker, communicating by a semi-lunar opening, dextral to free tip of gonotyl and bounded by wall of ventrogenital sac dextrally and gonotyl sinistrally, with ring of radial muscle-fibres (D.R.F.) (? dilators of dorsal chamber) inserted on wall of dorsal chamber, and running dorsad close against capusle o ventral sucker; without lateral pocket. Ventral sucker symmetric, median or slightly to right, small, 51 (43–56) × 55 (49–58) μm; ratio o.s./v.s. (lengths) 2.1–2.7; little modified, with large cavity directed ventrally or sinistro-ventrally, solidly muscular; armed with band 8–9 rows wide of 1.5 μm spines encircling rim, band typically on ventral face dextrally but on inner face of lip sinistrally. Gonotyl muscular, anucleate, unarmed; roughly circular in outline, 29 (23–33) × 30 (21–35) μm, flattened on dorsal face, convex on ventral face; arises sinistrally or postero-sinistrally; not penetrated by genital atrium. Genital atrium short, opens into dorsal chamber of ventrogenital sac, immediately dorsal to base of gonotyl and sinistral to mouth of ventral sucker.

Testes diagonal, subspherical, contiguous or slightly separated by coils of uterus, large; anterior testis 93 (80–110) × 104 (84–136) μm, posterior testis 107 (90–126) × 106 (87–136) μm, sperm ducts unite at seminal vesicle. Seminal vesicle one-chambered, sometimes constricted, extends to, or nearly to, ovary; proximal part large, 180 (76–270) × 83 (43–122) μm fusiform to ellipsoidal, with relatively thick (4–10 μm) wall of diagonal muscle-fibres, with inbulging valve about common entrance of sperm ducts; distal part variable, small 21 (10–33) × 22 (14–29) μm, with thinner wall of circular fibres. Prostatic ejaculatory duct 67 (58–82) × 22 (16–25) μm, with thick wall of longitudinal muscle-fibres and lining of inbulging ends of prostatic-gland ducts, opens into genital atrium through a short papilla (figure 21); prostatic-gland cells apparently closely invest duct.

Ovary subspherical, 78 (58–100) × 87 (68–115) μm, slightly to right; oviduct arises dorso-medially and runs posterad; seminal vesicle spherical, overlaps ovary dorsally, variable in size, 123 (66–160) × 119 (66–165) μm, with short duct that unites with oviduct and Laurer's canal; common vitelline duct enters fertilization canal near ootype; ootype median to ovary. Uterus with typical course; descends on left behind posterior testis for variable distance before crossing to right and turning anterad to posterior border of posterior testis, recurves dorsally and runs posterad. Vitelline follicles in 10–13 rosettes, mostly latero-ventral, absent dorsally, occasionally medial ventrally posterior to testes; extend anteriorly to between middle of posterior testis and middle of seminal vesicle on right side, and to between middle of posterior testis and middle of ovary on left; posteriorly usually do not reach ends of caeca; vitelline duct single, median, ventral; vitelline reservoir small, posterior to ootype. Eggs (50, uterine, not collapsed) 22 (20–25) × 12 (11–14) μm, with variable anopercular knob.

Excretory pore subterminal, ventral; excretory bladder tubular, typically exceeds slightly posterior border of posterior testis dorsally; bladder arms arise subterminally; mesostomate (see metacercaria).

Type host. Caspian tern, *Hydroprogne caspia* (Pallas).

Other hosts. White-capped noddy, *Anous minutus* Boie; sooty tern, *Sterna fuscata* L.; lesser crested tern, *Sterna bengalensis* Lesson; silver gull, *Larus novaehollandiae* Stephens.

LOCATION. Small intestine.

TYPE LOCALITY. Townsville, Queensland, Australia.

OTHER LOCALITIES. Townsville (gull, lesser crested tern); Heron Island, Queensland (white-capped noddy); Caloundra, Queensland (sooty tern).

DISPOSITION. U.S.N.M. holotype no. 72044, and paratypes 72045; B.M.(N.H.) paratype no. 1972.1.24.2; S.A.M. paratype no. E.889; M.P.M. paratype 19024; author's collection.

Remarks

The circular band of spines may vary in position and appearance, depending on the state of eversion of the ventral sucker. Thus, it may be ventral (apical), and clearly visible and of uniform width, or, inverted within the mouth of the sucker, especially sinistrally, and so appear to be of varying width (figures 18, 20*a*).

The five specimens from *Sterna fuscata* differ in several respects from all adults from other hosts. The differences can be summarized in tabular form (table 1).

TABLE 1. COMPARISON OF ADULTS OF *G. BEARUPI*

character, host	*Hydroprogne caspia* (type host)	*Sterna fuscata*
length/mm	1.39–1.90	1.51–1.72
width/μm	218–348	376–680
ratio o.s./v.s.	2.1 –2.7	1.5 –1.7
ventral sucker diameter/μm	43–58	68–83
state when fixed	alive	dead

Both groups are similar in total length. The difference in width is not significant, but results from the much greater number of eggs in specimens from *S. fuscata*. There appears to be, however, a significant difference between the two groups in the absolute size of the ventral sucker, and hence, in the ratio of oral to ventral sucker. But as in other characters, particularly those of the ventrogenital complex, the two groups are the same, they are considered to be conspecific. How much of the difference may have resulted from post-mortem changes is not known.

The seminal vesicle is unconstricted when greatly distended with sperm (figure 22), but in most specimens (figure 17), and particularly in those with little sperm, the seminal vesicle (figure 21) is clearly constricted, and comparable in form with the seminal vesicle of the related species, *fregatae*, *dollfusi*, *yehi*, *angelae* and *ussuriensis*. However, the distal part is relatively much smaller in *bearupi* than in the other species. As *bearupi* is here considered to be the most primitive in characters of the ventrogenital complex (see § III 3), the smallness of the distal part may also be primitive.

Diagnosis

Body elongate; forebody and hindbody not demarcated, of equal width. Oral sucker large; prepharynx nearly as long (maximum) as pharynx. Ventrogenital sac without lateral pocket, 26–33/100ths from anterior end, mouth symmetric; ventral sucker symmetric, unmodified, with circle 8–9 rows wide of 1.5 μm spines, ratio o.s./v.s. (lengths) 2.1–2.7; gonotyl hemispherical, not penetrated by genital atrium; prostatic ejaculatory duct relatively long; seminal vesicle one chambered, sometimes constricted. Vitellaria extend anteriorly to between middle of posterior testis and middle of seminal vesicle and posteriorly nearly to ends of caeca; eggs

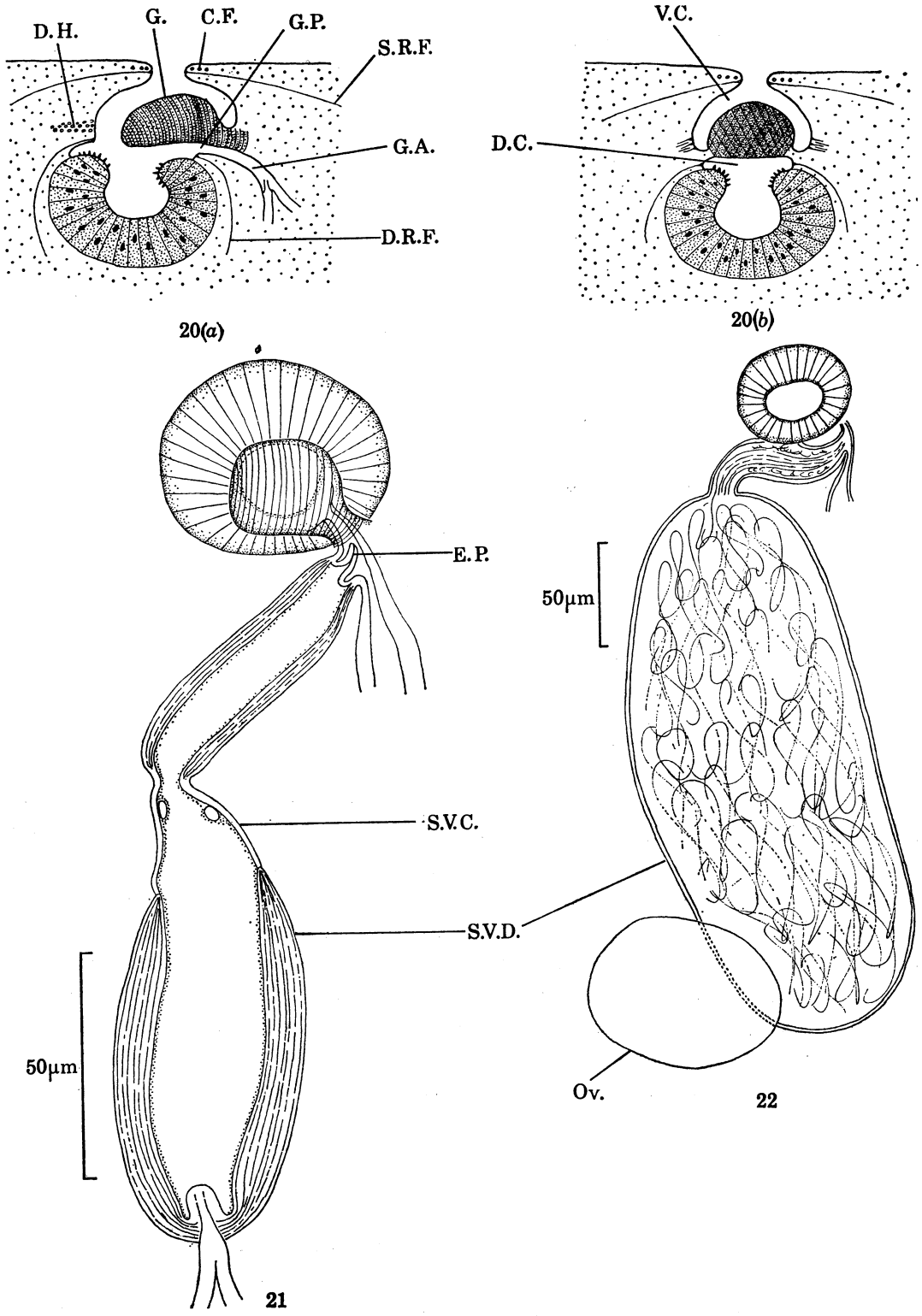


FIGURE 20. *G. bearupi*. Schematic sections of ventrogenital sac: (*a*) transverse, (*b*) sagittal.

FIGURE 21. *G. bearupi*. Seminal vesicle empty.

FIGURE 22. *G. bearupi*. Seminal vesicle distended with sperm.

22 (20–25) × 12 (11–14) μm. Excretory bladder extends to or just beyond posterior border of posterior testis.

The nearest species is *angelae* with which it shares a symmetric ventral sucker armed with a complete circle of minute spines, the absence of a lateral pocket, short excretory bladder, similar distribution of vitellaria, form of body, and one-chambered seminal vesicle with small distal and large proximal parts. However, the two species differ significantly in characters of the ventral sucker and seminal vesicle. In *bearupi*, the ventral sucker (figure 17) is proportionately smaller, ratio o.s./v.s. (lengths) 2.1–2.7, rounder, and has the spines in a circular band of uniform width (8–9 rows) and the seminal vesicle has a very small distal part; whereas in *angelae* (figure 8) the ventral sucker is proportionately larger, ratio o.s./v.s. (widths) 0.94–1.4, elongate, and has fewer rows of spines dextrally (3 rows) than sinistrally (8 rows), and the seminal vesicle has a prominent distal part.

Metacercaria (*figure* 23)

The following description is based on the examination of living specimens and of 36 whole-mounts, of which 10 were measured, of metacercariae from naturally infected fish.

The metacercaria is described in detail for two reasons, namely, to show that it is conspecific with *bearupi*, and to illustrate the advanced state of development attained by this stage.

Body 1.32 (1.08–1.43) mm long and 347 (286–434) μm wide, widest between bifurcation of gut and ventrogenital sac; forebody and hindbody not separated by constriction. Body closely covered with scales, larger and five-ribbed anteriorly and dorsally, becoming spines at about level of posterior testis and continuing to posterior end; absent pre-orally ventral to mouths of frontal glands. Cercarial pigment scattered throughout body, more abundant between caeca in forebody. Frontal-gland cells prominent, extend from pharynx to ventrogenital sac, most abundant between caeca; ducts inconspicuous; duct mouths form conspicuous transverse band across pre-oral spineless area. Tegumental glands numerous but inconspicuous, most abundant anteriorly and ventrally and about mouth of ventrogenital sac. Prepharyngeal and oesophageal glands not seen. Prominent sensory papillae about oral sucker and laterally over whole length of body.

Oral sucker subterminal, 111 (99–126) × 121 (111–134) μm. Prepharynx variable, 12–58 μm long. Pharynx 73 (62–89) × 52 (41–64) μm. Oesophagus short. Caeca simple, straight, extend almost to posterior end, dilated in forebody; caecal epithelium of columnar cells with contiguous bases and separated tips, with nucleus towards base and single large vacuole (droplet?) at apex.

Ventrogenital sac small, median, without lateral pocket; 35–41/100ths from anterior end; musculature not clear but apparently as in adult; mouth symmetric. Ventral sucker symmetric, with large cavity directed ventrally or sinistro-ventrally, solidly muscular; armed with 8–9 rows of minute spines encircling rim; 58 (41–68) × 58 (50–70) μm, ratio o.s./v.s. (lengths) 1.8–2.4. Gonotyl hemispherical, unarmed, anucleate, solidly muscular, not penetrated by genital atrium; 39 (33–47) × 34 (31–35) μm. Genital atrium short, opens into ventrogenital sac immediately dorsal to gonotyl.

Testes diagonal, separated, small but with indications of early spermatogenesis; anterior testis 56 (43–68) × 52 (39–70) μm; posterior testis 67 (45–85) × 51 (41–78) μm; sperm ducts united at level of ovary into short common sperm duct or at proximal end of seminal vesicle. Seminal vesicle constricted, extends posteriorly to level of ovary; proximal part with thick

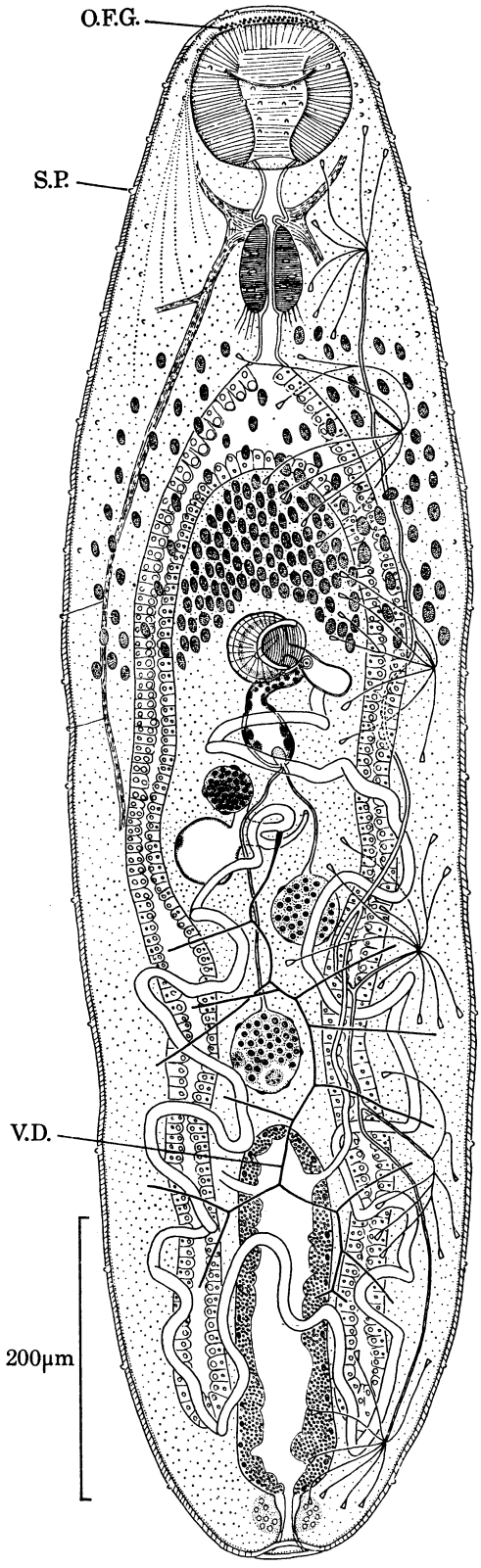


FIGURE 23. *G. bearupi.* Metacercaria (details from life).

outer layer of diagonal muscle-fibres and thin inner layer of circular muscle-fibres, 59 (39–84) × 37 (31–41) μm; distal part smaller, with thinner wall of circular fibres, not clearly separated from prostatic ejaculatory duct except in shape of nuclei in lining. Prostatic ejaculatory duct elongate, transverse, with thick wall of outer longitudinal and inner circular muscle-fibres, with lumen filled by inbulging ends of prostatic-gland ducts, opens into genital atrium dorsally through conical papilla; gland-cell bodies not seen.

Ovary submedian on right; 37 (29–48) × 38 (31–48) μm; oviduct arises dorso-medially, first part non-muscular, second part dilated with strong circular fibres; oviduct, duct of seminal receptacle and Laurer's canal unite postero-medial to ovary. Seminal receptacle small, posterior to ovary, 52 (39–64) × 51 (43–64) μm; with muscle fibres (dilators?) radiating out from wall into parenchyma. Laurer's canal opens in mid-line dorsally. Common vitelline duct enters just before ootype. Uterus coils about region of ootype, then descends ventral to caecum on right almost to posterior end, crosses excretory bladder ventrally in anteriorly arching loop, ascends on left ventral to caecum, loops ventrally across seminal vesicle and enters genital atrium by way of short thick-walled metraterm. Common vitelline duct runs posterad, ventrally between testes; gives rise to 10–13 branches ending in follicle rudiments.

Excretory pore terminal, opens through elongate sphincter into bladder. Excretory bladder tubular, with irregular thick lining filled with small inclusions of uniform size; rarely reaches posterior border of posterior testis. Bladder arms rise subterminally and usually asymmetrically; each runs forward ventral to caecum, and divides between the middle of the anterior testis and the anterior border of the ovary, into anterior and posterior collecting tubules, each of which gives rise to three groups of flame cells. Flame-cell formula (derived from one individual) $2[(7+7+7)+(11+7+8)]$.

Metacercarial cysts thin walled, hyaline, 506–734 × 329–430 μm, for eight cysts.

Host. Half-beak, *Hyporhamphus* sp.

Location. In cysts in mesentery near heart.

Locality. Heron Island, Capricorn Group, Queensland.

Disposition. U.S.N.M. no. 72047; B.M.(N.H.) no. 1972.1.24.3; M.P.M. no. 19025; author's collection.

The inclusions in the epithelial lining of the excretory bladder looked like droplets in living metacercariae; but in stained wholemounts, they appeared as collapsed spheres, rather like the collapsed eggs in the uterus of mounted adults. It would appear from this that the inclusions are bounded by a layer that perhaps hardens in alcohol, and then collapses during dehydration. Thus, these inclusions are neither simple (lipid) droplets nor calcareous concretions, such as are commonly found in many metacercariae.

Comparison of the metacercaria with the adult reveals the advanced stage of development attained by the reproductive system of the former. The various organs are developed, ducts are patent, and the ventrogenital complex is fully formed. All that is wanting is eggs, sperm, and vitelline cells.

Comparison of measurements (table 2) shows that: (i) the largest metacercaria is longer than the smallest ovigerous adult, (ii) young adults (type series) are narrower than metacercariae, (iii) the forebody does not change, but the hindbody lengthens as the uterus fills with eggs, (iv) oral and ventral sucker do not grow, the increase in the ratio o.s./v.s. apparently is a result of dilatation rather than growth of the oral sucker, and (v) the testes apparently continue to grow uniformly as the worm grows (cf. *renincola*).

A curious difference between the two is seen in the course of the uterus, which, in the metacercaria, descends to the right and ascends to the left of both testes, but in the adult typically passes the anterior testis on the right, crosses the mid-line between the testes, and passes the posterior testis on the left. It would appear that as the uterus fills with eggs and lengthens, it loops in a regular manner about the testes.

TABLE 2. COMPARISON OF ADULT AND METACERCARIA OF *G. BEARUPI*

character, stage	metacercaria	adult (type series)
body length/mm	1.08–1.43	1.39–1.90
width/μm	286–434	218–348
forebody length/μm	444–525	435–580
ratio forebody/total	1.35–0.41	0.26–0.33
oral sucker/μm	99–126 × 111–134	109–126 × 130–155
ventral sucker/μm	41–68 × 50–70	43–56 × 49–58
ratio o.s./v.s. (lengths)	1.5–2.4	2.1–2.7
anterior testis/μm	43–68 × 39–70	80–110 × 84–136
posterior testis/μm	45–85 × 41–78	90–126 × 87–136

(*d*) *Galactosomum cochleare* orth. emend.

Synonyms

Distoma cochleariforme (*sterniae*) Rudolphi, 1819 (*Sterna minuta*, *S. cantiaca*, *Sterna* sp.; Brazil, descr.; types Berlin, Vienna).

Distoma cochlear Diesing, 1850 (re-descr. of Rudolphi's specimens).

Distoma diesingi Cobbold, 1861 (new name for *D. cochlear* Diesing).

Microlistrum cochlear (Diesing) Braun, 1901; Braun, 1902, Fig. 36, Pl. 3 (re-descr. of Rudolphi's specimens); Odhner, 1910, Fig. (re-descr. of Rudolphi's specimens).

non Microlistrum cochlear (Diesing) Timon-David, 1935 (syn. of *Knipowitschetrema echinatum* Timon-David, 1955).

Galactosomum cochlear (Diesing) Travassos, 1929; Morozov, 1952 (syn. of *Galactosomum cochleariforme*); Hutton & Sogandares-Bernal, 1960 (possibly synonymous with *Galactosomum fregatae*); Cable, Connor & Balling, 1960, Figs. 16, 17, Pl. 3 (*Thalasseus maximus maximus*; Puerto Rico; descr.).

non Galactosomum cochlear (Diesing) Dollfus & Capron, 1958; syn. of *Galactosomum dollfusi*, *q.v.*

Galactosomum cochleare has been collected only twice, once by Natterer many years ago, and a second time by Cable *et al.* (1960). Although Natterer's specimens, described by Rudolphi (1819), have been redescribed three times, by Diesing (1850), Braun (1902) and Odhner (1910), the ventrogenital complex has not been described fully. For this reason, some of Natterer's specimens are redescribed below, and compared with a specimen and the description of Cable *et al.* (1960) to confirm their identification and correct some minor errors in their description.

Description (*figures* 25, 79)

The following brief description is based on two whole worms and a fragment containing the ventrogenital complex, all three dead when fixed and not flattened. Measurements are given of both whole worms.

With the characters of the genus. Body elongate, 3320, 2920 μm long; distinctly divided into short lanceolate flattened forebody, 910, 1030 μm long and 298, 460 μm wide, and long, subcylindrical hindbody 2410, 1890 μm long and 450, 460 μm wide.

Forebody scaly; most scales and spines lost. Gland cells not seen in forebody between caeca. Forebody with numerous dorso-ventral fibres between caeca and lateral to pharynx and prepharynx, and transverse fibres, deep to body-wall musculature ventrally, running from margin of body laterally to level of medial border of caeca. Without specialized dorso-ventral fibres or dorsal, or ventral pit.

Oral sucker small, 97, — μm long and 113, 153 μm wide. Prepharynx short, infolded forming fornix over anterior end of pharynx. Pharynx large, 104, 130 μm long and 94, 97 μm wide; with two groups of postero-lateral retractors running back dorsal to caeca, and protractors apparently closely investing prepharynx. Caeca narrow, straight or nearly so, extend almost to posterior end.

Ventrogenital sac median, at junction of forebody and hindbody, 27/100ths, 35/100ths from anterior end, ventrogenital sac and ventral sucker together occupy whole of intercaecal space; with lateral pocket; mouth simple, symmetric; musculature poorly developed, dextral hemisphincter apparently absent. Ventral sucker symmetric, sucker-like, with cavity reduced in diameter and variable in depth, presumably eversible; 110, 117 μm long and 117, 120 μm wide, ratio o.s./v.s. (lengths) 0.88, —; with thick capsule of circular fibres enclosing parenchymatous medulla traversed by numerous radial fibres running from walls of rim and cavity to outer capsule; and with two transverse bands of fibres, one anterior and one posterior, running from wall of cavity to outer capsule at right angles to radial fibres; rim and sides (but not bottom) cavity armed with slender 3.5–5.0 μm spines forming a broad circlet; mouth of cavity directed ventro-medially. Gonotyl arises postero-sinistrally; base overhangs genital pore, apex overlies cavity of ventral sucker; bilobed, with large linguiform ventral lobe with dorsal groove running from base over genital pore to free tip, and small antero-dorsal lobe.

Testes large, rounded, entire; occupy whole of intercaecal space; anterior testis 363, 292 μm long and 282, 298 μm wide; posterior testis 353, 353 μm long and 320, 310 μm wide; separated by coils of uterus. Sperm ducts unite at seminal vesicle. Seminal vesicle two-chambered; proximal thin walled, sinuous, sacculated; distal with thicker wall of prominent circular fibres, subreniform, shorter than proximal, with strong flexure between chambers, such that axes of two portions form a right angle. Prostatic ejaculatory duct arises ventro-terminally, curves forward medio-anterad; short, slightly dilated; opens into genital atrium via long papilla. Bodies of prostatic-gland cells massed between ventral sucker and flexure in distal chamber of seminal vesicle, largely intercaecal. Genital atrium short; does not enter gonotyl.

Ovary rounded, submedian on right; anterior border at or behind posterior end of seminal vesicle; 156, 139 μm long and 162, 185 μm wide. Seminal receptacle large, transversely oval, immediately behind ovary; 133, 113 μm long and 214, 220 μm wide. Course of uterus typical; ascending arm with several transverse loops ventral to seminal vesicle; enters genital atrium ventral to male duct. Vitellaria follicular, largely lateral; extend anteriorly to or almost to posterior border of ovary, and posteriorly almost to ends of caeca; interrupted lateral to testes on both sides, or sinistral to anterior testis and dextral to posterior testis. Eggs (10, uterine) 28.4 (27.2–29.8) × 15.4 (14.4–16.1) μm.

Excretory pore terminal. Excretory bladder not visible.

HOST. *Sterna* sp.

LOCATION. Intestine.

LOCALITY. Brazil.

DISPOSITION. Berlin, Coll. Rud., no. 1498.

Comparison with the description of Cable *et al.* (1960), and with one of Professor Cable's specimens in my collection, showed agreement in most characters, except that the genital atrium does not enter the gonotyl, and spines on the ventral sucker are absent in the bottom of the cavity.

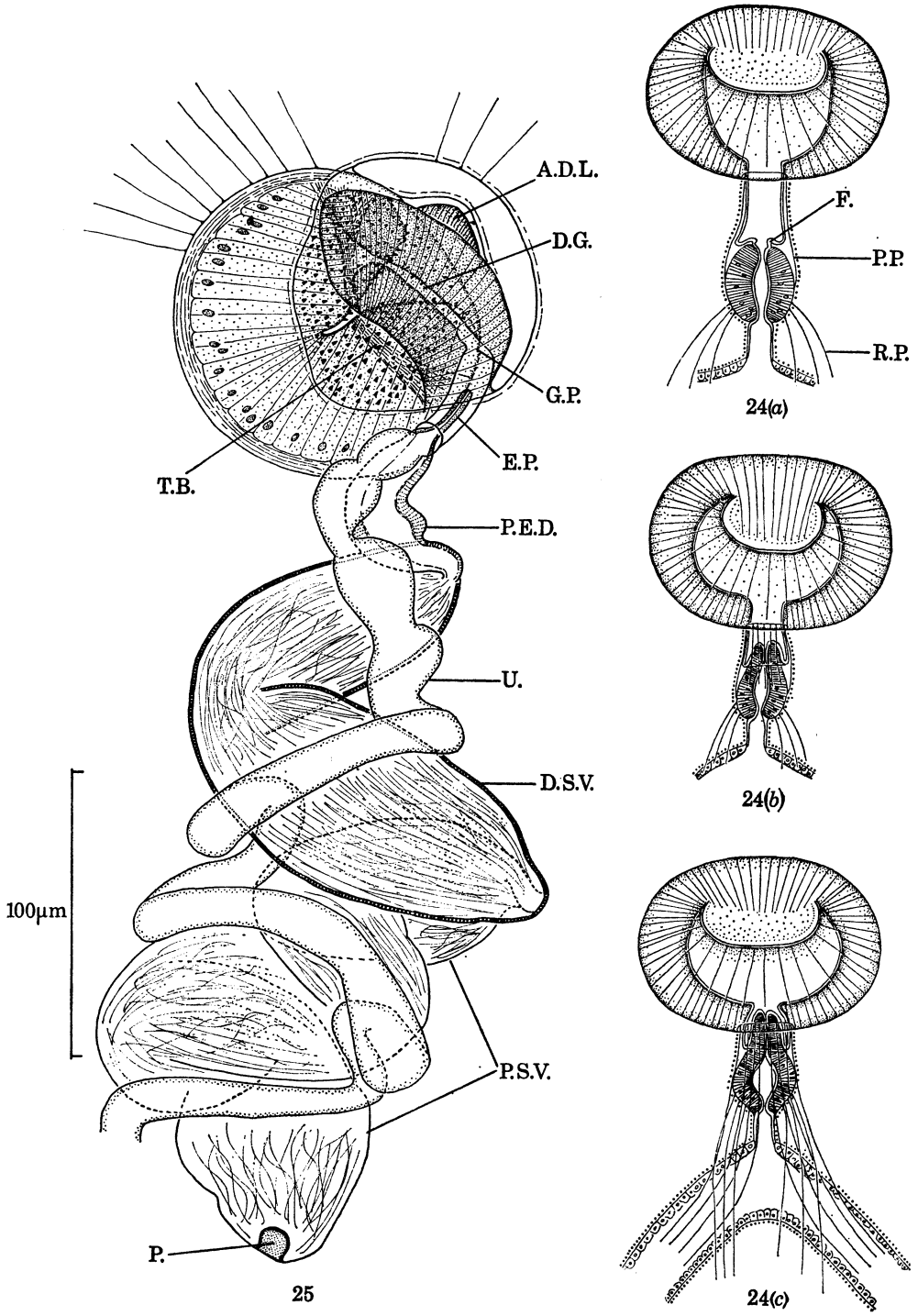


FIGURE 24. *G. bearupi.* Movement of pharynx (*a*) at rest, (*b*) partly protracted, (*c*) fully protracted (free-hand).
FIGURE 25. *G. cochleare.* Ventrogenital complex (Berlin, no. 1498).

Examination of the specimen from Professor Cable revealed some details of the musculature of the ventrogenital sac not seen in Rudolphi's specimens. Thus, the mouth of the ventrogenital sac is enclosed by a band of superficial circular fibres. Some of the outermost fibres on each side posteriorly leave the circular band and run latero-anterad dorsal to the muscles of the body wall. Immediately dorsal to the circular fibres is a sheet of separated fibres arising from the anterior margin of the mouth, and running antero-dorsad close to the ventrogenital sac and ventral sucker. There is no dextral hemisphincter encircling the ventrogenital sac. A few stout fibres radiate out into the parenchyma from the capsule of the ventral sucker over the antero-dextral quarter, and from the wall of the ventrogenital sac opposite the antero-dorsal lobe of the gonotyl.

Diagnosis (*supplemented from Cable* et al. 1960)

Body elongate, divided into short lanceolate forebody and long subcylindrical hindbody. Oral sucker small; prepharynx short, about as long as pharynx. Ventrogenital sac well behind gut bifurcation, at junction of forebody and hindbody, 27–35/100ths from anterior end; with lateral pocket; ventral sucker orientated transversely, sucker-like with reduced cavity and parenchymatous medulla, armed with wide circle of 3.5–5.0 μm spines; gonotyl overhangs genital pore, with large linguiform dorsally grooved lobe overlapping ventral sucker and small antero-dorsal lobe laterally; seminal vesicle two-chambered, proximal thin-walled sinuous, distal reniform with thicker wall of circular fibres; prostatic ejaculatory duct short and narrow. Vitellaria lateral, extend from posterior border of ovary almost to ends of caeca; absent lateral to testes on one or both sides. Eggs 28.4 (27.2–29.8) × 15.4 (14.4–16.1) μm. Excretory bladder tubular, reaches posterior testis.

(*e*) *Galactosomum cochleariformum* orth. emend.

Synonyms

Distoma cochleariforme Rudolphi, 1819 (in part) (*Pelecanus aquila* (*Fregata aquila*); Brazil; descr.; types Berlin, Vienna); Diesing, 1850 (re-descr. of Rudolphi's specimens).

Microlistrum cochleariforme (Rudolphi) Braun, 1901; Braun, 1902, Fig. 35, Pl. 3 (re-descr. of Rudolphi's specimens); Odhner, 1910 (tax.).

non Microlistrum cochleariforme (Rudolphi) Joyeux & Baer, 1928; Dubois & Mahon, 1959. syn. of *Galactosomum timondavidi*, *q.v.*

Galactosomum cochleariforme (Rudolphi) Pratt, 1911, Figs. 1–5 (*Fregata aquila*; Tortugas, Florida, U.S.A.; descr.); Linton, 1928, Fig. 52, Pl. 7 (*F. magnificens*; Tortugas, Florida, U.S.A.; descr.); Manter, 1930 (*F. aquila*; Tortugas, Florida, U.S.A.); Hutton & Sogandares-Bernal, 1960, Fig. 2*b* (*F. magnificens rothschildi* Mathews; Florida, U.S.A.; descr.); Cable, Connor & Balling, 1960, Figs. 11–15, Pl. 3 (*Sula leucogaster leucogaster* (Boddaert); Puerto Rico; descr.).

Cercarioides cochleariforme (Rudolphi) Witenberg, 1953.

The host in the citations of Rudolphi & Manter was probably *Fregata minor*, a wide-ranging species common in the Caribbean and not *Fregata aquila*, a species restricted to Ascension Island.

In his original description of specimens collected by Natterer in Brazil, Rudolphi (1819) considered that those from terns differed from those from the frigate bird, and called the former *Distoma cochleariforme* (*sterniae*). Diesing (1850) re-examined Rudolphi's specimens, decided that the ones from terns were distinct, and proposed the name *D. cochlear* for them. Braun (1902)

also re-examined Rudolphi's specimens and agreed with Diesing that they represented two species.

Description (*figures* 26, 27, 80)

The description is based on five specimens from different sources. The diagnosis is supplemented from Cable *et al.* (1960). Measurements (range) are given for the five specimens.

With the characters of the genus. Body 4820–6350 μm long; distinctly divided into short, spatulate forebody 1570–2120 μm long and 1500–1790 μm wide, concave ventrally; and cylindrical or subcylindrical elongate hindbody 3240–4230 μm long and 1030–1080 μm wide; ratio (lengths) forebody/hindbody 1:1.9 to 1:3.3.

Body with small, closely set scales anteriorly, becoming spines on hindbody and extending to posterior end; extreme anterior end unarmed, with 7–8 rows minute scales ventrally between unarmed area and oral sucker. Gland cells not seen in forebody between caeca. Dorsoventral fibres numerous in forebody, especially between caeca, but neither dorsal nor ventral pit present.

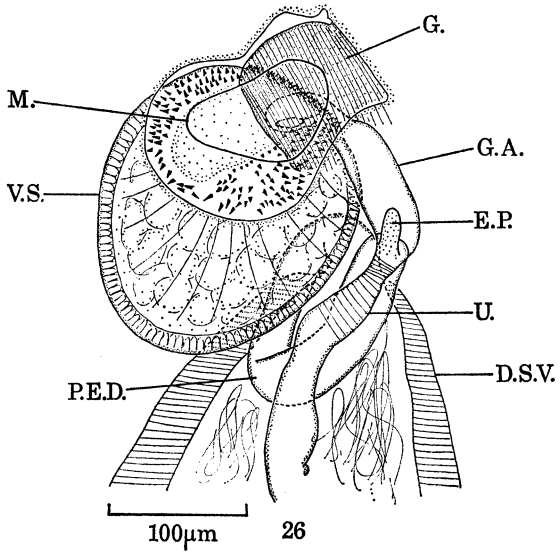
Oral sucker 220–324 μm long and 240–280 μm wide. Prepharynx short and wide; forming ventrally incised fornix at anterior end of pharynx. Pharynx 210–260 μm long and 140–210 μm wide; with protractors closely investing wall of prepharynx and two groups of postero-lateral retractors running back dorsal to caeca. Caeca slightly sinuous or straight, not inflated, extend almost to posterior end.

Ventrogenital sac small, median, just in front of junction of forebody and hindbody, 23–35/100ths from anterior end; with small lateral pocket. Mouth asymmetric, crescentic or comma-shaped; with large, rounded, muscular anterior lobe, with diagonal fibres (D.F.). Musculature of sac includes well-developed dextral hemisphincter (D.H.) arising near base of gonotyl, encircling mouth dextrally, inserted anteriorly and antero-sinistrally; fibres radiating out from the wall, especially laterally and anteriorly (A.F.), into the parenchyma; fibres (D.A.F.) arising from wall of sac dorsal to dextral hemisphincter and running forward. Ventral sucker symmetric, sucker-like, with reduced but variable cavity and parenchymatous medulla traversed by radial fibres, with thick capsule of circular fibres; axis inclined forward and to the left; 170–220 μm long and 170–190 μm wide; ratio o.s./v.s. (widths) 1.4–1.6; armed with stout spines up to 11 μm long in two groups on and within rim of cavity on either side, groups joined by 1–2 rows of spines anteriorly and posteriorly. Gonotyl arises postero-sinistrally; bilobed, with smaller dorso-medial lobe bearing genital pore dorsally, and larger ventro-lateral lobe. Genital atrium short, pierces base of gonotyl and runs mediad in dorso-medial lobe.

Testes tandem or slightly diagonal, entire or lobed, separated by ascending and descending arms of uterus, occupy most of intercaecal space. Seminal vesicle two-chambered; proximal smaller than distal; long axes form acute angle; proximal chamber thin-walled, saccate, transverse, on left anterior to ovary, joined to distal chamber by discrete, slender duct with prominent circular muscle-fibres; distal elongate, fusiform, with very thick inner circular layer and thin outer longitudinal layer of muscle-fibres. Prostatic ejaculatory duct elongate, slender; loops posteriorly, opens into genital atrium via a conical papilla.

Ovary transversely elliptical, on right, at or behind level of proximal chamber of seminal vesicle. Seminal receptacle immediately behind ovary, transversely elongate. Course of uterus typical; with ascending and descending arms passing anterior testis on right; crossing between testes, and passing posterior testis on left; behind posterior testis descending arm dextral,

ascending arm sinistral; ascending arm with two transverse loops anterior to ovary; terminal loop with outer longitudinal and inner circular muscle-fibres; with prominent sphincter at entrance into genital atrium. Vitellaria follicular, follicles in rosettes; lateral throughout whole length, with a few follicles exceeding medial border of caeca dorsally and ventrally; extend anteriorly on right to between anterior border of ovary and posterior third of distal chamber of seminal vesicle, on left to between middle of ovary and middle of distal chamber of seminal vesicle; extend posteriorly to, nearly to, or beyond ends of caeca, but not beyond coils of uterus. Eggs (10, uterine) 31.0 (29.8–32.4) × 16.0 (14.5–17.0) μm.



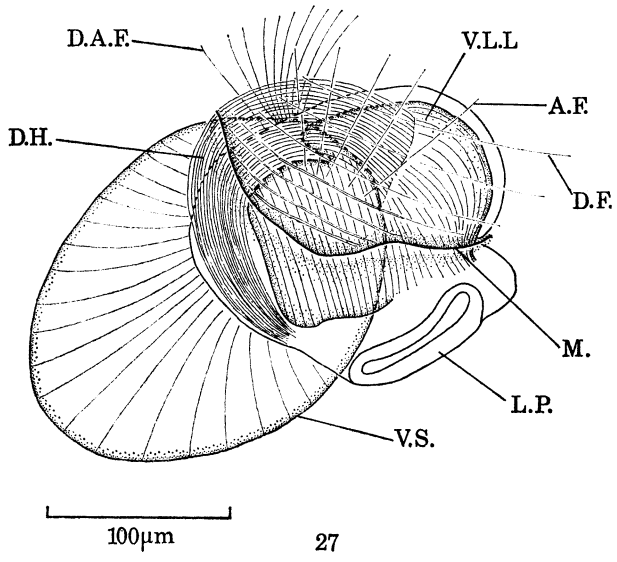


FIGURE 26. *G. cochleariformum.* Syntype, ventrogenital complex (Berlin, no. 1500).

FIGURE 27. *G. cochleariformum.* Musculature of ventrogenital sac (free-hand).

Specimens examined

Brazil	ex intestine *Pelecanus aquila* (*Fregata aquila*); coll. by Natterer, Berlin, coll. Rudolphi no. 1500	1 specimen type
Florida, U.S.A.	ex intestine *F. magnificens* (Linton 1928); U.S.N.M. no. 7943	1 specimen
	ex *Fregata aquila* (Manter 1930); author's colln	2 specimens
	ex intestine *F. magnificens rothschildi* Mathews (Hutton & Sogandares-Bernal 1960); author's colln	1 specimen
Puerto Rico	ex posterior intestine *Sula leucogaster* (Cable *et al.* 1960); U.S.N.M. no. 38212 (Fig. 11, Pl. 3, Cable *et al.* 1960); coll. Cable, author's colln	2 specimens

Linton's specimen was not included among those described above. Rather, it was examined to see whether Witenberg (1929, p. 223) was correct in suggesting that it belonged to *spinetum.* It does not, and is clearly *cochleariformum.*

Remarks

The single type specimen from the Berlin Museum differs from the other specimens examined, and from the description of Cable *et al.* (1960), in several features, some at least of which may be ascribed to the poor state of preservation of the specimen, now nearly 200 years old, and to the fact that it was probably dead but not flattened, when fixed. Thus, in the type (figure 80), the testes are entire and rounded, as described and figured by Pratt (1911), whereas in the specimen from Hutton & Sogandares-Bernal, also unflattened, they are distinctly lobed. As lobing of

testes frequently results from forcing the testes against the widely spaced dorso-ventral muscle-fibres, especially when worms are flattened, as are the specimens of Manter and of Cable, perhaps the difference between the type and the specimen of Hutton & Sogandares-Bernal is the result of relaxation in death of the muscle fibres in the type, but contraction during fixation in the latter.

The form of the testes is not an important character. More important are differences in the ventrogenital complex. In the type (figure 26), the gonotyl is simple and a lateral pocket could not be seen, whereas all of the other specimens (figure 27) have a lateral pocket and a gonotyl of complex form. But, as in other characters, especially those of the ventral sucker and seminal vesicle, all specimens agree, these differences are put down to the poor state of the type.

The excretory bladder and bladder arms could not be traced in the specimens available. According to Cable *et al.* (1960), the tubular bladder extends only to the posterior testis, and the bladder arms extend almost to the oral sucker and turn posteriorly before dividing (i.e. stenostomate).

The body is distinctly divided into a short wide forebody and a long, slender hindbody, the ratio of whose lengths is 1:3.3 in both unflattened specimens. But in three flattened specimens, the hindbody is shorter and wider, and the ratio varies from 1:1.9 to 1:2.2. The ratio is even lower, namely 1:1.1, in the specimen figured (Fig. 11, Pl. 3) by Cable *et al.* (1960). Thus, flattening greatly distorts the body proportions, as well as altering the shape of the testes.

Diagnosis

Body elongate, distinctly divided into short, wide, ventrally concave forebody and long, narrow, subcylindrical hindbody, up to three times as long as forebody. Prepharynx shorter than pharynx. Ventrogenital sac well behind gut bifurcation, just in front of junction of forebody and hindbody, 23–35/100ths from anterior end in unflattened specimens, with lateral pocket; ventral sucker smaller than oral sucker, sucker like, with reduced cavity and parenchymatous medulla, armed with band of 11 μm stout spines on rim widening laterally to form two lateral masses of spines; gonotyl variable, two parted, with genital atrium opening dorso-medially; seminal vesicle two-chambered, proximal chamber thin-walled and saccate, distal chamber elongate fusiform with thick wall of circular fibres; prostatic ejaculatory duct slender, elongate, looped posteriorly. Vitellaria in rosettes, lateral, extend anteriorly to between middle of ovary and middle of distal chamber of seminal vesicle, posteriorly to about ends of caeca. Eggs 31.0 (29.8–32.4) × 16.0 (14.5–17.0) μm. Excretory bladder extends to posterior testis; bladder arms stenostomate.

G. cochleariformum is closest to *cochleare* and *spinetum* in form and spination of the ventral sucker, and in having a lateral pocket and a short excretory bladder. Although dissimilar in gross appearance, the seminal vesicle is fundamentally similar in all three species, being two-chambered with proximal thin-walled and distal thick-walled chambers.

G. cochleariformum is not related to *Cercarioides*, despite a superficial resemblance in body shape.

(*f*) *Galactosomum darbyi*

Synonyms

Galactosomum darbyi Price, 1934, Figs. 3, 4, Pl. 1 (*Pelecanus occidentalis occidentalis* L.; Dominica; descr.; types U.S.N.M. no. 38699, 38700); Yamaguti, 1939 (proposed transfer to *Stictodora*).
Sobolephya darbyi (Price) Yamaguti, 1958.

The position of *darbyi* has remained equivocal since it was first described. Price (1934) pointed out that *darbyi* and *johnsoni*, which he described at the same time, were close to the genus *Stictodora*, and suggested that further discoveries might bridge the gap and result in synonymizing *Stictodora* and *Galactosomum*. Yamaguti (1939), on the basis of Price's description, proposed the transfer of *darbyi* to *Stictodora* without making the new combination, and later (1958) formally transferred it to the genus *Sobolephya*, which is probably a synonym of *Stictodora*.

Similarities between *G. darbyi* and *Stictodora sensu* Price include: (i) long prepharynx and distinct oesophagus, (ii) vitelline follicles scattered among coils of uterus, (iii) ventral sucker armed with relatively large spines, and (iv) small size. Of these, the last-named may be particularly significant in producing similarities that are more apparent than real. If a fluke, for example, a species of *Galactosomum*, is reduced in size, then there is less room for the vitelline follicles and so these may be crowded among the coils of the uterus. Possibly, the ventral sucker underwent relatively greater reduction than did its spines. And finally there appears to be an inverse relationship between total size and length of prepharynx among species of *Galactosomum*.

Re-examination of the holotype and six paratypes, all of which are poor specimens dead when fixed, revealed only two features not described by Price (1934), namely that the ventral sucker (gonotyl of Price) is parenchymatous, and that its apex is uniformly covered with minute spines. But as these characters are not of generic significance, they do not help to resolve the position of *darbyi*.

Through the kind offices of Dr J. M. Kinsella, I have been able to study 10 specimens of what are undoubtedly *darbyi*, collected from the type host. Although dead when fixed and macerated, especially anteriorly, these specimens (described below) show additional features of the ventrogenital complex, and especially of the male system (muscular seminal vesicle), that are consonant with the generic diagnosis of the genus *Galactosomum*, to which *darbyi* is here returned.

Description (*figures* 28, 29, 81)

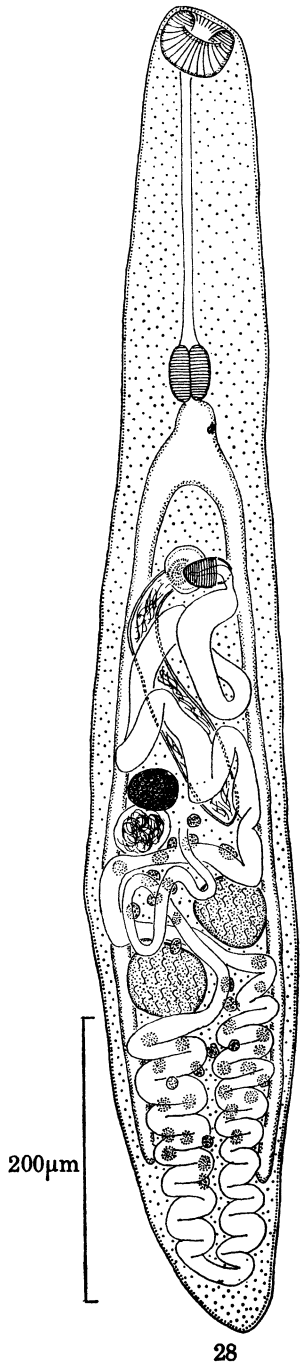
As six of the 10 specimens have macerated anterior ends, measurements of the series are incomplete and are expressed as a range.

With the characters of the genus. Body elongate, 868–973 μm long; forebody 340–422 μm long, tapering slightly; hindbody tapering posteriorly, 127–146 μm wide, wider than forebody. Spines (scales?) lost.

Oral sucker 38–45 μm long and 33–53 μm wide. Prepharynx 151–206 μm long. Pharynx 36–41 μm long and 24–30 μm wide. Oesophagus present, short. Caeca slender, extend to within 85–126 μm of posterior end.

Ventrogenital sac median, 37–43/100ths from anterior end and 32–58 μm behind bifurcation of caeca; lateral pocket absent, mouth large. Ventral sucker dextral, axis dorso-ventral; nearly spherical, 27–33 μm long and 24–32 μm wide; with reduced eversible elliptical cavity lined with < 2 μm spines, everted forms an elliptical uniformly spined dome; ratio o.s./v.s. (widths) 1.6–1.8. Gonotyl simple, tongue-like tip overlies ventral sucker; 23×15 μm; genital atrium enters gonotyl and opens dorsally and subterminally.

Gonads in third quarter of body. Testes large, rounded, diagonal, contiguous, or separated by coils of uterus; anterior testis sinistral, 41–64 μm long and 42–53 μm wide; posterior testis dextral, 45–59 μm long, and 44–57 μm wide. Seminal vesicle one-chambered, large; 155–211 μm long and 30–41 μm wide; with relatively thin wall, fusiform, inclined to the right, with



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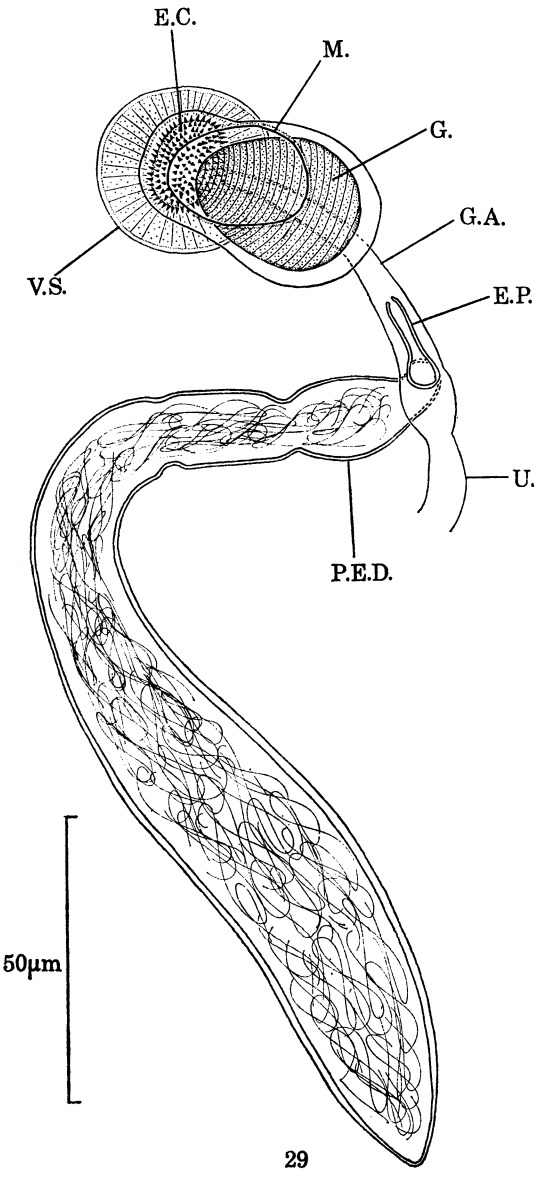


29

FIGURE 28. *G. darbyi.* Whole worm (ventral).

FIGURE 29. *G. darbyi.* Ventrogenital complex of specimen in figure 28 (semi-schematic).

elongate anterior portion transverse, in some a slight constriction dextrally in transverse portion (incipiently constricted). Prostatic ejaculatory duct ellipsoidal; 20–30 μm long and 9–21 μm wide; separated from seminal vesicle by constriction, runs sinistrad or ventrad; opens into genital atrium via long papilla.

Ovary dextral, opposite posterior end of seminal vesicle; 24–38 μm long and 32–44 μm wide. Seminal receptacle postero-dorsal to and overlapping ovary; 35–50 μm long and 42–68 μm wide. Uterus with typical course, with transverse loop ventrally across seminal vesicle; poster-

iorly exceeds caeca but does not reach posterior end. Vitelline follicles scattered at all levels from ventral to dorsal surface among coils of uterus; extend anteriorly to ovary, posteriorly to or beyond ends of caeca. Eggs (20, uterine) 22.0 (21.2–23.0) × 12.0 (11.0–12.7) μm.

Excretory bladder not seen.

HOST. *Pelecanus occidentalis* L.

LOCATION. Small intestine.

LOCALITY. Miami, Florida, U.S.A. new locality.

Host collected by D. J. Forrester, 4. ii. 1971.

Parasite collected by J. M. Kinsella PEL–1.

DISPOSITION. U.S.N.M. no. 72048; B.M.(N.H.) no. 1972.1.24.4; M.P.M. no. 19026; author's colln.

Remarks

In some specimens, the seminal vesicle exhibits a slight constriction in the first part of the transverse limb, suggestive of a constricted condition. But, unfortunately, the specimens are not good enough to allow this point to be confirmed from the direction of muscle fibres on either side of the constriction.

Diagnosis

Body elongate, slender. Oral sucker large; prepharynx distinctly longer than pharynx. Ventrogenital sac 37–43/100ths from anterior end, lateral pocket absent; ventral sucker symmetric, parenchymatous, ratio o.s./v.s. (widths) 1.6–1.8, with eversible cavity completely lined with minute spines; gonotyl simple; genital atrium enters gonotyl and opens subterminally and dorsally. Gonads in third quarter; testes diagonal; seminal vesicle one-chambered, with flexure. Vitellaria among coils of uterus at all levels from dorsal to ventral surface; extend from ovary to or beyond ends of caeca. Eggs 22 (21–23) × 12 (11–13) μm. Excretory bladder unknown.

(*g*) *Galactosomum dollfusi* sp.nov.

Synonym

Galactosomum cochlear Dollfus & Capron (not Diesing 1850), 1958 (*Sterna hirundo* L.; Senegal; no descr.).

Dollfus & Capron's material, although neither abundant nor in a good state of preservation, differs specifically from *G. cochlear* as herein described, and from all other species in the genus, and so is proposed as a new species, named in honour of Professor R. P. Dollfus.

Description (*figures* 30–32, 82)

The following description is based on the holotype and five paratypes, all of which apparently were dead when fixed, but not flattened. Measurements (ranges incomplete) are given for the holotype and three paratypes.

With the characters of the genus. Body moderately elongate, 1.13–1.53 mm long; forebody shorter and narrower than hindbody, forebody 226–328 μm wide, hindbody 234–426 μm wide. Body scales/spines lost. Gland cells abundant between bifurcation of gut and ventrogenital sac; ducts not seen.

Oral sucker subterminal, 87–74 μm. Prepharynx variable, as long or longer than pharynx, forming ventrally incised fornix at entrance to pharynx. Pharynx 66–100 × 50–66 μm. Oesophagus very short. Caeca straight, extend almost to posterior end.

Ventrogenital sac 28–31/100ths from anterior end, and one ventral-sucker length behind bifurcation of gut; mouth oval, without muscular thickening on right; lateral pocket absent. Muscle fibres associated with ventrogenital sac comprise (i) circular fibres (C.F.) about mouth of ventrogenital sac, (ii) dextral hemisphincter (D.H.) arising dorsally from full width of base of gonotyl, encircling ventrogenital sac counter-clockwise, and inserted on wall of ventrogenital sac sinistrally near base of accessory lobe of gonotyl, (iii) separated fibres anteriorly (A.F.) running dorsad, (iv) group of fibres (A.D.F.) arising from mouth dextrally ventral to dextral hemisphincter and curving anterad, (v) group of fibres (P.F.) arising from wall dextrally, dorsal to dextral hemisphincter, and running posterad, and (vi) a group of fibres (D.P.F.M.) arising from base of gonotyl ventrally, curving ventrally and then anteriorly, and inserted on posterior margin of mouth. Ventral sucker symmetric, slightly elongate, parenchymatous; 60–89 × 55–89 μm, ratio o.s./v.s. (lengths) ≈ 1.0; with reduced, elongate cavity bounded by two lateral, slightly swollen lips each bearing an elongate patch of minute slender spines 2.5 μm long. Gonotyl unarmed, solidly muscular arises sinistro-posteriorly; of two parts, postero-ventral linguiform body, 23–41 × 25–31 μm, bearing genital pore dorso-terminally, and antero-dorsal finger-like accessory lobe (F.L.) 43–64 × 19–27 μm, arising from base of gonotyl proper. Genital atrium short; formed by union of ejaculatory duct and uterus at base of gonotyl; penetrates gonotyl and opens dorso-terminally, opposite cavity of ventral sucker.

Testes rounded, diagonal, largely fill intercaecal space, separated by coils of uterus; sperm ducts not seen. Seminal vesicle one-chambered, constricted; proximal part elongate, fusiform, 137–254 × 64–107 μm, extending to level of ovary, with thick outer layer of diagonal fibres and thin inner layer of circular fibres; distal part rounded, with thinner wall of circular muscle-fibres, 33–80 × 33–76 μm. Prostatic ejaculatory duct 33 μm long, with thick wall of longitudinal muscle-fibres opens into genital atrium through conical papilla; bodies of prostatic-gland cells not seen.

Ovary submedian on right, opposite proximal end of seminal vesicle. Seminal receptacle postero-dorsal to and contiguous with ovary. Uterus with typical course. Vitellaria in rosettes in two longitudinal rows on either side of body; anteriorly extend to between ovary and anterior testis on right, to or slightly beyond ovary on left; posteriorly exceed caeca but not coils of uterus; follicles from each side meet in mid-line, dorsally and ventrally, between ovary and anterior testis, between testes and posterior to posterior testis; follicles absent or interrupted sinistral to anterior testis and dextral to posterior testis. Eggs (10, uterine) 28.7 (27.2–29.8) × 16.7 (14.5–18.7) μm.

Excretory pore subterminal, dorsal; excretory bladder tubular, does not reach posterior border of posterior testis; bladder arms arise terminally, ? run forward to level of pharynx.

Host. *Sterna hirundo* L.

Location. Intestine.

Locality. Rufisque, Senegal.

Disposition. U.S.N.M. holotype no. 72049, paratype no. 72050; Lille 2 paratypes; author's colln., 2 paratypes.

Remarks

In the holotype (figure 30), the distal part of the seminal vesicle is not rounded and clearly marked off from the proximal part, although its presence is indicated by circular muscle-fibres. However in the four paratypes, it is dilated with sperm and clearly set off from the proximal part.

Also in the holotype (figure 30), the accessory lobe of the gonotyl is largely obscured by the gonotyl proper, but in one of the paratypes (figure 32), its form and relationship to the gonotyl are more easily seen.

In some specimens, which were probably dead before fixing, both the ventral sucker and the gonotyl, together with its accessory lobe, are protruded through the mouth of the ventrogenital sac, presumably as they are in copulation. The ventral sucker and the gonotyl are directed ventrally and the long accessory lobe of the gonotyl, antero-ventrally.

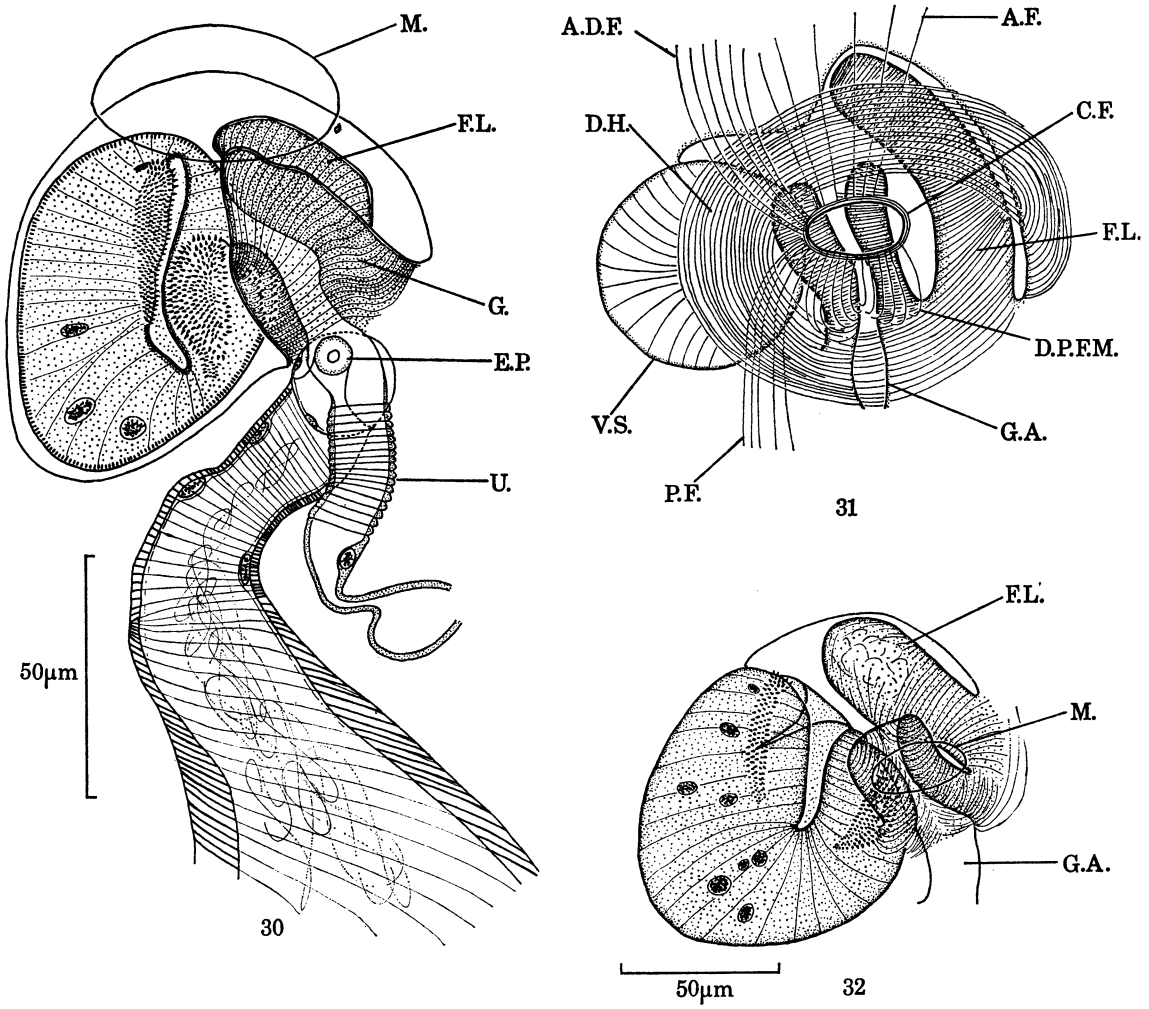


FIGURE 30. *G. dollfusi.* Holotype, ventrogenital complex.

FIGURE 31. *G. dollfusi.* Musculature of ventrogenital sac (free-hand).

FIGURE 32. *G. dollfusi.* Paratype, ventrogenital complex.

Diagnosis

Body moderately elongate, forebody shorter and narrower than hindbody. Prepharynx as long or longer than pharynx. Ventrogenital sac without lateral pocket, 28–31/100ths from anterior end and about one ventral-sucker length behind caecal bifurcation, mouth symmetric; ventral sucker about same length as oral sucker, symmetric, parenchymatous, with reduced elongate cavity bounded by two lateral lips each bearing an elongate patch of 2.5 μm spines

gonotyl bears genital pore dorso-terminally, with large digitiform antero-dorsal accessory lobe; seminal vesicle one-chambered, constricted, proximal part thick walled and elongate, distal part thin walled and rounded; prostatic ejaculatory duct short. Vitellaria extend anteriorly to or slightly beyond ovary, and posteriorly beyond ends of caeca; meet mid-ventrally and mid-dorsally except over gonads. Eggs 27–30 × 15–19 μm. Excretory bladder short, does not reach posterior border of posterior testis.

G. dollfusi differs distinctly from *cochleare*, with which it was first identified, in form of body, spination of ventral sucker, and form of seminal vesicle. In the last-named character, it resembles *bearupi*, *yehi* and *fregatae*. In form and spination of the ventral sucker, it is close to *yehi* and *sanaensis*, but differs from the latter in form of the seminal vesicle and extent of the excretory bladder.

G. dollfusi and *yehi* are so alike that they were at first thought to be the same; however, the marked difference in the form of the gonotyl, simple in *yehi* but with accessory lobe in *dollfusi*, clearly separates the two. In addition, the ventral sucker of *dollfusi* is relatively larger than in *yehi* (ratio o.s./v.s. *dollfusi* ≈ 1.0; *yehi* 1.6–1.8), and there appear to be significant differences in the musculature of the ventrogenital sac, as reflected in the shape of the mouth of the sac, namely oval in *dollfusi* and crescentic in *yehi*.

(*h*) *Galactosomum fregatae*

Synonyms

Galactosomum fregatae Prudhoe, 1949, Figs. 3–5 (*Fregata magnificens rothschildi* Mathews; Trinidad; descr.; types B.M.(N.H.) 1933.3.22.49–85); Chandler, 1951 (*F. magnificens rothschildi* Mathews; Texas, U.S.A.; descr.).

Galactosomum puffini Caballero, Grocott & Zerecero (not Yamaguti, 1941), 1954, Figs. 11–13 (*Pelecanus occidentalis californicus* Ridgway; Canal Zone, Panama; descr.) new syn.

Galactosomum canis Yamaguti, 1954, Fig. 2 (dog; Macassar; descr.; types M.P.M. 22301); Dubois & Mahon, 1959 (syn. of *G. puffini*) new syn.

Galactosomum agrachanensis Saidov, 1954, Figs. 2, 3 (*Chlidonias hybrida* (Pallas); Dagestan, U.S.S.R.; descr.; syntypes Moscow Helm. Lab. INV. N. 120); Dubois & Mahon, 1959 (valid) new syn.

Galactosomum puffini Cable, Connor & Balling (not Yamaguti, 1941), 1960, Fig. 18 (*Thalasseus maximus maximus*, *Sterna albifrons antillarum* Pallas, *Sula leucogaster leucogaster* (Boddaert); Puerto Rico; descr.) new syn.

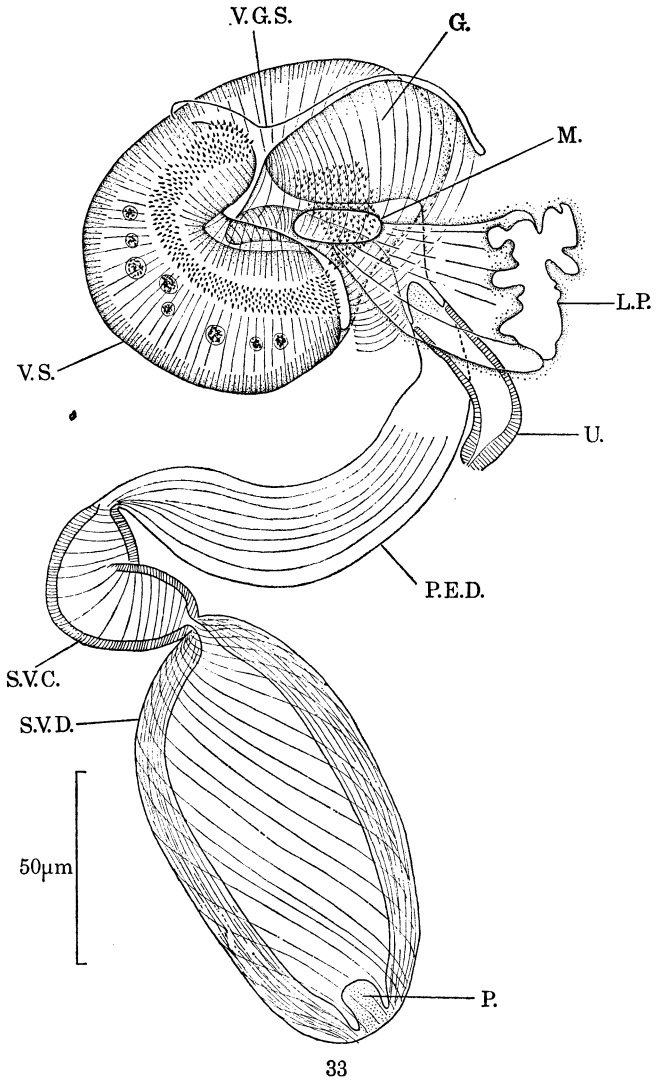
Galactosomum sp. Hutton & Sogandares-Bernal, 1960, Fig. 2*f* (*Larus atricilla* L.; Florida, U.S.A.; no descr.) new syn.

Galactosomum puffini Lumsden & Zischke (not Yamaguti, 1941), 1963, Figs. 16–18 (*Larus atricilla* L.; Louisiana, U.S.A.; descr.) new syn.

Galactosomum puffini Bravo-Hollis (not Yamaguti, 1941), 1967, Figs. 1–3 (*Larus occidentalis* Audubon; Baja California, Mexico; descr.) new syn.

Galactosomum puffini Nasir & Marval (not Yamaguti, 1941), 1968, Fig. 2 (*Larus atricilla*, L.; Cumana, Venezuela; descr.) new syn.

Hutton & Sogandares-Bernal (1960), in addition to listing *Galactosomum* sp. from *Larus atricilla* in Florida, mention that they compared this species with specimens of *Galactosomum* herein identified as *G. fregatae*, collected by them from *Larus argentatus smithsonianus*, *Pelecanus occidentalis carolinensis*, *Fregata magnificens rothschildi*, and with a specimen in their collection



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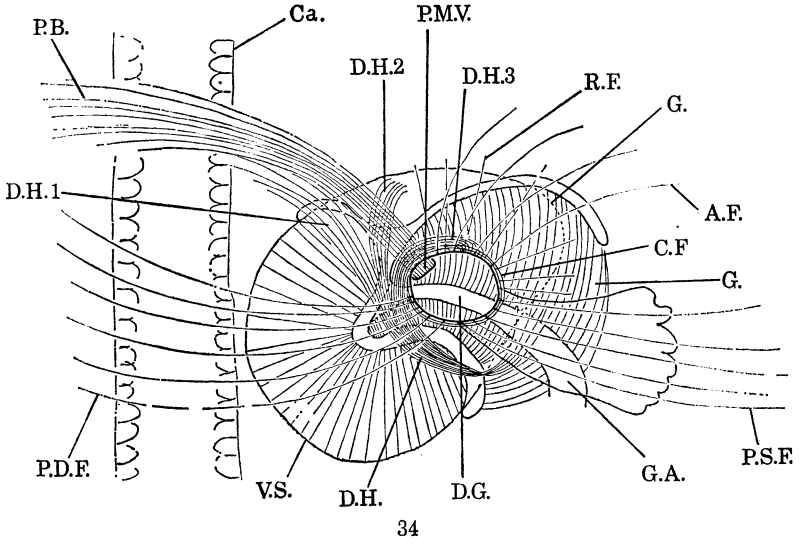

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FIGURE 33. *G. fregatae*. Syntype, ventrogenital complex.

FIGURE 34. *G. fregatae*. Musculature of ventrogenital sac (free-hand).

identified as *puffini* from *Pelecanus occidentalis californicus* from the Gulf of Panama. The last-named specimen was figured (figure 18) by Lumsden & Zischke (1963) who say that it was identified as *puffini* by Sogandares-Bernal and verified by Yamaguti. I have seen this specimen (figures 38, 39) and compared it with the type specimens of *fregatae* (figures 33, 36) and find them to be conspecific.

G. puffini, as redescribed herein, is distinct from *fregatae* in the form of the gonotyl and the form and spination of the ventral sucker.

Description (*figures* 33–39, 83)

The following description is a composite one, based on the material listed below in 'Specimens examined', except for Saidov's *agrachanensis* which were dead when fixed and had been strongly flattened. Ideally, this should be a re-description of the type specimens, but these, as Prudhoe (1949) has pointed out, were macerated when fixed, and are not good enough for full description; however, the ventral sucker in the syntypes (figures 33, 35) is identical in form and spination with that described below, and the diagnosis given agrees in all points with the types. Measurements are given for 10 specimens (marked with asterisk in list of 'Specimens examined').

With the characters of the genus. Body not distinctly divided but often with slight constriction behind ventrogenital sac; 1.1–2.3 mm long; forebody shorter than hindbody (ratio roughly 1:2), wider than hindbody in smaller specimens, narrower in larger; forebody without either dorsal or ventral pit or specialized dorso-ventral muscle-fibres.

Body closely covered with scales anteriorly, becoming spines at about level of ventrogenital sac; scales/spines markedly larger lateral to caeca than intercaecally between level of gut bifurcation and ventrogenital sac ventrally; with three rows pre-orally; extend to posterior end.

With scattered pigment granules in forebody. Frontal-gland cells abundant intercaecally anterior to ventrogenital sac; ducts open in transverse series in apical spineless area.

Oral sucker subterminal, 95 (66–126) × 106 (85–119) μm. Prepharynx variable, usually as long or longer than pharynx, forming ventrally incised fornix at mouth of pharynx. Pharynx 88 (68–119) × 61 (47–95) μm. Oesophagus short. Caeca simple, straight, extend almost to posterior end.

Ventrogenital sac large, median, not more than twice its length behind bifurcation of gut; mouth small, 29–36/100ths from anterior end, usually ventral to gonotyl, with outer circular (C.F.) and inner dorsally curving radial muscle-fibres anteriorly (R.F.) and sinistrally. Additional muscle-fibres of ventrogenital sac comprise, (i) dextral hemisphincter (D.H.) arising from base of gonotyl dextrally, crossing ventral to ventral sucker, and dividing into three roots, one (D.H.1) turning dextrad to join papillary band (P.B.), a second (D.H.2) turning dorsad dorsal to papillary bundle and inserted near anterior border of ventral sucker, and a third (D.H.3) turning sinistrad ventral to papillary bundle and inserted on wall of ventrogenital sac anterior to mouth; (ii) papillary band (P.B.) arising in papilla within mouth antero-dextrally and running laterad ventral to right caecum; (iii) three groups of widely spaced fibres, dilators of the mouth, one (A.F.) arising anteriorly and curving to the left, a second (P.S.F.) arising postero-sinistrally and running laterad ventral to lateral pocket, and a third (P.D.F.) arising both superficially and deeply from postero-dextral corner of mouth and running anterolaterad. Ventral sucker large 92 (60–126) × 124 (97–163) μm, ratio o.s./v.s. (lengths) 0.83–1.46 and (widths) 0.73–1.0; solidly muscular, with large shallow cavity; asymmetric,

with lip dextrally enlarged ventrally and overhanging dextral portion of cavity and lip sinistrally depressed and obsolete; armed with small spines 1.5–2.5 μm long in two separate groups, a band of 6–8 rows on external (ventral) margin of raised dextral lip, and a patch of spines on inner face of depressed sinistral lip, dorsal to gonotyl. Gonotyl unarmed, solidly muscular, curves to right toward cavity of ventral sucker; genital atrium excentric, nearer right (posterior) margin; narrower right wall of genital atrium ends in extensible digitiform projection (De.P.) overlying or projecting into cavity of ventral sucker; arises postero-sinistrally, pierced by genital atrium which opens mid-dorsally at base of groove extending to free tip. Genital atrium short, wall with outer longitudinal and inner circular muscle-fibres, formed by union of uterus and ejaculatory duct at base of gonotyl; pierces gonotyl and opens dorsally and subterminally, opposite cavity of ventral sucker.

Testes rounded, tandem to oblique, do not fill intercaecal space; contiguous or separated slightly by arms of uterus; sperm ducts separate, unite at seminal vesicle. Seminal vesicle one-chambered, constricted; proximal part elongate, fusiform, with very thick wall of diagonal muscle-fibres in two layers at right angles to one another, thick, outer counter-clockwise and thin, inner clockwise layer (as viewed from proximal end), extends posteriorly to ovary; distal part rounded, with appreciably thinner wall of circular muscle-fibres, proximal part inclined to right, distal to left, forming obtuse angle. Prostatic ejaculatory duct transverse, elongate; with thick wall of outer longitudinal muscle-fibres and inner layer of thinner circular muscle-fibres; pierced by ducts of prostatic gland cells lying on either side, lumen with prominent lining formed by inbulging ends of gland-cell ducts; entrance from seminal vesicle guarded by valve-like papilla, similar to that at proximal end of seminal vesicle; ejaculatory duct short, with wall of circular muscle-fibres, opens into genital atrium on right at tip of short papilla.

Ovary elongate, with long axis paralleling that of proximal part of seminal vesicle; median or slightly to right. Seminal receptacle spherical, highly variable in size, dextro-posterior to and dorsally overlapping ovary. Uterus of typical course; terminal part of uterus with short, thick cuff of circular muscle-fibres; coils of uterus exceed caeca laterally. Vitelline follicles in rosettes; extend intra- and extra-caecally to or beyond ovary anteriorly (extending further forward on left), and to or beyond the ends of the caeca posteriorly. Eggs (10, uterine) 31.0 (29.7–32.3) × 15.7 (15.3–16.1) μm, thick shelled, without anopercular thickening.

Excretory pore subterminal, dorsal; excretory bladder tubular, usually does not reach posterior border of posterior testis (figure 37); bladder arms arise latero-terminally; apparently stenostomate.

Remarks

The position of the ventrogenital sac was remarkably constant in the 10 specimens from various hosts, varying from 29/100ths to 36/100ths of the total length from the anterior end. According to Cable *et al.* (1960), the hindbody is much shorter in non-ovigerous specimens. In two non-ovigerous syntypes, the forebody was longer (54/100 and 49/100ths) than in two ovigerous syntypes (36/100 and 45/100ths). Comparison of outlines of an immature (figure 37) and a mature and large adult (figure 38) shows the great increase in size (width more than length) of the hindbody.

The two patches of spines on the ventral sucker may be variously disposed with respect to one another, depending on the degree of eversion of the semilunar dextral lip. In most well-fixed specimens (figure 33), the long band of spines is on the mid-ventral margin of the dextral

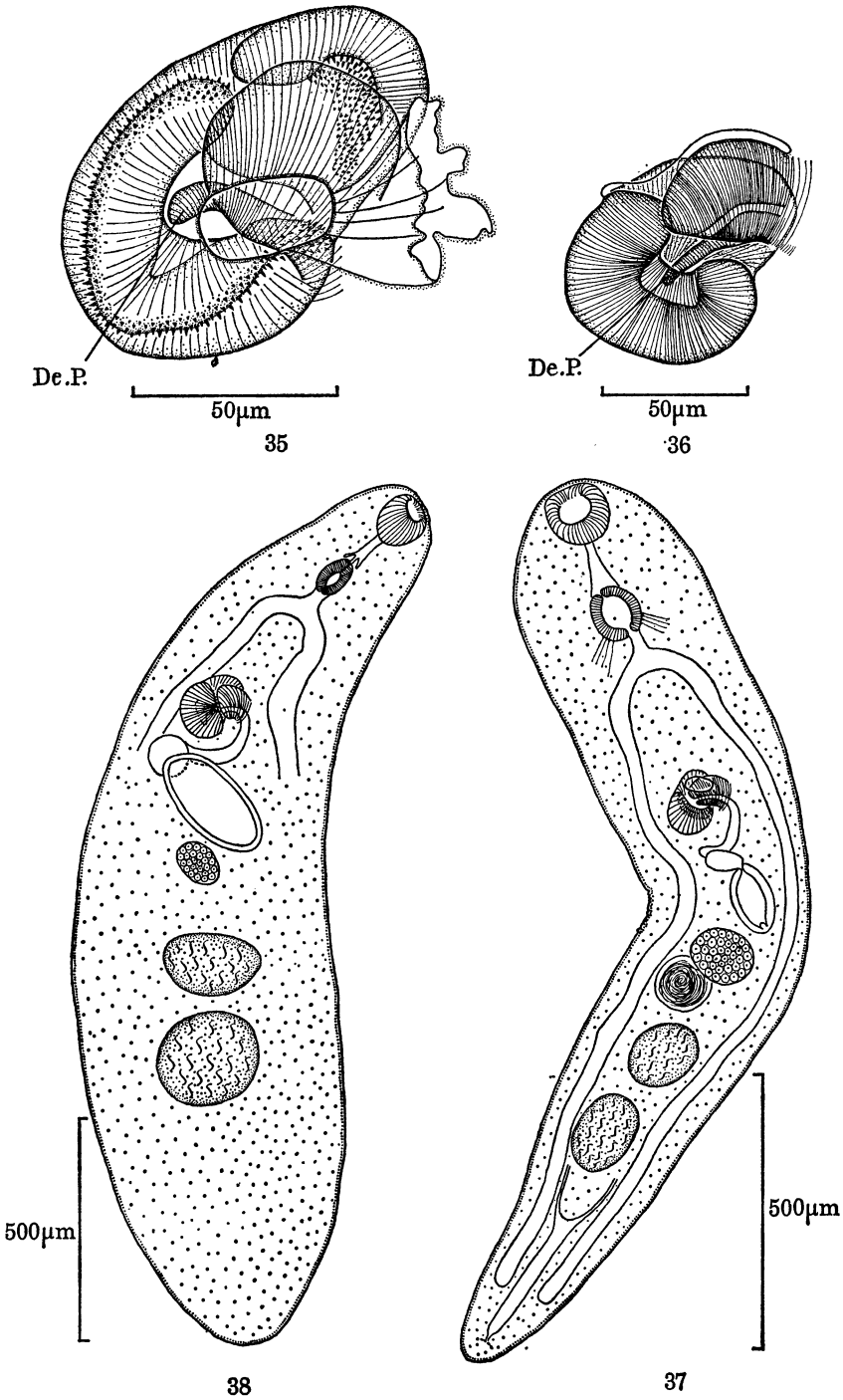


FIGURE 35. *G. fregatae*. Syntype, ventrogenital complex.

FIGURE 36. *G. fregatae*. Syntype, ventral sucker and gonotyl.

FIGURE 37. *G. fregatae*. Immature adult (*Galactosomum* sp. of Hutton & Sogandares-Bernal, 1960).

FIGURE 38. *G. fregatae*. Ovigerous adult.

lip, distinctly separate from the patch of spines on the sinistral portion. In some specimens (figure 41), the dextral lip is rolled inwards so that the band of spines is on the medial face of the dextral lip, not at first sight separate from the sinistral patch. And in others (figure 35), the dextral lip is turned outwards, so that the band of spines lies peripherally on the outrolled lip and the patch of spines is removed sinistrad. But in all states, the ventral sucker shows the specific disposition of spines in a dextral band and a sinistral patch, and except in strongly flattened specimens shows the two-parted form.

The digitiform process arising from the free end of the right side of the dorsal groove on the gonotyl is variable in form and extent, being sometimes short and scarcely recognizable (figure 33), sometimes short (figure 35), and occasionally much elongated (figure 36). Possibly it functions, in the extended state, as a guide to introduce the gonotyl between the ventral sucker and gonotyl of another worm.

A narrow, thin-walled duct between the seminal vesicle and the prostatic ejaculatory duct, as described and figured (Fig. 18, Pl. 4) by Cable *et al.* (1960), was not seen in the syntypes of *fregatae* and *agrachanensis*, nor in the other specimens examined, including the deposited specimen of Cable *et al.*, which appears to be the one they illustrate. Instead, the prostatic ejaculatory duct and seminal vesicle were separated by a short constriction (figure 33).

Comparison

Specimens examined

Trinidad	ex intestine *Fregata magnificens rothschildi* Mathews (Prudhoe 1949), B.M.(N.H.) 1933.3.22.49–85	10 syntypes
Panama	ex bursa *Pelecanus occidentalis californicus* L. (labelled *Galactosomum puffini*) coll. by Sogandares-Bernal in 1956. Coll. Sogandares-Bernal P56–39–1–A; coll. Ching. Specimen in Fig. 16 of Lumsden & Zischke (1963) U.S.N.M. no. 72051	5 specimens* (1 sectioned) (1 measured)
	ex intestine *Pelecanus occidentalis californicus* L. (labelled *Galactosomum puffini*) (Caballero *et al.* 1954). Mexico no. 25–17	2 specimens
Puerto Rico	ex intestine *Thalasseus m. maximus* (Boddaert) (labelled *Galactosomum puffini*) (Cable *et al.* 1960). U.S.N.M. no. 38214. Coll. Cable, 52–04–23–01, author's colln	3 specimens* (2 measured)
U.S.A., Florida	ex rectum *Larus atricilla* L.	1 specimen*
	ex *Larus argentatus smithsonianus* new host U.S.N.M. no. 72052	1 specimen*
	ex *Fregata magnificens rothschildi* Mathews. (All labelled *Galactosomum* sp.) (Hutton & Sogandares-Bernal 1960). Coll. Hutton; author's colln	2 specimens* (1 measured)
Louisiana	ex rectum *Larus atricilla* L. (labelled *Galactosomum puffini*) (Lumsden & Zischke 1963); author's colln	4 specimens*
Texas	ex intestine *Fregata magnificens* Mathews (Chandler 1951), Rice University	6 specimens
U.S.S.R.	ex intestine *Chlidonias hybrida* Pallas (*Chlidonias leucopareia* (Temminck)) (labelled *Galactosomum agrachanensis*) (Saidov 1954); Moscow, Helm. Lab. Inv. no. 120	3 syntypes
Ceylon	ex intestine domestic dog coll. by D. W. W. Kannangara. Colombo	2 specimens
Macassar	ex intestine domestic dog (labelled *Galactosomum canis*) (Yamaguti 1954); M.P.M. 22301	holotype and 10 paratypes

Mexico	ex intestine *Larus occidentalis* Audubon (labelled *Galactosomum puffini*) (Bravo-Hollis 1967); Mexico, 220–L	2 specimens
Venezuela	ex small intestine *Larus atricilla* (labelled *Galactosomum puffini*) (Nasir & Marval 1968); U.S.N.M. no. 62936	1 specimen

In all of the specimens examined, there are two separate groups of spines on the ventral sucker, not three as suggested by Prudhoe (1949) and as described by Cable *et al.* (1960) and by Lumsden & Zischke (1963), nor a complete circle as described by Yamaguti (1954).

The gonotyl in this, as in all species of *Galactosomum* examined, is unarmed. Presumably, Prudhoe (1949) and Caballero *et al.* (1954) misinterpreted the spines on the sinistral portion of the ventral sucker as being on the gonotyl.

The three syntypes of *agrachanensis*, although badly fixed and strongly flattened show (figures 40, 41) those features of the ventrogenital complex characteristic of *fregatae*, except that the ventrogenital sac is closer to the gut bifurcation, probably as a result of flattening.

The types of *canis* agree with *fregatae* in size, form and proportions, in the form of the seminal vesicle and extent of the vitellaria. Although dead when fixed and strongly flattened so that the ventrogenital sac and lateral pocket are grossly distended by sperm and the ventral sucker everted and flattened (figure 42), the types show a transversely elongate ventral sucker with two separate groups of spines, a semicircular band on the reflexed dextral lip and a patch in the reduced cavity sinistrally, and a gonotyl with digitiform process. It is clear that *canis* is a synonym of *fregatae*.

In view of the significance often attached to egg size, particularly in accounts in which the ventrogenital complex is not fully described, it is instructive to look more closely at the size of eggs of the various lots of *fregatae* and to compare these with measurements made by others who have examined the same material. This comparison is made in table 3, which is derived from seven lots of specimens, from four different species of host. These specimens fit the concept of *fregatae* as expressed in the diagnosis, and hence variation in egg size is within the limits of the species.

The table is not complete. Neither Hutton & Sogandares-Bernal (1960) nor Lumsden & Zischke (1963), who both examined Sogandares-Bernal's specimens from Panama, gave measurements of the eggs, and I failed to measure the eggs in the specimens of Caballero *et al.* (1954). Nevertheless, a number of points emerge from this limited comparison.

First, that there are minor differences between measurements of specimens from different hosts and localities, but that these are of the same order as differences between individuals from the same host (lots 2, 3 and 7).

Secondly, that although the two sets of measurements of syntypes (lot no. 1) agree closely, there is a surprising disparity between the two sets for lots 2, 3 and 6, especially for 3. Three factors probably contribute to this difference, namely, individual variation, eggs selected for measurement and calibration of the microscope. As Sogandares-Bernal (1959) has pointed out, it is necessary to select eggs lying as nearly as possible in the horizontal plane as tilted eggs measure significantly less than in fact they are; it should also be stated whether eggs are collapsed, as this affects the width.

Errors in calibration, together with individual differences in how measurements are made, probably account for differences sufficiently large to appear significant taxonomically. For

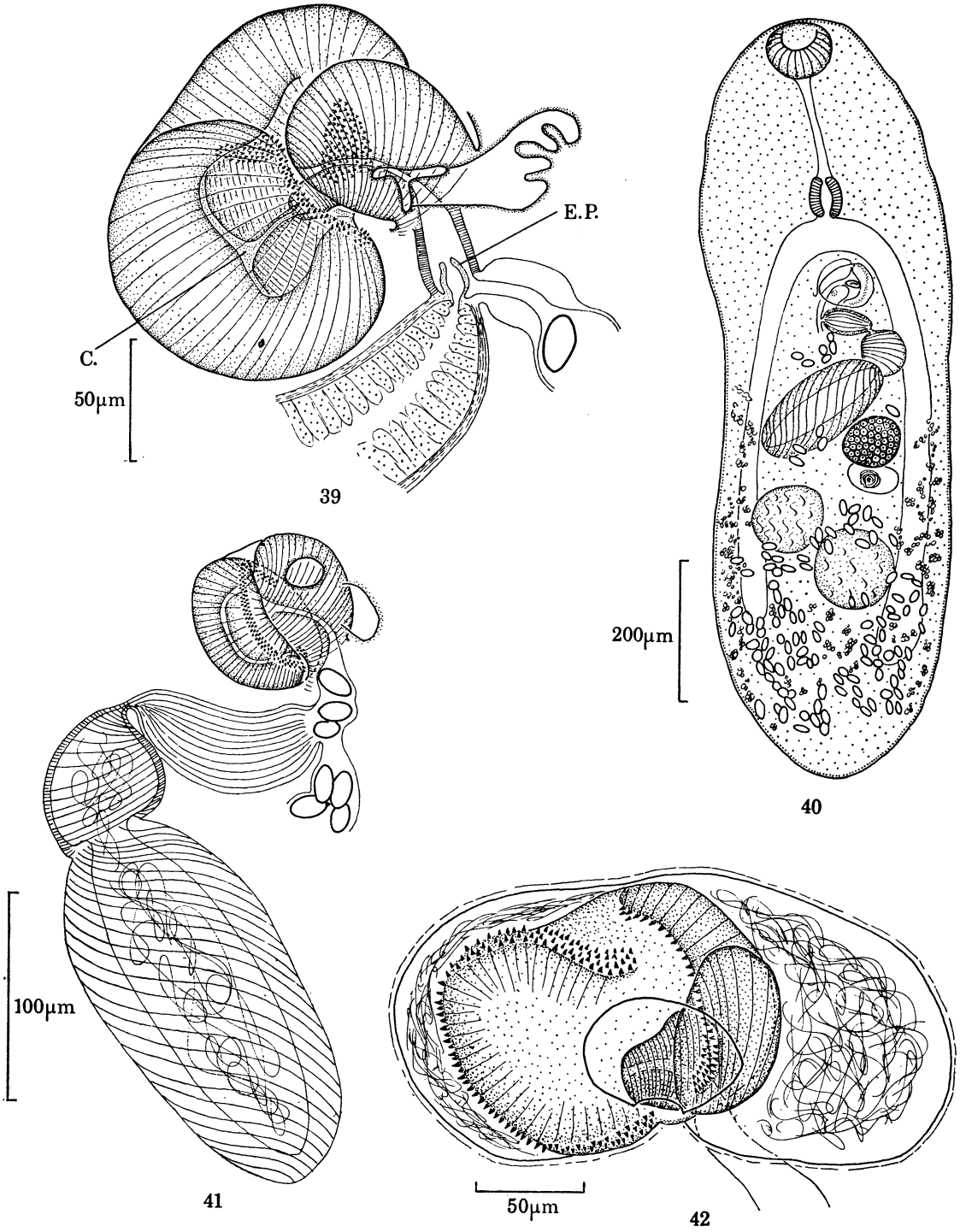


FIGURE 39. *G. fregatae.* Ventrogenital complex of *G. puffini* of Hutton & Sogandares-Bernal, 1960.

FIGURE 40. *G. agrachanensis.* Syntype (dorsal).

FIGURE 41. *G. agrachanensis.* Syntype, Ventrogenital complex (ventral).

FIGURE 42. *G. canis.* Holotype, ventrogenital complex.

example, Lumsden & Zischke (1963) identified the specimens of lot 3 as *puffini* rather than as *fregatae* partly on the basis of a difference in egg size, a difference not found in the present study.

It would seem that each worker, myself included, has his own combination of error, and that as a result comparison of measurements is significant only if all measuring has been done by one person.

TABLE 3. COMPARISON OF EGG SIZE/μM OF *G. FREGATAE*

	published figures	present study
lot 1, syntypes		
Fregata magnificens, Trinidad	30–32 × 13–15 (Prudhoe 1949)	31.0 (29.7–32.3) × 15.7 (15.3–16.1)
no. measured	100	10
lot 2		
Thalasseus maximus, Puerto Rico	25–29 × 11–14 (Cable *et al.* 1960)	30.6 (29.9–31.5) × 14.7 (14.0–15.7)
no. measured	—	10
	—	29.5 (28.9–30.6) × 13.8 (13.6–15.3)
no. measured	—	10
lot 3		
Larus atricilla, Louisiana, U.S.A.	22–25 × 14 (Lumsden & Zischke 1963)	28.1 (27.5–29.0) × 15.3 (14.5–16.2)
no. measured	—	10
	—	26.8 (26.4–27.2) × 14.0 (13.6–14.5)
no. measured	—	10
lot 4		
Pelecanus occidentalis, Panama	— (Hutton & Sogandares-Bernal 1960)	27.6 (25.3–29.8) × 14.2 (12.8–15.3)
no. measured	—	10
lot 5		
Pelecanus occidentalis, Panama	23 × 13–15 (Caballero *et al.* 1954)	—
no. measured	—	—
lot 6		
Larus occidentalis, Baja California, México	25 × 13 (Bravo-Hollis 1967)	28.0 (27.2–29.8) × 15.0 (13.6–16.1)
no. measured	—	10
	—	27.5 (27.2–29.0) × 14.9 (13.6–16.1)
no. measured	—	10
lot 7 (types, *canis*)		
dog	Yamaguti (1954)	26.0 (23.8–28.0) × 14.9 (13.6–16.1)
Celebes	24–27 × 14–15	
no. measured	—	10
	—	23.6 (22.9–24.6) × 13.7 (12.7–15.3)
no. measured	—	10

Diagnosis

Body strap shaped, often with slight constriction posterior to ventrogenital sac; forebody and hindbody of roughly equal width. Prepharynx as long or longer than pharynx. Ventrogenital sac large, median, not more than twice its length behind caecal bifurcation, with lateral pocket; mouth small, 29–36/100ths from anterior end, musculature complex with prominent dextral hemisphincter. Ventral sucker large, ratio o.s./v.s. (lengths) 0.83–1.46; asymmetric, solidly muscular; with reniform dextral lip bearing 6–8 rows of minute spines in band, and flattened sinistral portion, dorsal to gonotyl, bearing patch of minute spines. Gonotyl with variable terminal process. Genital atrium enters gonotyl, opens dorsally in groove. Seminal vesicle one-chambered, constricted, thick walled. Vitellaria extend anteriorly to or beyond

ovary; posteriorly to or beyond ends of caeca. Eggs 25–32 × 13–16 μm. Excretory bladder short, not exceeding posterior border of posterior testis.

G. fregatae is closest to *angelae* in possessing a transversely elongate ventral sucker with reduced cavity and raised dextral lip; however, the two species differ distinctly in spination of the ventral sucker and form of the gonotyl, and in addition in the position and musculature of the ventrogenital sac, form of the seminal vesicle, and anterior extent of vitelline follicles.

G. fregatae and *puffini* are similar in the form of the seminal vesicle and prostatic ejaculatory duct and distribution of vitelline follicles, but differ distinctly in the form of the gonotyl and the form and spination of the ventral sucker.

(*i*) *Galactosomum humbargari*

Synonyms

Galactosomum humbargari Park, 1936, Figs. 6–11, Pl. 44 (*Larus californicus* Lawrence; Dillon Beach, California, U.S.A.; descr.; types untraceable); Olson, 1955 (pers. comm. to Yamaguti, 1958) Figs. 7, 8 (metacercaria in *Leuresthes tenuis*; adult expt. in *Hydroprogne caspia* Pallas; California, U.S.A.); Dubois & Mahon, 1959, Figs. 9, 10 (*Larus occidentalis occidentalis* Audubon; California, U.S.A.; descr.); Ching, 1960 (*L. heermanni* Cassin, *L. glaucescens* Naumann, *L. philadelphia* (Ord); Washington State, U.S.A.; no descr.).

Although Park's types could not be traced, and his (1936) description is brief, there seems little doubt that the material examined belongs to *humbargari*, especially as the singular features of the ventral sucker (two gonotyls of Park) and of the gonotyl (rudimentary ventral sucker of Park) are adequately illustrated by him.

The re-description is based on wholemounts of 14 specimens from a variety of hosts. Measurements are given of the only two specimens that are both well fixed and unflattened.

Description (*figures* 43–45, 84)

With the characters of the genus. Body elongate, strap shaped; 1530, 1550 μm long; forebody flattened, ventrally concave, with constriction between bifurcation of caeca and ventrogenital sac; forebody about ¼ length of body, 266, 274 μm wide, without pit or specialized dorso-ventral fibres; hindbody subcylindrical, bluntly rounded posteriorly, 282, 363 μm wide.

Body covered with small scales, becoming spines at level of ovary and extending to posterior end; absent over anterior end, with three rows pre-orally. Frontal glands present; cell bodies largely intercaecal anterior to ventrogenital sac; ducts open in two staggered rows across unarmed anterior end. Pigment granules scattered in parenchyma anterior to bifurcation of caeca.

Oral sucker small; 81 × 88 μm, 91 × 97 μm. Prepharynx 81, 94 μm; about as long as pharynx; with ventrally incised fornix. Pharynx 65 × 39 μm, 71 × 36 μm. Caeca narrow, straight, with contiguous epithelium extend almost to posterior end.

Ventrogenital sac median, transversely oval mouth 25–26/100ths from anterior end; without distinct lateral pocket, but with sinistral wall folded. Musculature of sac includes (i) dextral hemisphincter (D.H.) arising from base of gonotyl postero-ventrally and encircling sac clockwise, first rising toward the ventral surface dextrally, then sinking deeper anteriorly and returning to the base of the gonotyl deep on the sinistral wall, (ii) small group of fibres (A.D.B.) arising ventral to (i) apparently from wall of sac antero-dextrally and running laterad or antero-laterad close to ventral surface, and (iii) fibres arising from the mouth anteriorly (A.F.) and

posteriorly (P.F.). Ventral sucker solidly muscular; large, 130 × 100 μm, 123 × 123 μm, occupies 3/4 of intercaecal space, ratio o.s./v.s. (lengths) 0.62, 0.73; axis inclined antero-ventrally; cavity reduced to semicircular slit, dorsal lip enlarged anteriorly; with anterior face flattened; armed with continuous, or laterally interrupted, band of 4–5 μm spines on outer (ventral) face of ventral lip and inner (ventral) face of dorsal lip, band widest on ventral lip, narrowest laterally. Gonotyl large, variable in shape, with broad base and narrow apex; base arises from wall of sac posteriorly and sinistrally, but is attached to capsule of ventral sucker anteriorly; with prominent groove in dextral face, giving C- or U-shaped cross-section; genital pore in base of gonotyl postero-sinistrally near mouth of ventral sucker. Genital atrium short, 53 μm.

Testes large, rounded, intercaecal, diagonal, well separated from each other and from ovary by coils of uterus; anterior testis 81 × 97 μm, 104 × 120 μm; posterior testis 100 × 104 μm, 97 × 152 μm. Sperm ducts unite at seminal vesicle and enter via small papilla. Seminal vesicle two chambered; first chamber large, 71 × 81 μm, ellipsoidal, sinistral, anterior or antero-sinistral to ovary, thin walled, opens into second chamber through short narrow duct; second chamber cylindrical, 81 × 65 μm, curved, runs dorso-anterad, dextral to first chamber and anterior to ovary, wall 6–7 μm thick with prominent circular-fibres, separated from prostatic ejaculatory duct by short narrow constriction. Prostatic ejaculatory duct long, 146 × 32 μm, 195 × 36 μm; sinuous, appearing sacculate; without prominent imbulging gland cells; without papilla at entrance into genital atrium; gland-cell bodies intercaecal lateral to prostatic ejaculatory duct.

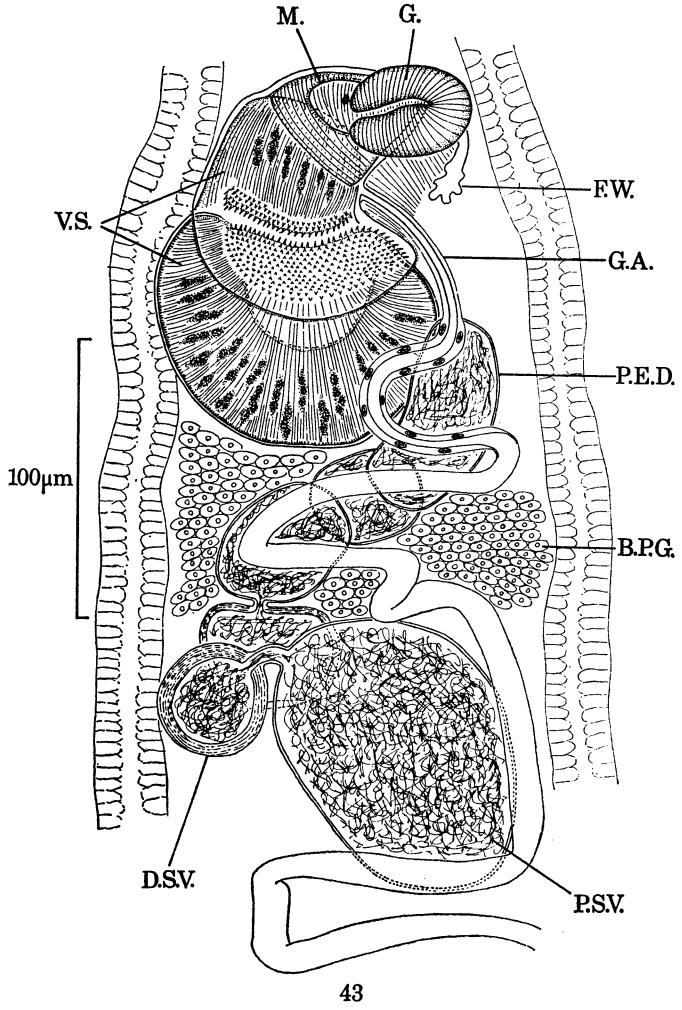
Ovary median, 87 × 104 μm, 117 × 139 μm; seminal receptacle postero-dextral to ovary, 87 × 81 μm, 107 × 133 μm. Ootype and Mehlis gland postero-sinistral to ovary. Uterus with typical course; coils overlap gonads dorsally and ventrally; with two loops ventrally over seminal vesicle and prostatic ejaculatory duct; short terminal portion with strong circular fibres; opens into genital atrium ventral to male opening. Vitellaria in rosettes confined among coils of uterus from ventral to dorsal surface; anteriorly extend to between middle and posterior border of ovary, posteriorly to or almost to posterior limit of uterine coils; vitelline duct apparently single. Eggs (10, uterine) 29.8 (29.0–31.4) × 16.5 (15.3–17.8) μm. Excretory bladder not seen.

Specimens examined

California, U.S.A.	ex intestine *Larus occidentalis* Audubon (Dubois & Mahon 1959). Coll. Dubois	3 specimens
	ex intestine *Larus occidentalis* Audubon. Coll. Sogandares-Bernal	1 specimen
	ex *Hydroprogne caspia* (Pallas) expt. Olson (in Yamaguti 1958); det. W. E. Martin. Coll. Olson, no. 641	1 specimen
	ex *Larus* sp. coll. by J. Karl; U.S.N.M. no. 72054; coll. Ching	2 specimens
Washington State, U.S.A.	ex *Larus glaucescens* Naumann (Ching 1960). U.S.N.M. no. 72053 coll. Ching; author's colln	10 specimens
British Columbia new locality, Canada	ex intestine *Larus glaucescens* Naumann. Coll. by D. N. Jensen; coll. Jensen	39 specimens
	ex intestine *Aechmophorus occidentalis* (Lawrence) new host. Coll. by D. N. Jensen, 7. ii. 1959 no. 589; coll. Jensen	1 specimen
	ex intestine *Podiceps grisegena* new host. Coll. by D. N. Jensen Feb. 1962, no. 1775; coll. Jensen	1 specimen
	ex intestine *Phalacrocorax auritus* new host Maudarte Island. Coll. by D. N. Jensen 12. vii. 1960, no. 1055; coll. Jensen	2 specimens

Diagnosis

Body strap shaped, with constriction anterior to ventrogenital sac. Oral sucker small; prepharynx about as long as pharynx. Ventrogenital sac 25–26/100ths from anterior end, without lateral pocket; mouth symmetric. Ventral sucker large, ratio o.s./v.s. (lengths) 0.62–0.73; solidly muscular, with slit-like cavity and enlarged dorsal lip, with band of minute spines about mouth. Gonotyl attached to anterior face of dorsal lip of ventral sucker, with large dextral groove. Genital atrium opens at base of gonotyl. Seminal vesicle two-chambered,



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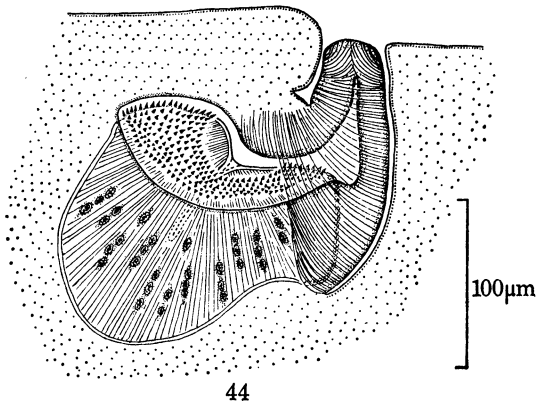

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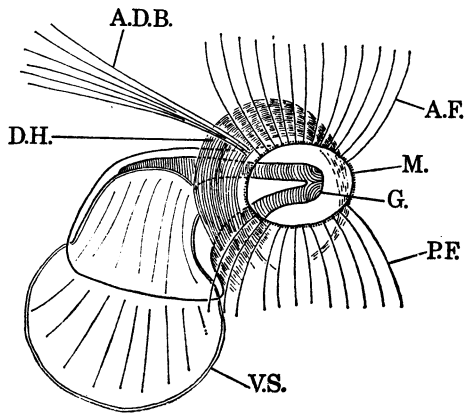

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FIGURE 43. *G. humbargari.* Ventrogenital complex (ventral).
FIGURE 44. *G. humbargari.* Ventrogenital complex (from left side).
FIGURE 45. *G. humbargari.* Musculature of ventrogenital sac (free-hand).

proximal large and thin walled, distal small and with thick wall of circular fibres. Prostatic ejaculatory duct long, sinuous. Vitelline follicles among coils of uterus at all levels from ventral to dorsal surface. Eggs 29–31 × 15–18 μm. Excretory bladder reaches posterior border of posterior testis.

G. humbargari differs from all other species in *Galactosomum* in the close association of gonotyl and ventral sucker, a condition approaching the fused ventral sucker – 'genital sucker'

complex of Morozov (1952). It is also unique in possessing a long prostatic ejaculatory duct together with a two-chambered seminal vesicle.

Remarks

The seminal vesicle and prostatic ejaculatory duct which exhibit important taxonomic characters, show clearly only in well fixed specimens, either unflattened or lightly flattened. In strongly flattened or macerated specimens, the seminal vesicle particularly does not show clearly as two-chambered. Hence, perhaps, Park's (1936) statement, '. . .seminal vesicle (seminal vesicle + prostatic ejaculatory duct). . .divided by one or two constrictions. . .'.

A few features of the metacercaria can be seen in Olson's stained preparation of encysted metacercariae. The excretory bladder reaches the posterior border of the posterior testis, the gonads are large but unripe, and the ventral sucker has attained the adult condition. Excysted, the metacercaria is probably more than a millimetre long, nearly as long as ovigerous adults. That is, it appears to be an advanced metacercaria, comparable with that of other species of *Galactosomum*.

(*j*) *Galactosomum johnsoni*

Synonyms

Galactosomum johnsoni Price, 1934, Figs. 1, 2 (*Sula leucogaster* (Boddaert); Puerto Rico; descr.; types U.S.N.M. nos. 38694, 38695).

Galactosomoides johnsoni (Price) Cable, Connor & Balling, 1960, Figs. 19, 20, Pl. 4 (*Sula leucogaster leucogaster* (Boddaert), *Thalasseus maximus maximus* (Boddaert); Puerto Rico; descr.) new syn.

Description (*figures* 46–48, 85)

The following brief account is based on a study of the type specimens and of three specimens from the series described by Cable *et al.* (1960). Measurements are given of two well-fixed specimens from the latter series.

With the characters of the genus. Body short, wide, flattened, ellipsoidal or egg shaped with narrow end anterior; length 800, 725 μm, width 330, 306 μm.

Body with scales anteriorly; becoming spines posterior to level of ventrogenital sac, and extending to posterior end; scales absent on anterior end and pre-orally. Frontal-gland cells not seen; ducts open in transverse series in anterior unarmed region. Pigment granules few, scattered in forebody.

Oral sucker relatively small; 60 × 66, 63 × 66 μm. Prepharynx longer than pharynx; 114, 152 μm long folded into ventrally incised fornix at entrance to pharynx. Pharynx 42 × 48, 32 × 54 μm, protractor fibres separate from wall of prepharynx, retractor fibres pass dorsal to caeca. Caeca simple, slender; end about midway between posterior border of posterior testis and posterior end.

Ventrogenital sac small, median, close to caecal bifurcation; with prominent lateral pocket sinistral to gonotyl; mouth of sac oval, sinistral or postero-sinistral to gonotyl, 38/100, 49/100ths from anterior end. Musculature of sac includes: (i) superficial fibres (S.S.F.) arising from mouth of sac sinistrally and fanning out sinistrad, ventral to lateral pocket; (ii) fibres (S.A.S.F.) arising from wall anteriorly and running anterad, then sinistrad, overlapping (i) ventrally; (iii) a group of fibres (S.H.) arising from wall postero-dextrally, curving counter-clockwise ventral or latero-ventral to lateral pocket, ventral to (i) and dorsal to (ii), appearing to end on

wall of sac ventrally and anteriorly at or near ventral sucker and (iv) a small, indistinct group of stout fibres (D.H.) arising from the muscular ventral wall of the sac between the ventral sucker and the mouth of the sac, curving sinistrad ventral to (ii) and attached to the wall o the sac antero-sinistral to the mouth. Ventral sucker small, rounded, bilaterally symmetric; 48 × 45, 54 × 48 μm, ratio o.s./v.s. (lengths) 1.3, 1.2, axis inclined antero-sinistrad; medulla parenchymatous, with well-separated radial fibres; cavity reduced to shallow U-shaped concavity ventro-sinistrally; armed with three groups of 2.5 μm spines, a single elongate slightly raised group on floor of cavity and a pair of circular patches borne on low prominences on the ventral lip. Gonotyl small, solidly muscular C-shaped, with anterior half thicker and mouth of C on right; arises dorsally, sinistral to ventral sucker. Genital atrium short; runs anterad then ventrad and opens in space bounded by gonotyl.

Testes large, irregularly rounded, diagonal, separated by coils of uterus. Seminal vesicle one chambered, divided by slight constriction into large posterior and smaller anterior portions; wall thin but muscular, apparently with diagonal fibres in posterior portion and circular fibres in anterior; runs antero-dextrad: posterior portion 97 × 52, 133 × 58 μm, anterior portion 32 × 26, 42 × 49 μm. Prostatic ejaculatory duct short and wide, inbulging ends of prostatic-gland cells small; papilla absent but valve-like constriction present at entrance into genital atrium.

Ovary rounded, dextral. Seminal receptacle large, anterior and dorsal to ovary. Ootype and Mehlis's gland median, medial to ovary. Vitelline follicles scattered among coils of uterus at all levels from ventral to dorsal surface; extend anteriorly to middle of ovary and anterior border of anterior testis, posteriorly to posterior end. Uterus with typical course, except that ascending and descending limbs form transverse series of loops posterior to posterior testis; terminal portion with well-developed circular fibres. Eggs (10, uterine) 36.2 (34.9–37.4) × 19.3 (18.7–20.4) μm large, flattened on one side.

Excretory pore terminal; excretory bladder (from Cable *et al.* 1960) sac shaped, extends almost to posterior testis.

Specimens examined

Puerto Rico ex small intestine *Sula leucogaster* (Boddaert) (Price 1934). U.S.N.M. no. 386895 — (paratypes, wholemounts and serial sections)

ex small intestine *Sula l. leucogaster* (Boddaert) (Cable *et al.* 1960). U.S.N.M. no. 38215, specimen figured 72055; author's colln 3 specimens

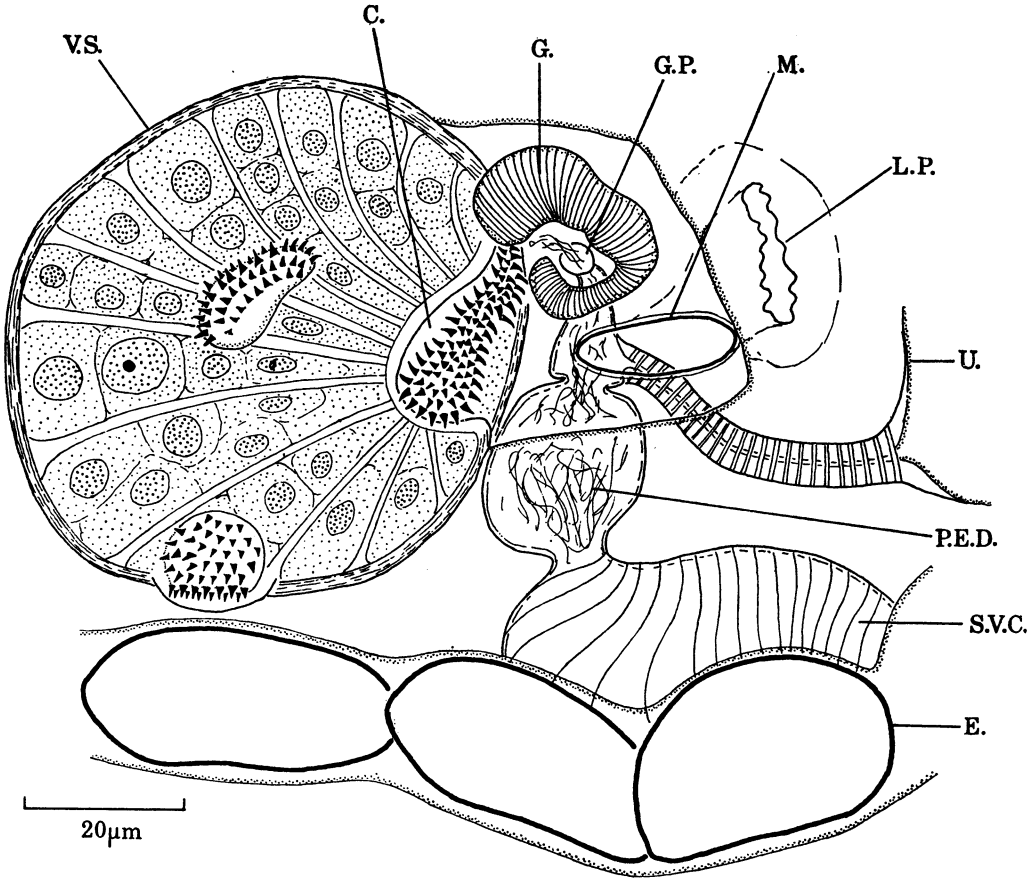
Remarks

According to Price (1934), the seminal vesicle is not constricted; however, the present study confirms the observation of Cable *et al.* (1960) that it is divided by a slight constriction.

In both paratypes and specimens from Cable it can be seen that the genital pore opens within the curve of the gonotyl (figure 46), and not, as Cable *et al.* (1960) state, on the tip of the gonotyl.

The ventral lip of the ventral sucker is clearly bilobed in the well-fixed specimen shown in figure 47; whereas in the paratype illustrated (figure 46) the two lobes are separated from each other and from the reduced cavity of the sucker. In a strongly contracted ventral sucker, it could be difficult to distinguish the three groups of spines.

The musculature of the ventrogenital sac is unusual, possibly because the sac itself is transversely elongate. The group of fibres partly encircling the sac sinistrally is unique to this species.



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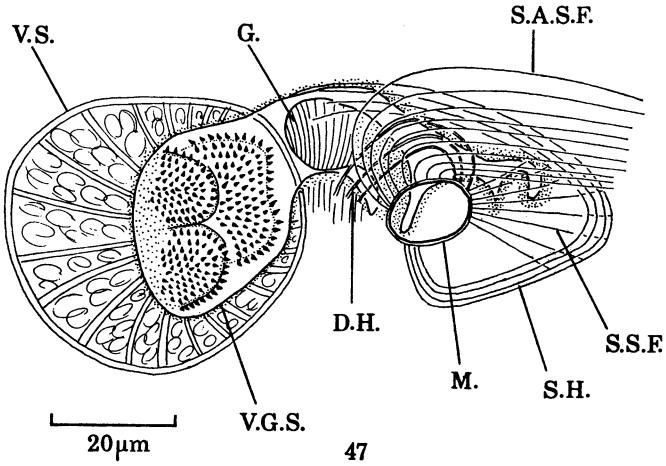

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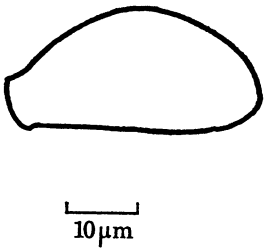

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FIGURE 46. *G. johnsoni*. Paratype, ventrogenital complex.

FIGURE 47. *G. johnsoni*. Ventrogenital complex (muscle fibres free-hand).

FIGURE 48. *G. johnsoni*. Asymmetric egg.

Diagnosis

Body short, wide, undivided. Oral sucker small; prepharynx longer than pharynx. Ventrogenital sac small; 38–49/100ths from anterior end; with lateral pocket. Ventral sucker small, rounded, parenchymatous; ratio o.s./v.s. (lengths) 1.2–1.3; with three groups of minute spines, one in reduced cavity and two on ventral lip. Gonotyl C-shaped; not pierced by genital atrium. Seminal vesicle one chambered, constricted. Seminal receptacle anterior to ovary. Vitellaria among coils of uterus at all levels from ventral to dorsal surface; extend from anterior border of ovary to posterior end. Eggs asymmetric; 36 (35–37) × 19 (19–20) μm. Excretory bladder short, does not reach posterior testis.

(*k*) *Galactosomum phalacrocoracis*

Synonyms

Galactosomum phalacrocoracis Yamaguti, 1939, Fig. 41, Pl. 23 (*Phalacrocorax pelagicus* Pallas; Tokusima and Matus, Japan; descr.; types M.P.M. no. 22001); *Dolgikh & Naidenova, 1967, Fig. lv (gills and adjacent muscle of *Diplodus annularis* L.; Black Sea, U.S.S.R.; descr.; metacercaria) cf. *lacteum*; Prudhoe, 1949 (syn. of *Galactosomum lacteum*); Dubois & Mahon, 1959 (syn. of *G. lacteum*); *Smogorzhevskaya, 1956, Fig. 6 (*Phalacrocorax carbo* (L.), *Ardea cinerea* L.; Dnieper delta, U.S.S.R.; descr.); *Smogorzhevskaya, 1961, Fig. 4 (*P. aristotelis* L.; Tarkhankyt, U.S.S.R.; descr.).

non Galactosomum sp. Bykhovskaya–Pavlovskaya. Smogorzhevskaya, 1961. Probable syn. of *G. ussuriensis q.v.*

Although neither of Smogorzhevskaya's (1956, 1961) records can be positively identified, for want of full descriptions of the ventrogenital complex, it would appear that her account of 1961 probably refers to *phalacrocoracis*, but that her account of 1956 refers to a different species possibly *lacteum*.

Description (*figures* 49, 50, 86)

The following brief description, based on eight paratypes, is given to supplement that of Yamaguti (1939), particularly in details of the ventrogenital complex. The specimens are slightly macerated and flattened, and have lost the body spines.

With the characters of the genus. Body elongate, slender; 5.17 (4.10–5.97) mm long; forebody 646 (540–774) μm wide, slightly narrower than hindbody 700 (580–790) μm wide, with slight constriction before and behind level of ventrogenital sac; forebody with conspicuous dorso-ventral muscle-fibres, most abundant between caeca.

Oral sucker large, 316 (306–330) μm long and 322 (284–346) μm wide. Prepharynx longer than pharynx. Pharynx 158 (145–171) μm long and 113 (81–139) μm wide; extrinsic muscle-fibres arise from posterior end and comprise protractors forming a loose sheath external to pharynx and prepharynx and attached to oral sucker, and two lateral groups of retractors that cross caeca dorsally.

Ventrogenital sac capacious 187 (158–232) μm long and 345 (278–420) μm wide, with large symmetric transversely oval mouth 45–50/100ths from anterior end; musculature comprises circular fibres, especially ventrally, and strongly developed radial fibres laterally, anteriorly and dorsally; lateral pocket absent. Ventral sucker on left, ratio o.s./v.s. (widths) 1.5 (1.2–1.7); 272 (242–323) μm long and 217 (184–251) μm wide, with rounded parenchymatous base and

asymmetric apex; apex divided into large armed dextral lobe, and small unarmed finger-like sinistral (medial) lobe overlapping gonotyl dorsally and with sinistral face embedded in parenchyma of body; dextral lobe with protrusible externo-dorsal prominence separated from ventral portion of dextral lobe by reduced cavity opening antero-medially and bearing spines apically and dorsally and some ventrally in reduced cavity between apex and prominence and with eversible spined pocket opening ventro-medially. Gonotyl anvil shaped, solidly muscular large; 135 (103–171) μm long and 207 (168–242) μm wide, as wide as ventral sucker; arises postero-sinistrally, genital atrium short, enters base and curves to right to open dorso-laterally opposite notch of ventral sucker; muscle fibres from base dextrally run ventro-anterad to posterior border of mouth of ventrogenital sac.

Seminal vesicle two-chambered; thick walled, both chambers with thick outer diagonal and thin inner circle layer of muscle fibres; distal chamber 194 × 129–558 × 226 μm about twice as long as proximal 97 × 74–258 × 136 μm; distal inclined to left, proximal to right. Prostatic ejaculatory duct relatively short and narrow, 113 × 47–242 × 32 μm with prominent longitudinal muscle-fibres.

Vitellaria in rosettes, primarily ventro-lateral, absent dorsally between caeca, one or two rosettes between caeca ventrally behind testes; duct from each rosette opens into single mid-ventral duct, which is joined at vitelline reservoir by short anterior duct from first two rosettes of follicles; extend anteriorly on right to level of ovary and on left to or beyond ovary to level of middle of distal chamber seminal vesicle. Eggs (20, uterine) 27.0 (25.4–29.0) × 14.2 (13.6–15.3) μm.

Uterus with atypical course; arises medial to ovary, coils loosely sinistral to ovary as far forward as distal chamber of seminal vesicle, crosses to right side behind ovary, loops ventrally on both sides beside and behind testes, turns dorsad on right at level of anterior testis to form prominent sinuous descending arm of post-testicular region, reaches posterior end, crosses to left and ascends dorsally on left, without crossing between testes, to level of seminal vesicle, loops across seminal vesicle ventrally and enters genital atrium ventral to ejaculatory duct by way of terminal portion with conspicuous circular muscle-fibres. Excretory bladder not seen.

Comparison

Specimens examined

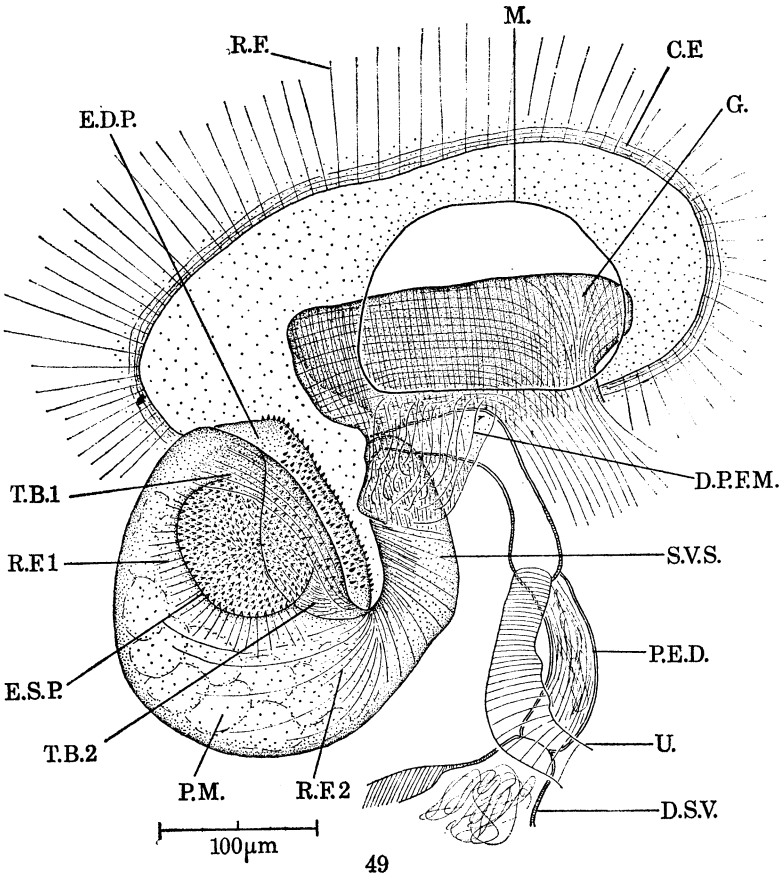
Washington new locality, U.S.A.	ex *Phalacrocorax* sp. coll. by H. L. Ching, 7. vii. 1959. Friday Harbor, author's colln	1 specimen

Although the single specimen from the U.S.A. is smaller (1.85 mm) than the types (4–6 mm), it agrees in form and proportions, and in possessing a large ventrogenital sac without a lateral pocket but with conspicuous radial muscle-fibres, a ventral sucker with spined pocket, and sinistral finger-like lobe, and an anvil-like gonotyl.

Remarks

The ventral sucker in most specimens has the spined pocket inverted and the spine-bearing portion of the apex not protruding (figure 49); but in one specimen (figure 50), the spine-bearing portion of the apex is inflated, the two lobes of the apex are appressed, and the spined pocket is everted, forming a disk with spines ventrally and marginally, but not dorsally.

The intrinsic musculature of the ventral sucker is complex, but obscure. The elements that can be discerned include: (i) an outer capsule of circular fibres; (ii) fibres (R.F. 1) radiating



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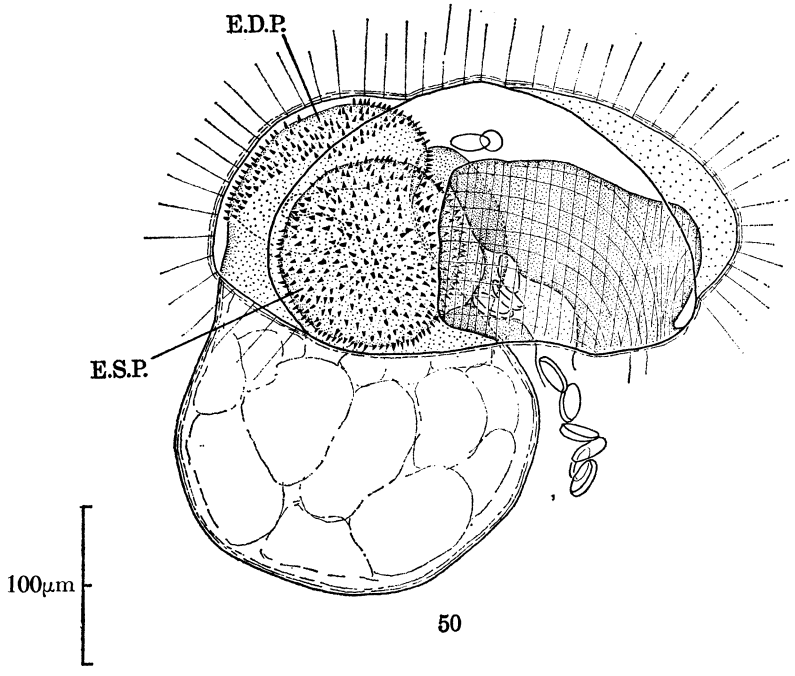

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FIGURE 49. *G. phalacrocoracis*. Paratype, ventrogenital complex.

FIGURE 50. *G. phalacrocoracis*. Paratype, ventral sucker with spined cavity everted.

out from the wall of the spined pocket into the parenchymatous medulla of the base; (iii) circular fibres in the wall of the spined pocket; (iv) radial fibres (R.F. 2) in the dextral lobe, becoming more numerous at bottom of notch between lobes; (v) a stout band of fibres (T.B. 1) arising from a point near the bottom of the notch on the left and fanning out over the apex dextrally, ventral to the spine-bearing prominence; (vi) a small group of fibres (T.B. 2) arising from the same point as (v), but running dextrad dorsal to the spined pocket, and (vii) a large, oval bundle of fibres dorsal to the spined pocket and to (vi), within the substance of the spine-bearing prominence.

The mouth of the spined pocket could not be seen clearly in any specimen, but from the position of the everted pocket (figure 50) and from suggestions of the mouth and of the muscle fibres used in eversion, it would appear to lie ventrally near the anterior margin of the ventral portion of the apex.

In the paratypes, the entrance of the ejaculatory duct into the genital atrium could not be seen clearly, but in the single North American specimen it appears to open through a papilla.

Diagnosis

Body elongate, narrow. Oral sucker large, prepharynx slightly longer than pharynx. Ventrogenital sac 45–50/100ths from anterior end, well behind caecal bifurcation, inflated, lateral pocket absent; ventral sucker asymmetric, parenchymatous, ratio o.s./v.s. (widths) 1.2–1.7, apex with armed dextral lobe with eversible spined pocket and small unarmed sinistral lobe; gonotyl anvil shaped. Seminal vesicle two-chambered, both chambers with thick layer diagonal fibres; distal chamber about twice as long as proximal. Vitellaria largely ventro-lateral; extend from level ovary or seminal vesicle to posterior end. Eggs 27.0 (25.4–29.0) × 14.2 (13.6–15.3) μm. Excretory bladder long, reaches posterior border of ovary.

G. phalacrocoracis is closest to the genotype, *lacteum*; indeed, it has been considered as a synonym of *lacteum* by Prudhoe (1949) and by Dubois & Mahon (1959). The differences between the two species might have been ascribed to the great difference in size (*phalacrocoracis* 4–7 mm; *lacteum* 1.3–3.0 mm), save that a small (1.85 mm) specimen of *phalacrocoracis*, one of a collection from the Pacific coast of North America, showed that the differences existed in worms of the same size.

TABLE 4. COMPARISON OF EGG SIZE/μM OF *G. PHALACROCORACIS* AND *G. LACTEUM*

G. lacteum	*G. phalacrocoracis*
22 × 11 (Jägerskiöld 1908)	24–27 × 12–13 (Yamaguti 1939)
22–26 × 11–13 (Prudhoe 1949)	—
22–26 × 10–14 (present work)	25–29 × 14–15 (present work)

While bearing a striking superficial resemblance to that of *lacteum*, the ventral sucker of *phalacrocoracis* differs significantly in having (i) an eversible, spined pocket opening apically, instead of a spined ventral groove; (ii) an apical prominence bearing spines apically and dorsally, separate from the spines of the pouch, rather than an apical knob spined ventrally and medially, and continuous with the spines of the reduced cavity; and (iii) a sinistral finger-like projection, absent in *lacteum*. Additional differences include: (i) the prominent zone of muscle fibres radiating out from the wall of the inflated ventrogenital sac, seen clearly in the 1.85 mm

adult, but not in specimens of *lacteum* of comparable size; (ii) a flat-topped, anvil-like gonotyl; (iii) no lateral pocket, and (iv) vitellaria usually exceed ovary anteriorly, rather than not exceeding the posterior border of the ovary. The difference in size of egg is not as marked as Yamaguti (1939) thought, as can be seen in table 4.

(*l*) *Galactosomum puffini*

Synonyms

Galactosomum puffini Yamaguti, 1941, Figs. 12–14 (*Puffinus leucomelas* (Temm.); Siriyazaki, Japan; descr.; types M.P.M. no. 22101).

Galactosomum puffii (*sic*!) Yamaguti. *Leonov, 1958 (*Sterna hirundo* L.; Kherson, U.S.S.R.; no descr.).

Galastosomum (*sic*!) *puffii* Yamaguti. *Leonov, 1956 (first record in Russia); *Belogurov, Leonov & Zueva, 1968 (*Larus argentatus* (Pont.); Sea of Okhotsk, U.S.S.R.; no descr.).

non Galactosomum puffini Yamaguti. Caballero, Grocott & Zerecero, 1954; Cable, Connor & Balling, 1960; Lumsden & Zischke, 1963; Bravo-Hollis, 1967; Nasir & Marval, 1968. All are synonyms of *G. fregatae*, *q.v.*

Description (*figures* 51, 52, 87)

The following brief re-description of the holotype and six paratypes is given to supplement the description of Yamaguti (1941). The specimens were apparently dead when fixed and the ventrogenital complex distorted in mounting, except in the holotype. Measurements are given of the seven type specimens.

With the characters of the genus. Body 1960 (1730–2300) μm long and 443 (387–483) μm wide; outline bottle-shaped, with short and narrow forebody occupying 22–30/100ths of length, and long, wide hindbody.

Forebody, especially between caeca, with numerous frontal-gland cells that open by long ducts in a transverse band just anterior to oral sucker. Oral sucker 61 (51–73) μm long and 61 (54–69) μm wide.

Ventrogenital sac small, about twice its diameter behind gut bifurcation, 22–30/100ths from anterior end; with lateral pocket; mouth symmetric. Ventral sucker symmetric, sucker like, with cavity; somewhat parenchymatous with separated radial fibres traversing medulla; 68 (60–74) μm long and 68 (59–83) μm wide, ratio o.s./v.s. (lengths) 0.84–1.0; armed with minute spines in two groups, a dextral U-shaped band of about eight rows of spines on lip and a small circular group postero-sinistrally just within cavity. Gonotyl unarmed, solidly muscular; about 3/4 as large as ventral sucker, pierced by genital atrium and bearing genital pore dorso-terminally. Genital atrium short, largely within gonotyl, opens terminally.

Seminal vesicle one-chambered, constricted; proximal part fusiform, with thick outer layer of diagonal fibres; distal part subglobular, with thinner wall of conspicuous circular-fibres; separated from prostatic ejaculatory duct by conical valve; prostatic ejaculatory duct long and wide, with conspicuous longitudinal fibres, lined by inbulging ends of prostatic-gland ducts. Ejaculatory duct short and narrow; opens into genital atrium ventral to uterus through conical papilla.

Seminal vesicle transversely elongate. Course of uterus typical. Vitelline follicles in rosettes; anteriorly to or slightly beyond ovary on right and to middle of proximal part of seminal vesicle on left; posteriorly almost to posterior end; lateral anteriorly, but scattered over full width

both ventrally and dorsally behind posterior testis. Eggs (20, uterine) 23.3 (22.1–23.8) × 13.7 (11.9–15.3) μm.

Excretory bladder not seen, but may not reach posterior testis as bladder arms can be traced back to half way between posterior testis and posterior end. Bladder arms divide into anterior and posterior collecting tubules at level of ventrogenital sac.

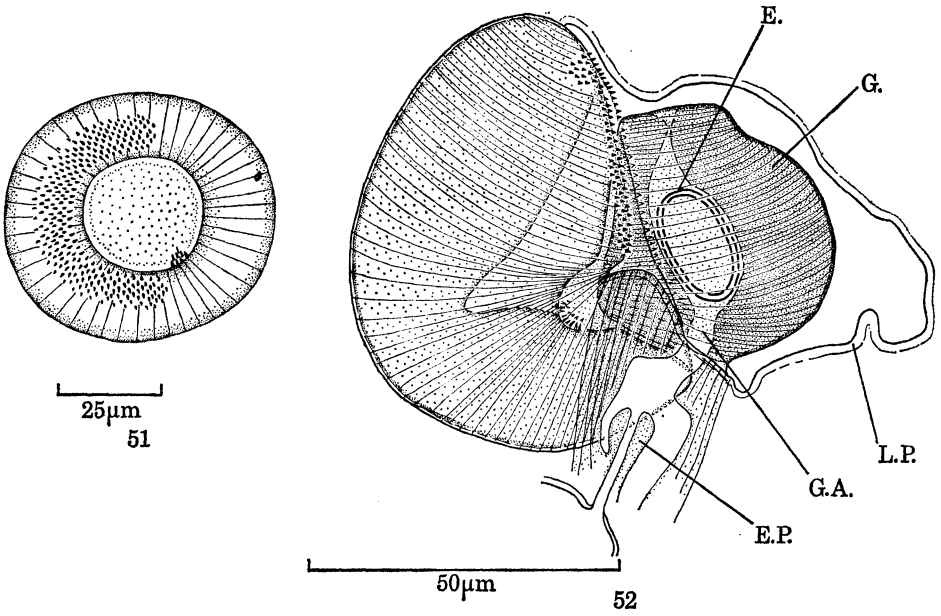


FIGURE 51. *G. puffini.* Holotype, ventral sucker (free-hand).
FIGURE 52. *G. puffini.* Paratype, ventrogenital complex.

Remarks

Numerous eggs in the ventrogenital sac of most specimens obscure both ventral sucker and gonotyl and render it impossible to see clearly the arrangement of spines on the ventral sucker. It is, however, clear that the ventral sucker is symmetric, has a large cavity and is armed with two groups of spines (figure 51).

The seminal vesicle in the six paratypes has a single axis, typical of a constricted seminal vesicle. In the holotype (figure 87), which is perhaps distorted, there are two axes, forming an obtuse angle.

Diagnosis

Body divided into short narrow forebody and long wide hindbody. Oral sucker small; prepharynx longer than pharynx. Ventrogenital sac 22–30/100ths from anterior end; lateral pocket present; ventral sucker symmetric, sucker like, ratio o.s./v.s. (lengths) 0.84–1.0, with dextral U-shaped band and sinistral patch of minute spines; gonotyl simple; genital atrium enters gonotyl and opens terminally. Seminal vesicle one chambered, constricted. Vitellaria extend from level of ovary or middle of seminal vesicle almost to posterior end. Eggs 23 (22–24) × 14 (12–15) μm. Excretory bladder long?

G. puffini is intermediate between *bearupi* with symmetric sucker, but with a continuous band of spines, and *fregatae* with two groups of spines, but with asymmetric ventral sucker. In *puffini*,

the gonotyl is simple, and the genital pore terminal, whereas in *fregatae* the gonotyl has a medially directed digitiform process adjacent to the genital pore, which is dorsal.

Additional differences that may be significant, between *puffini* and *fregatae*, two species often confused in the past, include (i) the smaller and narrower forebody in *puffini*, and (ii) the transversely elongate seminal receptacle in *puffini*, as opposed to the rounded seminal receptacle in *fregatae*.

According to Yamaguti (1941), the excretory bladder reaches the level of the seminal receptacle. I could not see the excretory bladder, but was able to trace the bladder arms back to a point well behind the posterior testis, indicating perhaps a short, entirely post-testicular bladder. Other features, such as form of ventral sucker and seminal vesicle, indicate affinity with the *bearupi*-group, which is characterized by a short bladder (see § III 3).

(*m*) *Galactosomum renincola* sp.nov.

The following species was found in both the bursa and ureters; however, the greatest number was found in the renal ureter. To call attention to this unusual site within the host, the name *Galactosomum renincola* is proposed.

Description (*figures* 53–59, 88)

The description is based on the type series (holotype and 9 paratypes), and sagittal sections of one worm. Additional notes are appended on 27 immature specimens from a sooty tern.

With the characters of the genus. Body 2.90 (2.02–3.52) mm long, distinctly divided into widened, spatulate, ventrally concave forebody 950 (730–1150) μm wide and narrower, thicker but flattened hindbody 770 (560–985) μm wide, hindbody widest anteriorly, and tapers slightly to posterior end; forebody shorter than hindbody, ratio, fore/hind 0.69 (0.61–0.87); forebody with large, deep unspined pit dorsally, anterior to ventrogenital sac and occupying most of intercaecal space, with roughly circular group of muscle fibres radiating outwards from wall of pit, and external to these a peripheral ventral band of circular fibres deep to inconspicuous radial-fibres; whole of area bounded by caeca and ventrogenital sac with numerous dorso-ventral fibres, but smaller and more widely spaced than in dorsal pit.

Body closely covered with scales anteriorly; becoming spines behind level of caecal bifucation; absent pre-orally, in dorsal pit, and immediately about mouth of ventrogenital sac; becoming smaller and finer posteriorly, but continuing to posterior end.

Frontal glands with numerous ducts, cell bodies in two lateral groups on each side, at level of pharynx; tegumental glands small, inconspicuous, numerous, especially in forebody ventrally, but absent intercaecally. Remnant of cercarial eyespot pigment present on either side of brain, pigment granules in scattered, intracellular clumps in forebody. Row of ducts opens into prepharynx ventrally; cell bodies not seen. Ducts from small, lateral gland cells open at pharyngo-oesophageal junction.

Oral sucker subterminal, large 302 (242–362) × 334 (266–403) μm. Prepharynx short and wide forming ventrally incised fornix at pharynx. Pharynx large, 168 (129–202) × 153 (129–185) μm. Oesophagus short, without epithelial lining. Caeca simple, straight, with tall columnar epithelium, extend almost to posterior end.

Ventrogenital sac small, median, at level of junction of fore- and hindbody, 38–47/100ths from anterior end; mouth small, with wall thickened anterodextrally by dextral hemisphincter (D.H.); radial fibres (R.F.) anteriorly, sinistrally and posteriorly originate deep in body,

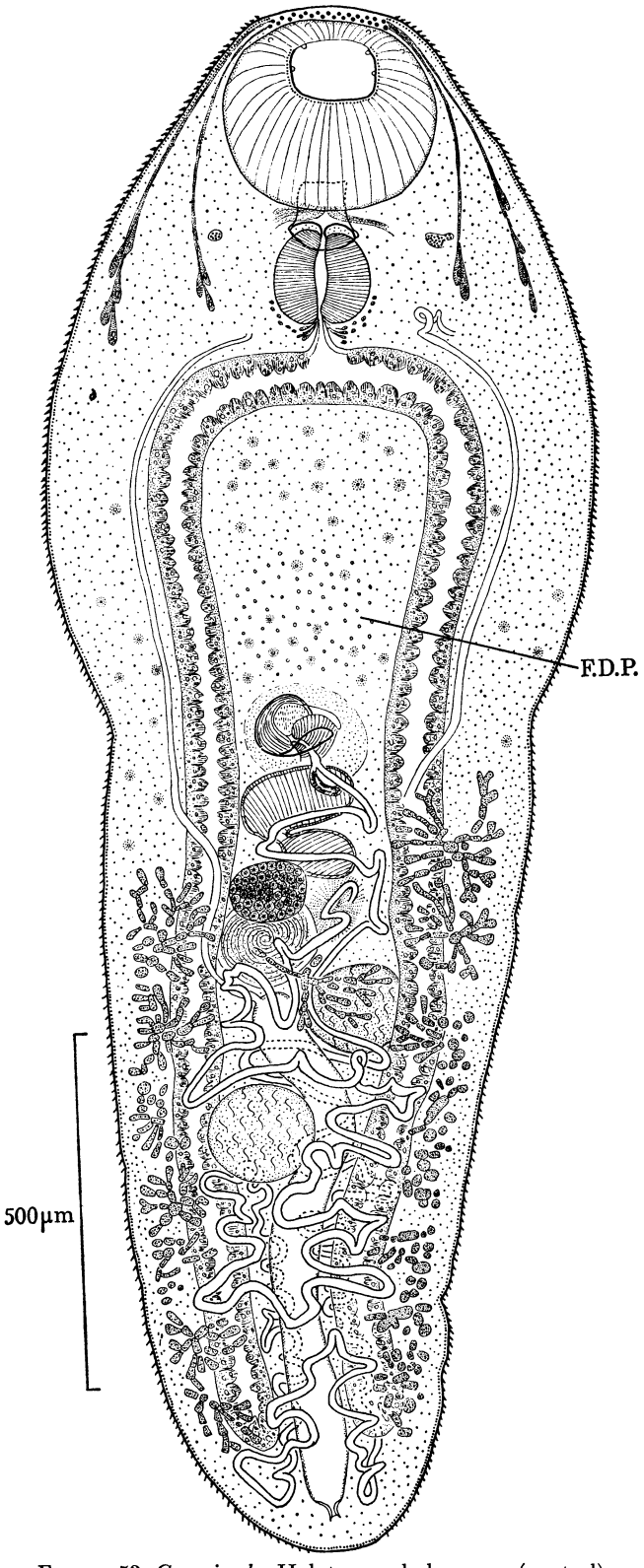


FIGURE 53. *G. renincola*. Holotype, whole worm (ventral).

peripheral to ventral sucker and ventrogenital sac, curve in ventrally to insertion on mouth of ventrogenital sac; thickened wall opposed to tip of gonotyl; without lateral pocket; largely filled by gonotyl and apical knob of ventral sucker. Ventrogenital complex surrounded by densely staining tissue clearly demarcated from parenchyma. Ventral sucker pyriform; ratio o.s./v.s. (lengths) 2.6–3.2; with embedded parenchymatous base 106 (76–119) × 100 (78–122) μm and large, unarmed muscular apical knob, 99 (80–124) × 104 (83–119) μm, projecting into ventrogenital sac; thick capsule of circular muscle-fibres at right angles to long axis; with no trace of cavity; axis inclined slightly forward and to left. Gonotyl 80 (62–107) × 77 (50–103) μm, unarmed, solidly muscular, conical, with base swollen anteriorly (sinistrally); arises from broad base postero-dorsally on left and curves toward apex of ventral sucker on right; bears genital pore dorso-terminally. Genital atrium short formed by union of uterus and ejaculatory duct immediately posterior to gonotyl; enters gonotyl, runs nearer ventral surface, and opens dorso-terminally, opposite apex of ventral sucker.

Testes small, slightly wider than long, do not fill intercaecal space, diagonal, separated; anterior testis sinistral, 125 (104–154) × 169 (122–246) μm; posterior dextral, 155 (119–202) × 165 (125–210) μm; sperm ducts run forward dorsally, unite at seminal vesicle. Seminal vesicle two-chambered, thick walled; long axis of proximal part inclined to right, forming acute angle with transverse long axis of distal part; proximal part oval to pyriform, with inbulging thickening (valve) about united entrance of sperm ducts, with outer layer of wall composed of diagonal muscle-fibres, 141 (92–193) × 106 (65–166) μm; distal part ellipsoidal to pyriform, with thick layer of circular muscle-fibres, 195 (134–256) × 119 (68–169) μm. Prostatic ejaculatory duct arises ventro-terminally on left and runs antero-dextrad to genital atrium, 39–47 × 21–23 μm; whole length lined with hair-like extensions of prostatic-gland ducts whose bodies form two small masses, one on either side of prostatic ejaculatory duct; ends in a short papilla projecting into genital atrium.

Ovary rounded 110 (74–134) × 135 (95–169) μm, to right of mid-line and nearer ventral surface; oviduct arises potero-medially on dorsal side. Seminal receptacle overlaps ovary postero-dorsally; variable in size; 138 (77–208) × 156 (119–210) μm; duct of seminal receptacle and Laurer's canal arise together from medial margin of seminal receptacle (figure 56); Laurer's canal thick walled, opens dorsally in mid-line, dorsal to ootype. Short oviduct unites with short duct of seminal receptacle and then, posteriorly, with common vitelline duct; enters ootype which is surrounded by Mehlis's gland and first coils of uterus. Vitelline follicles in rosettes, typically seven rosettes on right side and eight on left; largely ventro-lateral, occasionally meeting in mid-line ventrally behind posterior testis especially at posterior end, extend external to caeca to dorsal side, but seldom exceed medial border of caeca; extend posteriorly to, occasionally beyond, ends of caeca, but not beyond uterus; extend anteriorly on right to anterior border of ovary, and on left further forward to seminal vesicle or posterior border of ventrogenital sac; duct from centre of each rosette enters common mid-ventral longitudinal duct that runs forward between testes to small vitelline reservoir postero-dorsal to ootype. Uterus with typical course, largely intercaecal; descending arm posterior to testes continues posterad ventrally on left to about half way between posterior testis and posterior end, then crosses to right side, and turns anterad to posterior border of posterior testis, before descending to posterior end dorsally against medial face of right caecum; long terminal portion with thick muscular wall. Eggs (10, uterine) 27.5 (26.0–29.0) × 16.2 (16.0–18.0) μm; thick shelled, anopercular knob small or absent.

Excretory pore subterminal, dorsal; excretory bladder tubular, long; curves between testes dorsally and ends at posterior border of seminal receptacle; bladder arms arise terminally; apparently stenostomate.

TYPE HOST. Wedge-tailed shearwater, *Puffinus pacificus* (Gmelin).

OTHER HOSTS. Sooty tern, *Sterna fuscata* L.; white-capped noddy, *Anous minutus* Boie.

LOCATION. Renal ureter and bursa Fabricii of *Puffinus pacificus*; renal ureter, ureter, and large intestine of *Sterna fuscata*, bursa Fabricii and ureter of *Anous minutus*.

ABUNDANCE. In two of seven *Puffinus pacificus*, one bird with 14 adults in renal ureter, other with two adults in ureter distal to kidney; in four of seven *Anous minutus*, one or two adults in bursa of three birds, and one adult in ureter of fourth.

TYPE LOCALITY. Heron Island, Capricorn Group, Queensland (also *Anous minutus*).

DISPOSITION. U.S.N.M. holotype no. 72056, paratypes no. 72057, ex *Sterna fuscata* (figured), no. 72058; B.M.(N.H.) paratype no. 1972.1.24.5; S.A.M. paratype no. E. 890; M.P.M. paratype no. 19028; author's colln.

Remarks

The unusual location of adults of *renincola* calls for comment. First of all, it should be pointed out that, with the exception of the sooty tern, the hosts were examined while still warm; hence, it is evident that the ureter is a natural site of this species. No other species of *Galactosomum* or indeed of the family Heterophyidae, is recorded from the ureter; all are found in the gut.

When observed *in situ*, the worms were strongly flattened against the mucosa, especially the hindbody which in this state was as wide as the forebody. Even in such flattened worms, the dorsal pit is evident, but as the worms adhere by their ventral surface, the function of the dorsal pit is enigmatic.

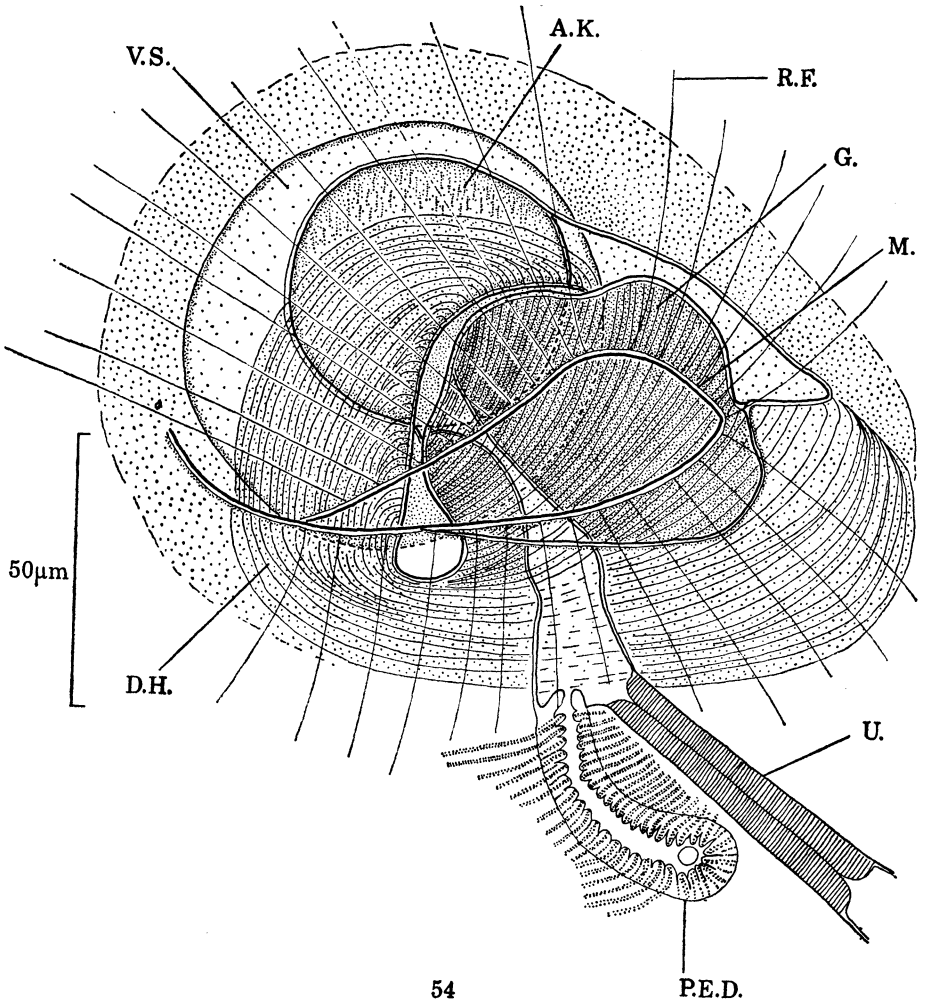
The dorsal pit (figure 55), a structure of problematic function, is a conspicuous feature of live worms *in situ* and of unflattened wholemounts; the pit itself disappears in flattened wholemounts, but the structure can be identified by the group of prominent dorso-ventral fibres (F.D.P., figure 53). In sections, the parenchymal cells adjacent to the pit are more granular than those deeper in the body. The dorsal pit is unique to *renincola*, although a ventral pit occurs in *sinuilactis*, *q.v.*

In living worms from bursa and ureter, the caeca are filled with bright red blood; however, no marked lesion of the mucosa was noted at the site of attachment of the oral sucker. Blood-feeding does not appear to have been described for other species of *Galactosomum* (see §V, p. 443).

The course of the uterus is fairly constant, except the first and ventral portion of the descending arm, which although usually dextral, may be sinistral. The dorsal portion of the descending arm and the post-testicular portion of the ascending arm fill with darker eggs in older flukes, and form two conspicuous sinuous masses.

Immature adults from the sooty tern range in size from 0.89 to 1.90 mm. In small specimens, less than 1.5 mm long, the forebody is longer than the hindbody (ratio fore/hind 1.0–1.47), whereas in the largest, 1.90 mm long, the forebody is shorter than the hindbody, and the ratio of fore/hind, 0.76 lies within the range, 0.61–0.87, of mature adults from a wedge-tailed shearwater.

The smallest immature adult (figure 58) has small, undeveloped gonads, and may approximate to the metacercaria. Larger immature adults (figure 59) show a great increase in the size of the gonads; indeed, these are relatively larger than those of early mature adults (figures 53, 57; cf. *bearupi*).



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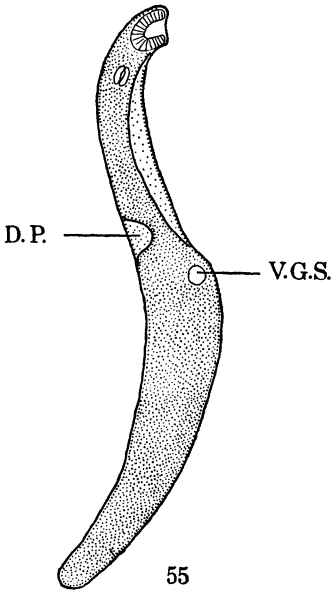

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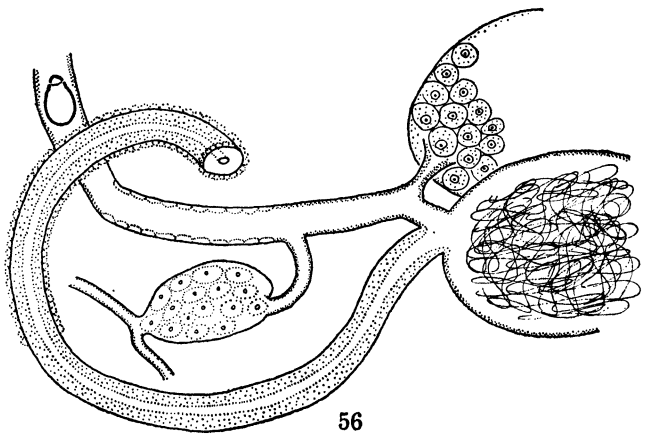


56

FIGURE 54. *G. renincola*. Holotype, ventrogenital complex.

FIGURE 55. *G. renincola*. Lateral aspect, showing dorsal pit (free-hand).

FIGURE 56. *G. renincola*. Female complex (free-hand).

Characters found to remain constant for both immature and mature specimens include (i) those of the ventrogenital complex, (ii) the extent of the excretory bladder, and (iii) the ratio of the lengths of the oral to the ventral sucker, namely 2.8–3.2 in mature adults and 2.8–3.4 in immature adults.

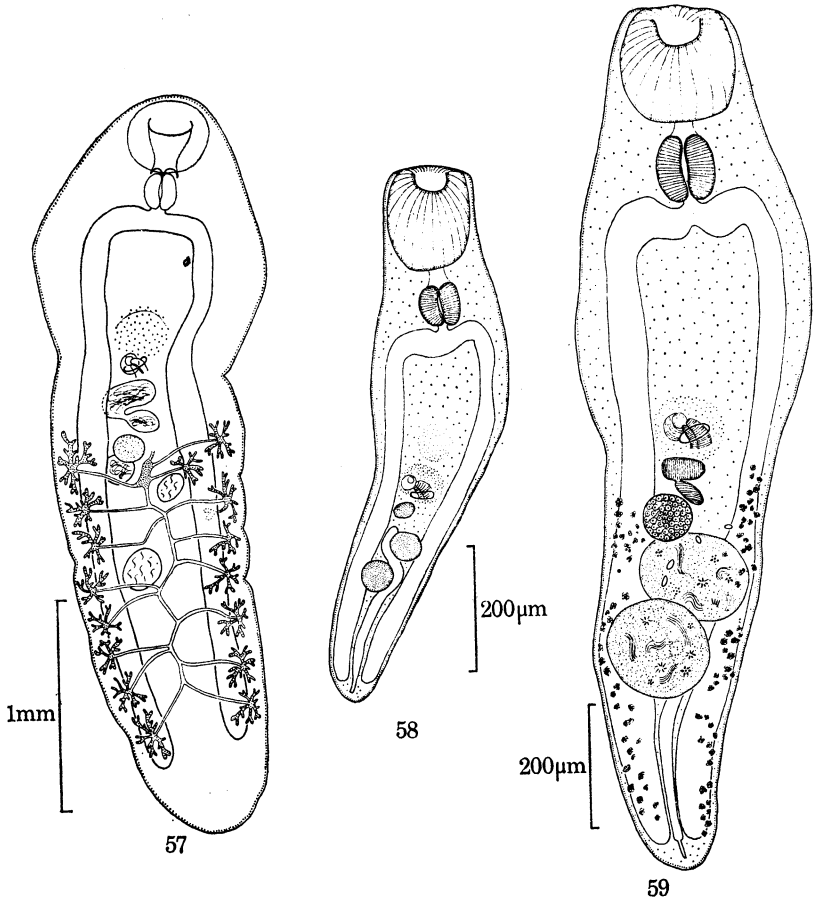


FIGURE 57. *G. renincola*. Paratype, vitelline system.
FIGURE 58. *G. renincola*. Immature adult.
FIGURE 59. *G. renincola*. Nearly mature adult.

Diagnosis

Body stout, forebody wider, and in mature adults shorter, than hindbody, with dorsal pit anterior to level of ventrogenital sac. Oral sucker large; prepharynx shorter than pharynx. Ventrogenital sac well behind gut bifurcation, at junction of forebody and hindbody; 38–47/100ths from anterior end. Ventral sucker smaller than oral sucker, ratio o.s./v.s. (lengths) 2.8–3.2; with unarmed apical knob, no cavity, and spherical parenchymatous base. Gonotyl simple; bears genital pore dorso-terminally. Seminal vesicle two-chambered, with transversely orientated distal part, with prominent circular fibres, forming acute angle with smaller proximal part, with prominent diagonal fibres; both parts moderately thick walled. Vitellaria extend to between anterior border of ovary and posterior border of ventrogenital sac; may exceed caeca posteriorly. Eggs 27.5 (26.0–29.0) × 16.2 (16.0–18.0) μm. Excretory bladder extends forward between testes to posterior border of seminal receptacle.

G. renincola differs from other species possessing a long excretory bladder in the following combination of characters: (i) forebody spatulate; (ii) dorsal pit in forebody; (iii) oral sucker

much larger than ventral sucker; (iv) ventral sucker unarmed, with apical knob, and (v) two chambers of seminal vesicle forming an acute angle, with distal > proximal.

G. renincola is, perhaps, closest to *lacteum*, with which it shares: (i) spatulate forebody; (ii) ventral sucker with apical knob; and (iii) o.s. ≫ v.s. but differs from it in having (i) apical knob unarmed; (ii) acute angle between chambers of seminal vesicle; (iii) dorsal pit, and (iv) anterior limit of vitellaria further forward.

(*n*) *Galactosomum sanaensis*

Synonym

Galactosomum sanaensis Kobayasi, 1942, Figs. 1, 2 (dog fed *Mugil cephalus* L.; Hainan Island; descr.).

The species is based on a single specimen that has apparently disappeared, as inquiries in Taiwan, where some of Kobayasi's specimens remained (J. K. Chiu, personal communication) and in Japan, failed to locate it. Nevertheless, as described and figured *sanaensis* differs from the species that I have seen at first hand and so is retained as valid.

Diagnosis (*from Kobayasi* 1942) (*figure* 89)

Body elongate, slender, wider posteriorly. Prepharynx longer than pharynx. Ventrogenital sac in first third of body, about twice its diameter behind the bifurcation of the gut. Ventral sucker slightly smaller than oral sucker, ratio o.s./v.s. (length) 1.4, symmetric, subspherical, with two patches of minute spines on the lip laterally. Gonotyl not described. Seminal vesicle '. . .runs transversely and irregular. . .'. Vitellaria exceed ovary anteriorly, reach posterior end. Eggs 24–27 × 14–18 μm. Excretory bladder extends forward between testes, exceeds anterior testis.

The sucker ratio was calculated from Kobayasi's measurement of the oral sucker, and the estimated length of the ventral sucker in his Fig. 2, the scale of which, by comparison with his Fig. 1, is 0.05 mm not 0.1 mm.

G. sanaensis, with its long excretory bladder differs from *lacteum*, *phalacrocoracis* and *renincola*, also with long bladder, in the form of the ventral sucker and the position of the ventrogenital sac. It resembles *puffini* in the ratio of oral and ventral suckers, and in the position of the ventrogenital sac; however, in *puffini*, spines on the ventral sucker are differently arranged.

The form of the ventral sucker, with its two spine patches, is similar to that of *yehi*, as redescribed herein, and *dollfusi*, but in both of these the excretory bladder does not reach the posterior testis.

(*o*) *Galactosomum sinuilactis* sp.nov.

Among material from cormorants collected in Brisbane and obtained from the Johnston Collection, from cormorants in South Australia, is what appears to be a new species of *Galactosomum*, for which the name *G. sinuilactis* is proposed. The specific name refers to the striking and characteristic sinuous form of the caeca.

The description is based on the type series (holotype and 11 paratypes), supplemented from a further 55 wholemounts, together with sagittal and transverse serial sections. Measurements (average and range) are given of the holotype and 11 paratypes. A brief description is appended of the metacercaria, based on material from the Johnston Collection.

Description (*figures* 60–64, 90)

With the characters of the genus. Body sole shaped, 2.87 (2.70–3.26) mm long; with spatulate forebody 850 (750–940) μm wide and elongate pointed hindbody 717 (590–750) μm wide;

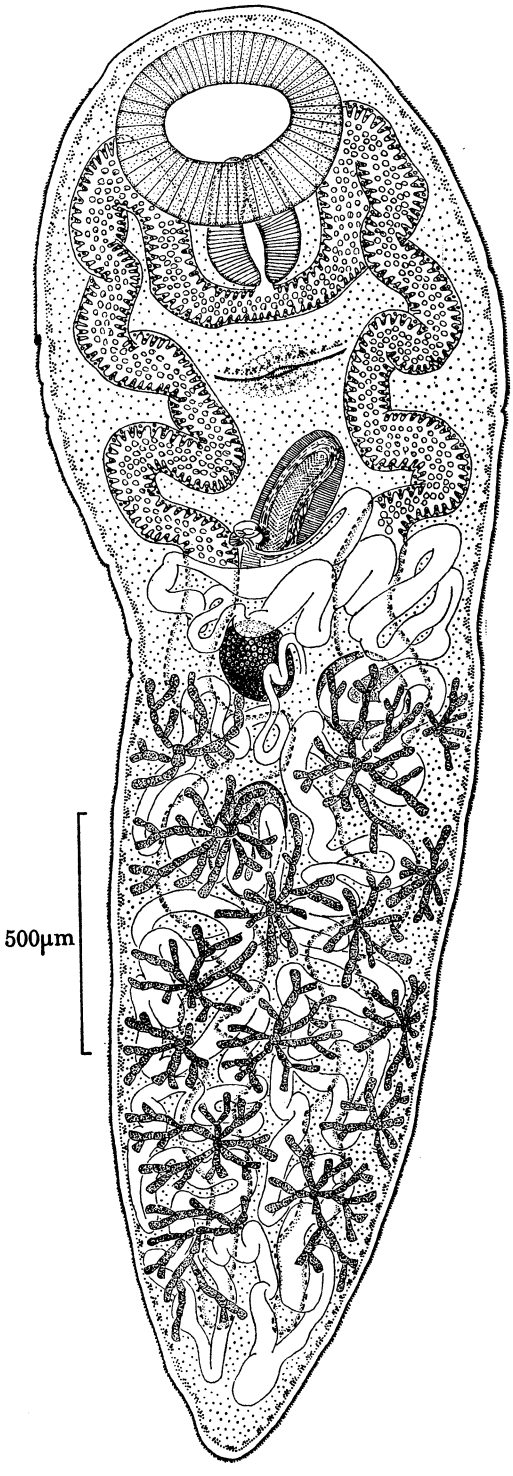
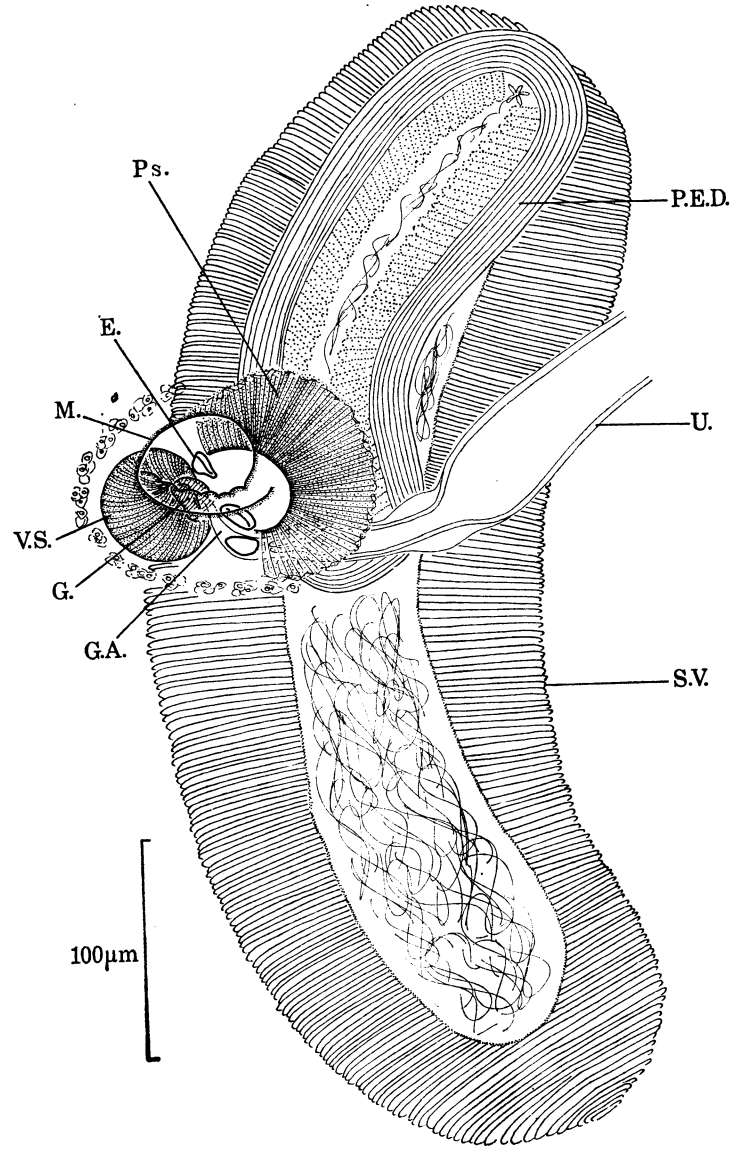


FIGURE 60. *G. sinuilactis*. Holotype, whole worm (ventral).



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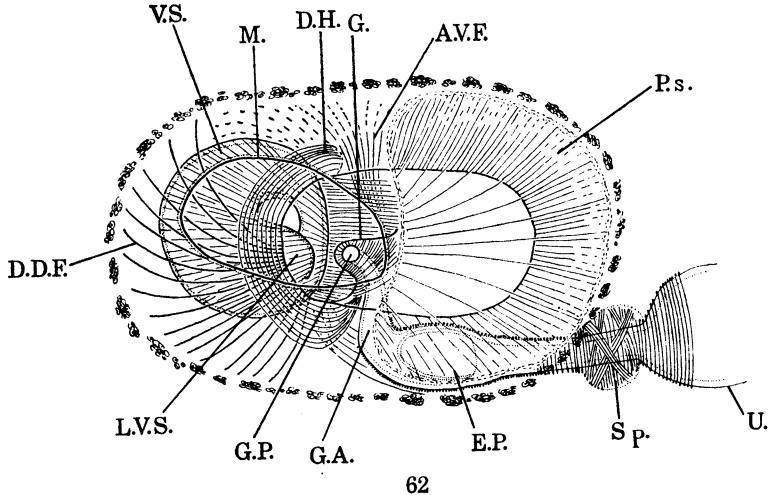


62

FIGURE 61. *G. sinuilactis*. Holotype, ventrogenital complex.

FIGURE 62. *G. sinuilactis*. Musculature of ventrogenital sac (free-hand).

function of forebody and hindbody just posterior to ventrogenital sac. Forebody flattened, concave ventrally, with concavity deepening into a ventral pit typically in area bounded by bifurcation of gut anteriorly and incurving caeca laterally. Ventral pit variable in shape and depth, often a transverse depression; body-wall muscles modified into a superficial ring centrally, framed by arching longitudinal fibres; dorso-ventral fibres radiate dorsad from ring; parenchyma internal to ring often granular (? glandular).

Body covered with small, slender spines (not scales); absent over anterior end and preorally; extend to posterior end; absent from posterior lip of ventrogenital sac. Frontal glands apparently absent; neither duct mouths nor cell bodies seen. Parenchyma of large contiguous, polygonal cells.

Oral sucker large, mouth opening ventrally; 410 (380–460) μm long and 440 (410–500) μm wide. Prepharynx very short, the whole forming a fornix, slit ventrally, about anterior end of pharynx. Pharynx large, 246 (226–274) μm long and 178 (129–210) μm wide; opens into prepharynx by antero-ventral longitudinal slit. Caeca large, sinuous; loop forward lateral to pharynx, then run posterad in regular series of sinuosities almost to posterior end; caecal epithelium of tall, columnar, separated cells.

Ventrogenital sac small, submedian, dextral, well behind bifurcation of gut, 35–41/100ths from anterior end; mouth transversely oval, usually symmetric; wall sinistrally sucker like, directed dextrally, with thick layer radial fibres but no capsule (pseudosucker). Musculature of mouth includes longitudinal fibres of body wall inserted on mouth anteriorly and forming loop about mouth laterally and posteriorly; longitudinal fibres, distinct from those of body wall, running postero-dorsally in posterior spineless lip; and enlarged, modified diagonal fibres (S.D.F.) of the body wall radiating out dextrally from mouth almost to lateral margin of body. Musculature of sac includes dextral hemisphincter (D.H.) arising from base of gontoyl posteriorly, half encircling sac dextrally, and forming shelf ventral to apex of ventral sucker dorsal to this a fan of separate fibres (D.D.F.) arising from wall of sac ventral to apex of ventral sucker, radiating out and forward and toward ventral surface; and fibres (A.V.F.) arising dorsal to anterior root of gonotyl and fanning out antero-ventrally. Dorsal floor of sac between ventral sucker and pseudosucker with strong transverse fibres continuous with base of gonotyl. Ventral sucker parenchymatous, with nuclei basal, embedded dextrally, with apex directed sinistroventrally; small 50 (42–56) μm long and 41 (32–47) μm wide, ratio o.s./v.s. (lengths) 6.8–9.3; with reduced cavity and swollen dextral lip; unarmed. Gonotyl small, with broad base arising from wall postero-dorsally and small rounded tip, 23–33 μm wide, bearing genital pore ventroterminally. Genital atrium short and curved; courses through length of gonotyl.

Testes diagonal, intercaecal, well separated from each other and from ovary, variable in shape; anterior testis on left, 177 (140–227) μm long and 149 (110–195) μm wide; posterior testis on right, 213 (165–276) μm long and 159 (120–195) μm wide. Sperm ducts unite at seminal vesicle; entrance guarded by small papilla projecting into lumen of vesicle. Seminal vesicle one-chambered cylindrical, curved, dorsal; with thick layer outer circular muscle-fibres; 476 (404–540) μm long and 198 (185–256) μm wide, wall 32–81 μm thick; extends anteriorly anterior to ventrogenital sac and posteriorly to or slightly beyond ovary; opens into prostatic ejaculatory duct via small, conical papilla. Prostatic ejaculatory duct large; 266 (256–292) μm long and 89 (78–100) μm wide, wall 16–19 μm thick; wall with thick layer of longitudinal muscle-fibres; lumen largely filled by elongate inbulging ends of prostatic-gland cells, cell bodies form sleeve externally; runs posterad or postero-dextrad, narrowing slightly, to

open into genital atrium under posterior margin of pseudosucker; opens via large papilla into genital atrium.

Ovary rounded, variable in shape, submedian and dextral, nearer ventral surface; 161 (136–198) μm long and 153 (130–175) μm wide. Ootype and Mehlis's gland postero-medial to ovary. Laurer's canal present, opens dorsal to Mehlis' gland. Seminal receptacle postero-dorsal to and overlapping ovary; variable in size and shape, 125 (52–162) μm long and 169 (110–218) μm wide. Vitellaria in 15–16 rosettes uniformly distributed ventrally from level of ovary to ends of caeca; vitelline duct single, median. Uterus with typical course; extensively coiled; ascending limb with dorsal loops running between excretory bladder and left caecum; terminal arm greatly dilated with eggs, turns mediad to enter genital atrium; terminal portion a short metraterm with strong circular-fibres, separated from uterus by prominent sphincter with circular and diagonal fibres. Eggs (10, uterine) 24.4 (23.0–25.5) × 12.2 (11.0–12.7) μm.

Excretory bladder long, extends to or beyond anterior border of ovary; excretory pore subterminal, dorsal. Bladder arms arise at level between testes, divide into anterior and posterior collecting tubules at level of anterior testis; system mesostomate; flame cells numerous, $N \approx 16$.

TYPE HOST. *Phalacrocorax varius* (Gmelin).

LOCATION. Bursa Fabricii and large intestine.

TYPE LOCALITY. Moreton Bay, Queensland, Australia.

DATE OF COLLECTION. 25.vii.1969.

COLLECTOR OF HOST. G. Groom and R. Greenhill.

DISPOSITION. U.S.N.M. holotype no. 72059, paratypes 72060, paratype figured 72061; B.M.(N.H.) paratype no. 1972.1.24.6; S.A.M. paratype no. E. 891; M.P.M. paratype no. 19029; author's coll. paratype no. 1357.

OTHER HOSTS AND LOCALITIES. *Phalacrocorax varius* (Gmelin) Kangaroo Island, South Australia, Aug. 1946; Port Gawler, South Australia, 5.vi.1946, author's coll.

Phalacrocorax fuscescens (Vieillot) Edithburgh, South Australia, 14.iv.1945, author's coll.

Seven *Phalacrocorax varius* from Moreton Bay were examined carefully to determine the distribution of the flukes. Of these birds, two lacked the bursa Fabricii and were uninfected. A total of 44 flukes were found in the five cormorants that possessed a bursa Fabricii, and of these only four flukes were found in the large intestine. Three of the four were small (table 5) and contained few eggs; the fourth was as large but contained fewer eggs than adults from the bursa. A further difference between the two groups was seen in the contents of the caeca. Those from the bursa had blood-filled caeca, whereas those from the large intestine did not (see § V). A comparable difference in development and site is suggested for *renincola* which, however, was found in the ureters in birds lacking a bursa.

One is tempted to suggest by analogy with monogenoids, that sinuous (elongated or enlarged) caeca and blood-feeding are related in *sinuilactis*, but against this is the combination of straight caeca and blood-feeding in *renincola*.

The ventral pit (figure 63), resembles the dorsal pit in *renincola*, in having granular parenchymal cells subjacent to it suggestive of glandular activity. The ventral pit appears to be related to attachment, as it was seen in living specimens that, during attempts to re-attach to the bursal mucosa, the pit deepened, as the forebody expanded laterally like a cobra's hood, eventually forming a concavity over the whole of the ventral surface of the forebody.

Diagnosis

Body sole shaped; with wide flattened, ventrally concave forebody and narrower, thicker hindbody; forebody with ventral pit posterior to pharynx. Oral sucker large; prepharynx shorter than pharynx. Ventrogenital sac small, dextral; 35–41/100ths from anterior end; sinistral wall a pseudosucker; dextral hemisphincter forms shelf dextrally over ventral sucker. Ventral sucker small, ratio o.s./v.s. (lengths) 7–9; unarmed, parenchymatous, with reduced cavity and swollen dextral lip. Gonotyl small, conical, genital pore opens ventro-terminally. Gonads small, separated; testes diagonal. Seminal vesicle one-chambered, cylindrical, with thick layer of circular fibres; extends anterior to ventrogenital sac. Prostatic ejaculatory duct posteriorly directed, with thick layer of longitudinal fibres. Vitellaria in rosettes uniformly

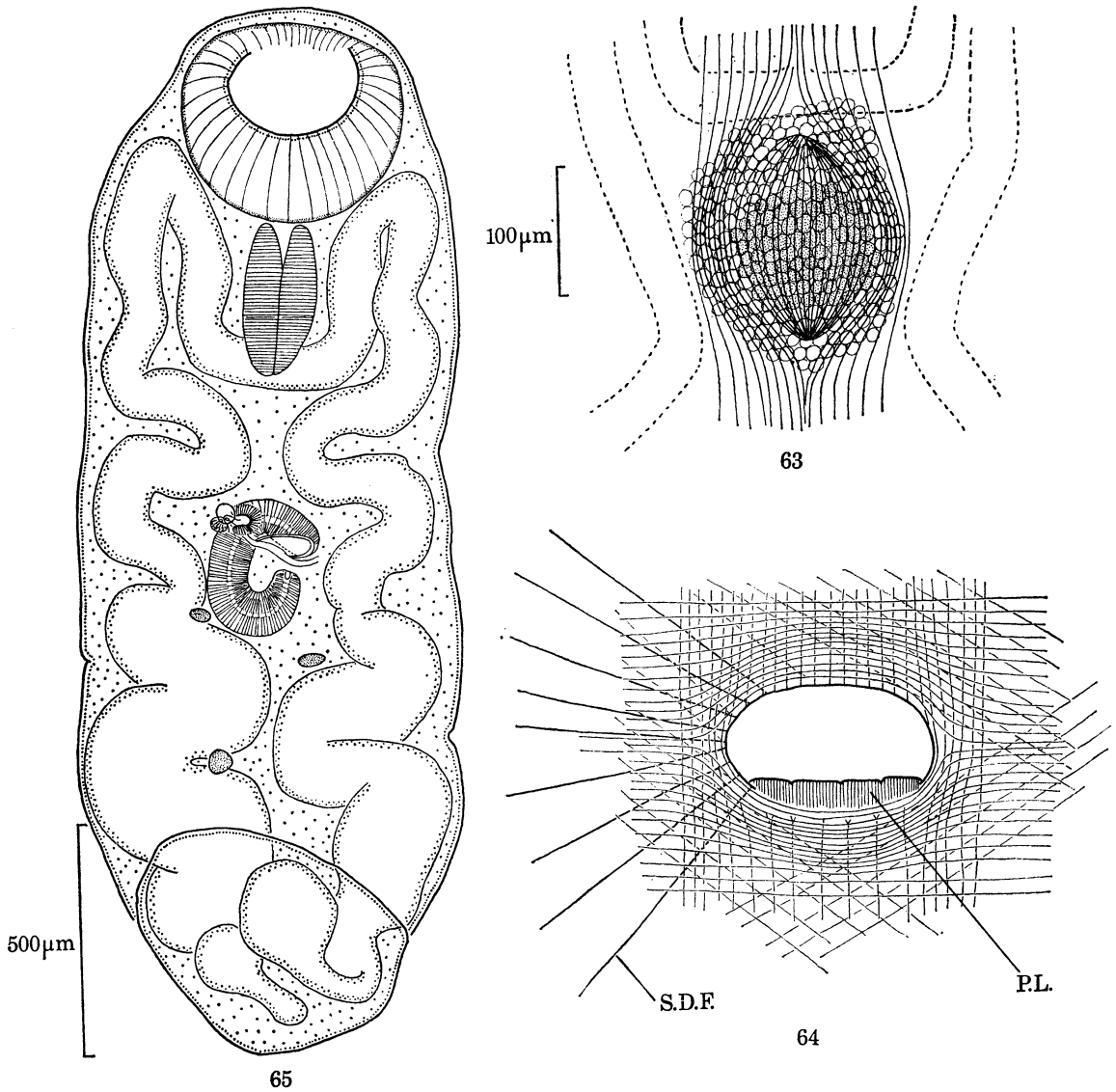


FIGURE 63. *G. sinuilactis*. Region of ventral pit (free-hand).

FIGURE 64. *G. sinuilactis*. Mouth of ventrogenital sac (free-hand).

FIGURE 65. *G. sinuilactis*. Metacercaria from *Haletta semifasciata*.

spaced ventrally from ovary to ends of caeca. Eggs 24.4 (23.0–25.5) × 12.2 (11.0–12.7) μm. Excretory bladder long, extends to or beyond ovary.

G. sinuilactis resembles *renincola* in body shape, long excretory bladder, small gonads, large oral sucker and pharynx, very short prepharynx, and small unarmed ventral sucker, but differs markedly in the form of the ventrogenital sac, seminal vesicle, and prostatic ejaculatory duct, and in the course of the caeca. Further similarities are the presence of a forebody pit, which is, however, ventral in *sinuilactis* but dorsal in *renincola*, and occurrence in the bursa Fabricii.

Metacercaria (*figure* 65)

HOSTS. *Haletta semifasciata*, *Platycephalus* sp.

LOCATION. In cysts on outer surface of gut.

LOCALITY. Adelaide, South Australia.

DISPOSITION. U.S.N.M. no. 72062; author's coll.

Description

Of the eight specimens available, one had been fixed alive but strongly flattened, and the remainder had been fixed dead and flattened slightly. Measurements are given of four specimens.

Closely resembles adult in shape of body and form of caeca. Reproductive system advanced; ventrogenital complex as in adult; in male system testes small and without sperm, seminal vesicle empty strongly curved C- or U-shaped; in female system ovary small, seminal receptacle small and empty, uterus fully formed, but coiling less extensive, vitelline duct not seen. Excretory bladder inflated, exceeds anterior border of ovary.

TABLE 5. COMPARISON OF METACERCARIA AND ADULT OF *G. SINUILACTIS*

	metacercaria	small adults (4 smallest)	large adults (type series)
total length/mm	2.58–3.44	1.72–2.04	2.70–3.26
forebody width/μm	775–920	590–635	750–940
anterior end to ventrogenital sac/μm	1130–1245	680–820	940–1150
oral sucker length/μm	322–452	258–346	380–460
oral sucker width/μm	412–525	290–340	410–500
pharynx length/μm	242–306	170–185	226–274
pharynx width/μm	153–169	97–137	129–210
ventral sucker length/μm	44–56	38–44	42–56
ventral sucker width/μm	41–50	32–36	32–47
ratio o.s./v.s. (lengths)	8.1–8.5	6.8–9.0	6.8–9.3
seminal vesicle length/μm	555	218–330	404–540
seminal vesicle width/μm	84–117	91–165	185–256

Remarks

As in metacercaria of other species of *Galactosomum*, and indeed of haplorchines in general, the metacercaria of *sinuilactis* is, but for the absence of sperm, eggs, and vitellaria, an adult in morphology. Comparison of metacercariae with the three smallest ovigerous adults and with adults containing many eggs (the type series) reveals that the metacercariae are larger than the smallest adults, and as large as fully ovigerous adults (table 5). This discrepancy may be explicable in two ways. First, the adults were alive when fixed, whereas the metacercariae,

from their appearance, were dead. As flukes swell after death, the metacercariae, which indeed look flaccid and cloudy, may be swollen, thus distorting their measurements. Secondly, it is possible that the metacercaria decreases in size (of body, but not of organs) following entry into the definitive host, as suggested earlier in the case of *lacteum*.

In all three groups, it can be seen that the ratio o.s./v.s. does not change significantly, and so contributes a stable taxonomic character.

(*p*) *Galactosomum spinetum*

Synonyms

Microlistrum spinetum Braun, 1901; Braun, 1902, Fig. 37, Pl. 3; Figs. 38, 39, Pl. 4 (*Rynchops nigra*; Brazil; descr.; types Berlin, no. 1606); Odhner, 1910 (re-descr. of Braun's specimens).

Galactosomum spinetum (Braun) Travassos, 1929 (as *G. spinectum*); Sogandares-Bernal, 1959 (*Rynchops nigra*; Florida; no descr.); Sogandares-Bernal & Hutton, 1960, Figs. 1–4 (metacercaria in *Hyporhamphus unifasciatus* (Ransoni); Florida; no descr.); MacInnis, 1966, Fig. 2 (*Gelochelidon nilotica aranea* (Gmelin); Florida; descr.).

Retevitellus spinetus (Braun) Cable, Connor & Balling, 1960, Figs. 21–23 (*Thalasseus maximus maximus*; Puerto Rico; descr.; t.o.d. of *Retevitellus* Cable, Connor & Balling, 1960).

Galactosomum spinectum (*sic*!) (Braun, 1901). Morozov (in Skrjabin, 1952); citation of *Fregata magnificus* as host is an error.

This species was found by Braun among material collected by Natterer in Brazil and lodged in Rudolphi's collection.

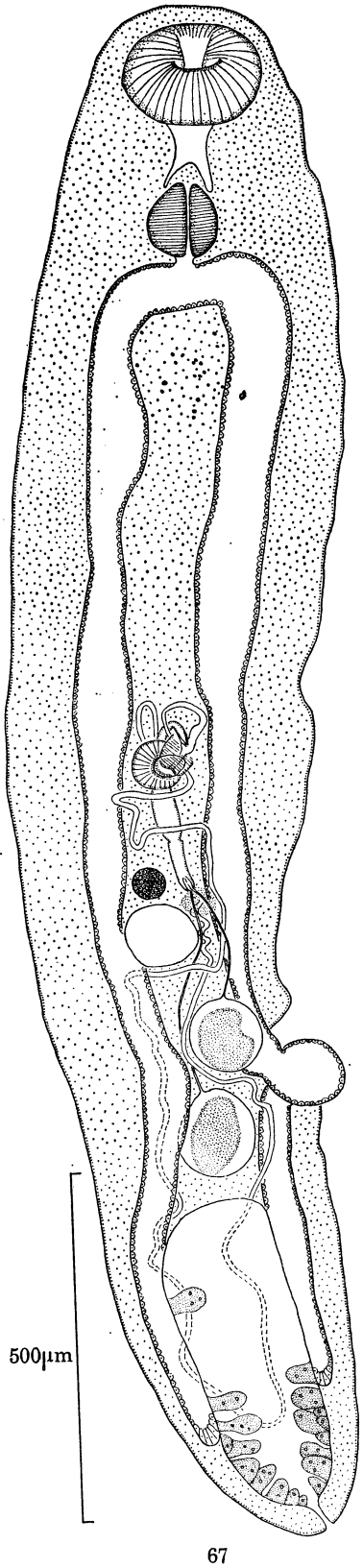
The description is based on three of Braun's six type specimens. These were re-described by Odhner (1910), but without details of the ventrogenial complex. Comparison is made with a specimen from and the description of Cable *et al.* (1960), with the undescribed specimens reported by Sogandares-Bernal (1959), and with specimens collected by R. Holliman in Florida. Measurements (range) are given of three syntypes. A brief description is given of the metacercaria recorded by Sogandares-Bernal & Hutton (1960).

Description (*figures* 66, 91)

With the characters of the genus. Body flattened leaf like, undivided; obovate lanceolate, widest at level ovary, tapering to ends, narrower posteriorly; 4.6–5.1 mm long and 0.89–1.27 mm wide. Forebody with numerous stout dorso-ventral muscle-fibres, abundant both inter- and extra-caecally, extending in decreasing number into hindbody to level of testes. Body scaly to level of anterior testis, spiny to posterior end; scales absent pre-orally between oral sucker and unarmed anterior tip. Gland cells not seen clearly, but frontal-gland cells apparently numerous intercaecally in forebody.

Oral sucker ventro-terminal, large; 204–240 × 250–270 μm. Prepharynx short, about same length as pharynx; protractors of pharynx closely invest wall. Pharynx large, 190–210 × 125–175 μm, as long as oral sucker; retractors of pharynx arise postero-laterally on each side and pass posterad both dorsal and ventral to caeca, but more numerous dorsally. Oesophagus very short. Caeca straight, end well short of posterior end.

Ventrogenital sac small, median, obscured by terminal coils of uterus; 33–38/100ths from anterior end; with simple postero-sinistral lateral pocket arising ventral to base of gonotyl, with small group of stout muscle-fibres arising from postero-lateral face of pocket dorsally and run-



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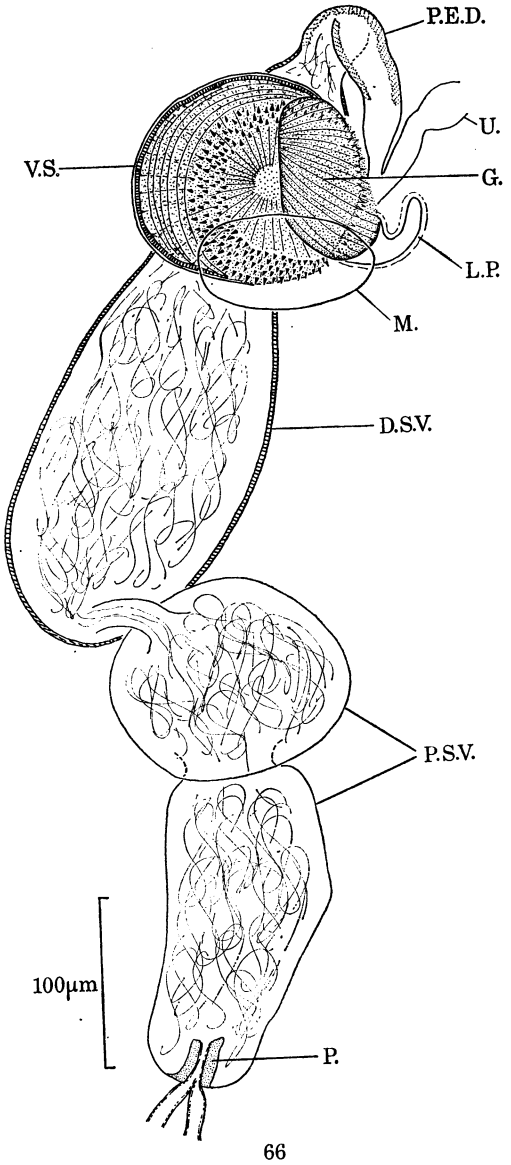

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FIGURE 66. *G. spinetum*. Syntype, ventrogenital complex.

FIGURE 67. *G. spinetum*. Metacercaria.

ning antero-laterad into parenchyma; mouth symmetric, encircled by well-developed circular muscle-fibres and with narrow dextral hemisphincter arising from wall posterior to gonotyl, encircling sac dextrally, and inserted on wall anteriorly. Ventral sucker small, 125 × 115–135 μm, ratio o.s./v.s. (lengths) 1.6, 1.9; axis inclined to left; with thick capsule of circular muscle-fibres and parenchymatous medulla traversed by separated radial fibres; sucker like, with reduced eversible cavity directed ventro-medially; with about 10 rows of 4–5 μm spines encircling apex and wall of cavity, with central small spineless area. Gonotyl simple, solidly muscular, overlaps apex of ventral sucker ventrally; short, with broad tip directed posteriorly or postero-dextrally, 85–95 × 45–50 μm; arises sinistrally or antero-sinistrally; overhangs genital pore, with dorsal groove extending from base ventral to genital pore to free tip. Genital atrium short, approaches base of gonotyl antero-sinistrally.

Testes elongate, indented, tandem; contiguous or separated by ascending arm of uterus. Seminal vesicle two-chambered; proximal thin walled, tortuous, with 2–3 wide, broadly joined sacculations, 185–240 × 95–145 μm; proximal end sinistral to ovary, joins distal chamber by short narrow duct; distal chamber with thicker wall of circular fibres, fusiform to clavate, narrowed anterior end extends to or beyond anterior border of ventral sucker, 306–370 × 90–130 μm. Prostatic ejaculatory duct short, narrow, recurved ventrally, opens into genital atrium via papilla; prostatic-gland cells in two submedian groups anterior to ventral sucker.

Ovary rounded, submedian on right. Seminal receptacle behind and contiguous with ovary. Vitellaria follicular, in rosettes; largely lateral, with a few follicles medial to caeca especially behind posterior testis; extend anteriorly to between posterior border of ovary and ventral sucker, posteriorly end a short distance behind posterior testis and well in front of ends of caeca. Course of uterus atypical; descends to right of anterior testis, crosses between testes, and descends on left to posterior end, ascends on right past both testes, passes ovary on left, loops across seminal vesicle ventrally, loops to right then to left anterior to ventrogenital complex, enters genital atrium from in front. Eggs (10, uterine) 25.3 (23.8–28.9) × 12.7 (11.9–13.6) μm.

Excretory pore terminal; excretory bladder tubular, extends anteriorly to or almost to posterior testis; bladder arms recurve at level of pharynx (? stenostomate).

Host. *Rynchops nigra* L.

Location. Intestine.

Locality. Brazil.

Disposition. Berlin, coll. Rud. no. 1606 syntypes.

Remarks

G. spinetum exhibits a number of unusual features, which together led Cable *et al.* (1960) to propose a new genus, *Retevitellus*, for this species. One of the more singular features, the arrangement of the vitelline ducts, has been found in a number of species, and is probably common to the genus *Galactosomum*. A second feature, the anterior extension of uterus and seminal vesicle beyond the ventral sucker, is shared in part with *sinuilactis*, in which the seminal vesicle extends anterior to the ventral sucker. Of the remaining features, shape of testes and limited post-testicular extent of vitellaria are not considered to be of more than specific importance. The remaining feature, shape, is peculiar to this species.

The flattened, leaf-like form of the body and the absence of any change in form or contour between forebody and hindbody is singular. It appears that in *spinetum* the whole of the body,

or at least the anterior two-thirds, is flattened by means of the abundant dorso-ventral fibres against the mucosa of the host's intestine, rather than just the forebody as in species such as *cochleariformum*.

Yet another odd, but minor, feature is seen in the course of the uterus, the ascending arm of which does not cross from right to left between the testes. The reason for this may lie in the great development of dorso-ventral muscle-fibres, which, assuming a development of the uterus from metacercaria to adult as described for *bearupi* (*q.v.*), may prevent looping of the ascending arm about the posterior testis as the uterus lengthens. Occasionally, the descending arm passes to the left of the anterior testis.

Comparison

Specimens examined

U.S.A., Florida	ex *Hyporhampus unifasciatus* John's Pass, Fla. (Sogandares-Bernal & Hutton 1960). Coll. Sogandares F59–35, author's colln	4 specimens (metacercariae)
	ex *Rynchops nigra* L. Little Gasparilla Pass, Fla. (Sogandares-Bernal 1959). Coll. Sogandares F59–25, author's colln	8 specimens (7 immature)
	ex *Larus atricilla* L. (laughing gull) new host Alligator Harbor, Fla. Oct. 1957, no. 452, coll. by R. Holliman, author's colln	2 specimens
Puerto Rico	ex *Thalasseus maximus*, no. 52042301 (Cable *et al.* 1960), author's colln	1 specimen

All of the above specimens agree with the types, particularly in characters of the ventrogenital complex, and are here considered to be conspecific. It is clear that the apex of the ventral sucker is not uniformly spiny, as suggested by Odhner (1910) and Cable *et al.* (1960), but has a wide band of spines encircling a small spineless area (base of cavity).

Measurements of 10 uterine eggs in each of three specimens suggests that egg size is constant. Thus, in a syntype 25.3 (23.8–28.9) × 12.7 (11.9–13.6) μm; in a specimen from Cable, 25.0 (23.8–25.5) × 13.9 (13.6–14.4) μm; and in a specimen from Holliman, 24.7 (23.8–25.5) × 13.8 (13.6–14.4) μm.

Diagnosis

Body flattened, lanceolate. Oral sucker large; prepharynx short. Ventrogenital sac 33–38/100 ths from anterior end, well behind caecal bifurcation, lateral pocket present; ventral sucker symmetric, parenchymatous, ratio o.s./v.s. (lengths) 1.6–1.9, armed with band of minute spines 10 rows wide; gonotyl simple; genital atrium opens dorsal to base of gonotyl. Testes large, lobed, tandem. Seminal vesicle two-chambered; proximal thin walled, tortuous; distal fusiform, with thick wall circular fibres, extends anterior to ventrogenital sac. Vitellaria largely lateral, from between ovary and ventral sucker to just behind posterior testis. Uterus extends anterior to ventrogenital sac. Eggs 25 (24–30) × 13 (12–14) μm. Excretory bladder short, may reach posterior border of posterior testis.

Metacercaria (*figure* 67)

A brief description is given, based on a single specimen from the material referred to by Sogandares-Bernal & Hutton (1960).

Body flattened; 2200 μm long and 470 μm wide; widest in forebody, hindbody not tapering as markedly as in adult. Spination as in adult.

Oral sucker 196 × 143 μm; prepharynx shorter than pharynx, forming ventrally incised

fornix posteriorly; pharynx 112 × 94 μm; oesophagus very short; caeca inflated, with low cuboidal epithelium.

Ventrogenital sac median, 50/100ths from anterior end, lateral pocket not seen, mouth large, symmetric, ventral to tip of gonotyl. Ventral sucker 70 × 76 μm, axis inclined to left, apex directed ventro-medially and armed with up to 10 rows of minute spines dextral to unspined apex and fewer rows sinistrally. Gonotyl simple, solidly muscular, arises antero-sinistrally and overlaps apex of ventral sucker ventrally; with dorsal, submedian groove extending from base ventral to genital pore to free tip. Genital atrium short, approaches base of gonotyl antero-sinistrally.

Testes large, rounded, entire; occupy whole of intercaecal space; with no indication of spermatogenesis. Sperm ducts unite at seminal vesicle. Seminal vesicle two-chambered, proximal thin walled, elongate, straight, with papilla about entrance of combined sperm ducts; distal with slightly thicker wall, fusiform. Prostatic ejaculatory duct recurves ventrally anterior to ventral sucker, opens into genital atrium via a papilla.

Ovary submedian, dextral. Seminal receptacle large, empty. Uterus fully developed, course as in adult.

Excretory pore terminal; excretory bladder tubular, inflated, extends almost to posterior testis, with discontinuous lining of large, granular cells; bladder arms appear to extend to and loop in the area beside the pharynx.

Host. *Hyporhamphus unifasciatus* (Ransoni).

Location. Visceral adipose tissue.

Locality. Florida, U.S.A.

Disposition. U.S.N.M. no. 72063.

Remarks

The lateral pocket, although not seen, is presumably present as it was clearly seen in small, non gravid adults, and may have been flattened against the ventral sucker dorsal to the gonotyl.

Comparison of metacercaria and adult

Although the number of specimens measured is small, comparison of the single metacercaria, with the adults listed under 'specimens examined' (three young adults from Sogandares-Bernal, and the three type specimens) does reveal something of the changes in size and proportion that accompany growth of the adult. Thus, the adults (4.6–5.6 mm) are 2.0–2.5 times as long as the metacercaria (2.2 mm). The position of the ventrogenital sac changes from 50/100ths in the metacercaria to 31–38/100ths in the adult, reflecting the relatively greater growth of the hindbody. While the body doubles or more in length, the oral sucker changes little, being 196 × 143 μm in the metacercaria and 195 × 225 to 240 × 270 μm in adults greater than 4.5 mm long. The ventral sucker increases from 70 × 76 μm in the metacercaria to 125 × 115–135 μm in the adult; the ratio o.s./v.s. (lengths) changes from 2.8 in the metacercaria to 1.6–2.1 in adults. Among the three young adults from Florida, there is a striking difference between the smallest, which lacks eggs, has an empty seminal receptacle, and a sucker ratio of 2.7, and the other two, which have eggs, sperm in the seminal receptacle, and a ratio of 2.0. This difference suggests that a part of the apparent increase in size of the ventral sucker may result from enlargement rather than growth following mating.

As in other species of *Galactosomum*, the metacercaria attains a level of development not far short of sexual maturity, and except for the smaller size of the seminal vesicle, does not differ from the adult in characters of the ventrogenital complex.

(*q*) *Galactosomum timondavidi*

Synonyms

Galactosomum timondavidi Pearson & Prévot, 1971, Figs. 1–3 (*Larus argentatus* (Pont.); Marseille, France; descr.; types U.S.N.M. no. 71993).

Microlistrum cochleariforme Joyeux & Baer (not Rudolphi, 1819 *sensu* Braun, 1902), 1928 (*Larus argentatus* (Pont.); Macedonia; no descr.).

Knipowitschetrema nicolai Dubois & Mahon (not Isaichikov, 1927), 1959, Fig. 11 (re-description of Joyeux & Baer's *cochleariforme*).

? *Knipowitschetrema echinatum* Gvozdev (not Timon-David, 1955), 1962, Fig. 6 (*Hydroprogne tschegrava* Kazakhstan, U.S.S.R.; descr.).

Reasons for the above synonyms were given by Pearson & Prévot (1971) and are not repeated here.

As only a single additional adult is at hand for study, a description is omitted and a brief diagnosis only given.

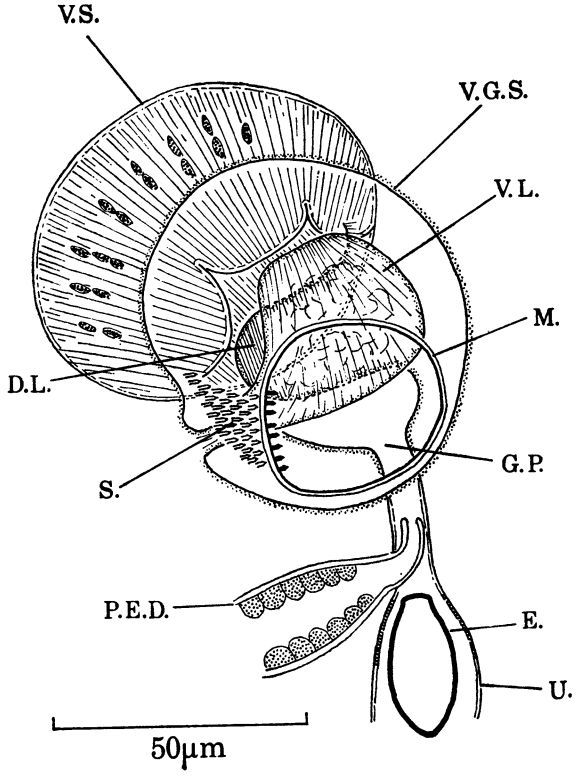


FIGURE 68. *G. timondavidi*. Ventrogenital complex.

Diagnosis (*figures* 68, 92)

With the characters of the genus. Body elongate, narrow, not divided into forebody and hindbody. Oral sucker large; prepharynx probably usually longer than pharynx; pharynx shorter than oral sucker. Ventrogenital sac small, median, 19–29/100ths from anterior end and

well behind caecal bifurcation; armed with stout 5 μm spines dextrally and posteriorly; without lateral pocket. Ventral sucker small, rounded, symmetric, unarmed, with large cavity; ratio o.s./v.s. (lengths) 2.3–2.5. Gonotyl bilobed; ventral lobe with loose arrangement of fibres internally, dorsal lobe soldily muscular. Genital atrium opens between lobes of gonotyl. Testes large, tandem. Seminal vesicle undivided, flask shaped; wall relatively thin but muscular, with outer diagonal fibres over most of length and outer circular fibres over short neck. Prostatic ejaculatory duct narrow; opens into genital atrium via short papilla. Ovary median or on right, at or behind posterior end of seminal vesicle. Vitellaria in rosettes, largely lateral, with some follicles ventrally between caeca; extend anteriorly to between anterior border of posterior testis and point posterior to posterior testis, posteriorly do not reach ends of caeca. Course of uterus variable at level of testes, fills body posterior to posterior testis. Eggs 25.8 (24.8–26.4) × 12.3 (11.1–14.5) μm. Excretory pore terminal; excretory bladder tubular, does not reach posterior testis.

The most singular feature of this species is the presence of spines on the wall of the ventrogenital sac.

Disposition. U.S.N.M. no. 72064.

(*r*) *Galactosomum ussuriensis*

Synonyms

Galactosomum ussuriensis Oshmarin, 1963, Fig. 27 (*Sterna albifrons* Pallas; Primorsk region, U.S.S.R.; location of types not known).

? *Galactosomum* sp. Bykhovskaya–Pavlovskaya, 1955, Fig. 6 (*Sterna hirundo* L.; Stalinabad, U.S.S.R.; descr.).

Although Oshmarin's types were not available, his description and figure leave little doubt that the Australian material described below is conspecific. Bykhovskaya–Pavlovskaya's single specimen has the appearance and proportions of *ussuriensis* as described below, except that the oral sucker is small (ratio o.s./v.s. 0.42); unfortunately, the spination of the ventral sucker is only briefly alluded to.

Description (*figures* 69–72, 93)

The description is based on the study of 32 wholemounts and sagittal sections of one adult. Measurements (range) are given of four well-fixed and unflattened specimens from a Caspian tern.

With the characters of the genus. Body elongate, narrow, flattened, with rounded ends; 2.65–3.31 mm long; width of forebody 282–380 μm, of hindbody 290–338 μm, and at level of ventrogenital sac 290–362 μm, with slight constriction anterior and posterior to ventrogenital sac.

Body with scales anteriorly, becoming spines behind posterior testis and extending to about ends of caeca; absent from anterior end and pre-orally. Pigment granules scattered in parenchyma at level of pharynx. Frontal glands prominent in space bounded by caeca anterior to ventrogenital sac; ducts pass dorsal and ventral to caeca, open in transverse row in apical unarmed area.

Oral sucker large; 183–186 μm long and 201–208 μm wide. Prepharynx variable; 75–164 μm long; forms ventrally incised fornix about entrance to pharynx. Pharynx 100–110 μm long and 84–97 μm wide. Oesophagus very short. Caeca straight, extend almost to, to, or beyond coils of uterus.

Ventrogenital complex large, occupies whole intercaecal space. Ventrogenital sac large; 32–36/100ths from anterior end; without lateral pocket, with slight folding sinistrally; mouth median or slightly to left, typically asymmetric, with lip and subjacent wall thickened antero-dextrally by large oval mass of muscle fibres (A.D.M.) not arising from gonotyl. Musculature of sac also includes: (i) stout band (S.H.) arising from antero-dextral mass, half-encircling sac deep to mouth sinistrally, and fanning out postero-dextrad from point posterior to sac; (ii) separated fibres (D.D.F.) radiating out from the sac dextrally, dorsal to large mass and rising to the ventral surface; and (iii) two groups of separated fibres, one anterior (S.A.F.) and one postero-sinistral (P.S.F.), fanning out from the mouth of the sac. Ventral sucker asymmetric, axis inclined sinistro-ventrad; ventral lip reduced, not covering large variable cavity ventrally; lip enlarged posteriorly with parenchymatous medulla, rest of sucker solidly muscular; armed with 5 μm spines on outer face of lip in two discrete groups, a posterior triangular patch and an anterior band; length (long axis) 188–236 μm, width 107–133 μm, ratio o.s./v.s. (lengths) 0.8–1.0. Gonotyl large, solidly muscular; 120–143 μm long and 87–117 μm wide; arises dorso-sinistrally, with single stout band of fibres entering base postero-sinistrally; tip variously lobed or folded, overlies cavity of ventral sucker. Genital atrium short; does not enter gonotyl; opens into ventrogenital sac dorso-lateral to gonotyl, anterior to root of gonotyl, opposite posterior lip of ventral sucker.

Testes large, rounded, contiguous, slightly diagonal; anterior testis 149–178 μm long and 130–169 μm wide; posterior testis 162–195 μm long and 143–172 μm wide. Seminal vesicle one chambered, constricted; proximal part with thick (10 μm) layer diagonal fibres, with papilla at entrance of sperm ducts, 194–243 μm long and 117–146 μm wide; distal part with thinner wall of prominent circular fibres, 58 μm long and 65–68 μm wide. Prostatic ejaculatory duct cylindrical, sinuous, with prominent longitudinal-fibres; 113–130 μm long and 36 μm wide; papilla absent at entrance into genital atrium.

Ovary large, slightly to right, 97–120 μm long and 110–130 μm wide. Seminal receptacle postero-dextral to ovary; contiguous with ovary and anterior testis; variable in size, 62–165 μm long and 71–152 μm wide. Vitellaria in rosettes arising from single vitelline duct; anteriorly first rosettes dextral to anterior testis and sinistral to posterior testis; behind posterior testis rosettes largely lateral, with arms extending to mid-line ventrally and dorsally; extend posteriorly to or nearly to ends of caeca. Uterus of typical course; post-testicular coils short, largely intercaecal. Eggs (20, uterine) 21.2 (20.4–22.1) × 12.4 (11.1–13.6) μm.

Excretory pore terminal; excretory bladder tubular, reaches posterior border of posterior testis.

Specimens examined

Australia	ex small intestine, *Larus novaehollandiae* Stephens. New host, coll. by A. J. Bearup, July 1960, Townsville, Queensland; new locality	7 specimens
	S.P.H.T.M. Mn. 1478	5 specimens
	U.S.N.M. no. 72066	2 specimens
	ex small intestine *Hydroprogne caspia* (Pallas) new host, coll. by A. J. Bearup, 29. i. 1959; Townsville, Queensland; author's colln	2 fragments
	ex small intestine *Hydroprogne caspia* (Pallas), coll. by J. C. Pearson, 14. i. 1968; Townsville, Queensland; U.S.N.M. no. 72065; M.P.M. no. 19030; author's colln	5 specimens
	ex small intestine, *Sterna fuscata* L., new host, coll. by J. C. Pearson, 20. viii. 1968; Caloundra, Queensland, B.M.(N.H.) no. 1972.1.24.7, 8; author's colln	12 specimens

Comparison

Oshmarin's (1963) description is difficult to follow as he refers to all structures within the genital atrium (ventrogenital sac) as parts of a genital sucker, thus combining in a single organ the ventral sucker, gonotyl, and antero-dextral muscle mass. It would appear that of the five lobes he describes and figures, the two spine-bearing lobes are parts of the ventral sucker, the anterior unarmed lobe is the mass of muscle fibres on the wall of the sac, and the middle and posterior unarmed lobes together are the gonotyl. Other features, such as the form of the seminal vesicle, disposition of gonads, distribution of vitellaria, and form of post-testicular uterus correspond closely with Australian specimens.

Remarks

The ventral sucker and gonotyl appear to be highly mobile and present a variety of appearances in fixed material. Thus, the ventral sucker may open out (figure 69) so that the spine patches are on the outer face of the lip anteriorly and posteriorly; or it may be contracted so that the anterior lip folds into the cavity and the posterior lip bulges medially, in such a way that both spine patches are on the rim of the sucker and are directed sinistrally (figure 70).

The gonotyl may be ellipsoidal (figure 69) or pyriform (figure 71) in outline; its free tip may be variously lobed (figure 71) or folded (figure 69), and when protracted through the mouth of the ventrogenital sac (figure 70), it may present a complex picture of lobes and folds.

The mouth of the ventrogenital sac is typically asymmetric and shaped like a curved teardrop (figure 69); but its shape is variable and may assume a nearly symmetric form (figure 71).

The seminal vesicle when empty (figure 69) has a narrow constriction between the two parts suggestive of the two-chambered condition, but this widens as sperm fills the vesicle until the two parts are broadly joined (figure 72).

The absence of a papilla on the ejaculatory duct was confirmed in sections. As pointed out in the Introduction, this is the only species for which there is clear evidence of its absence.

Diagnosis

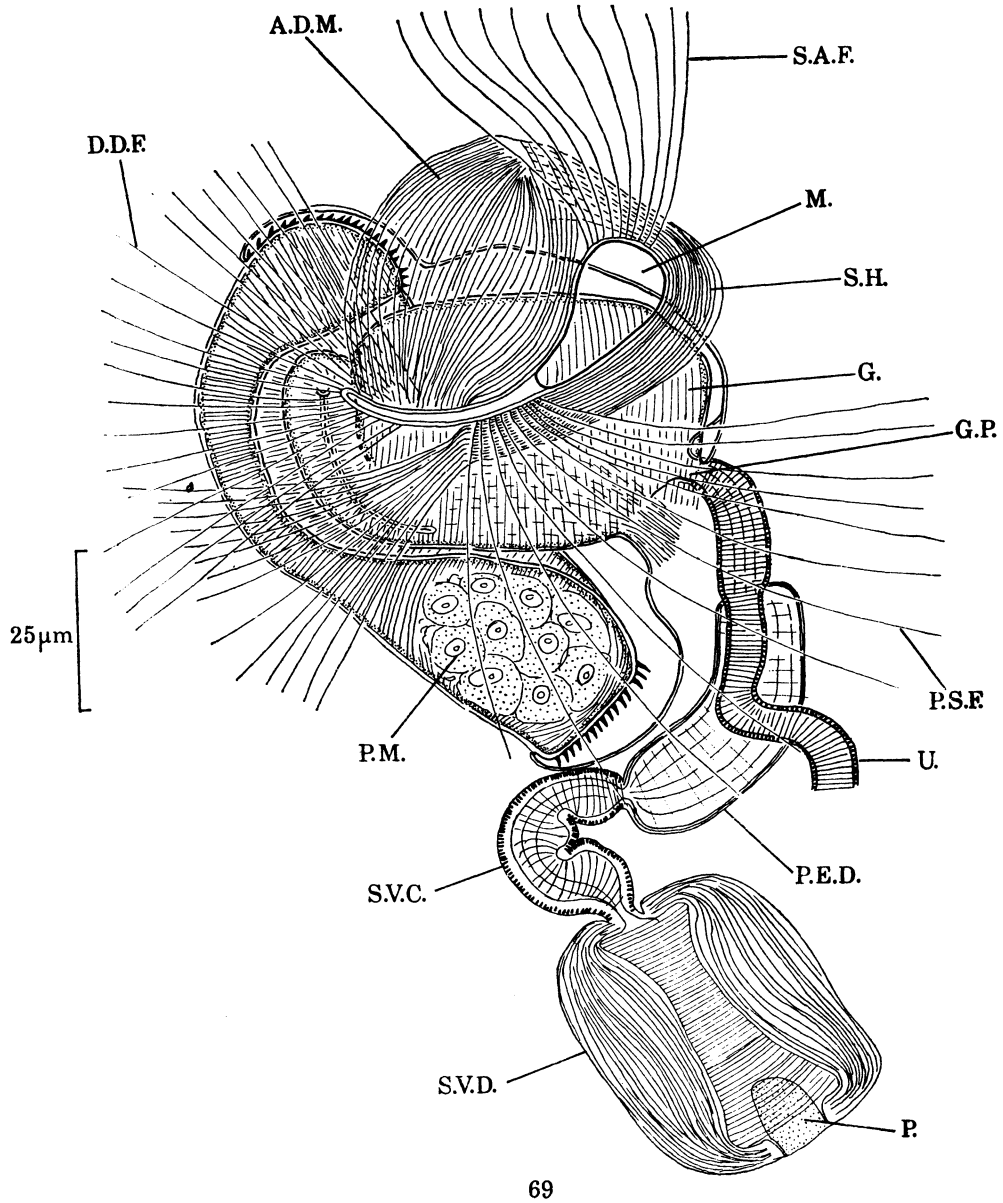
Body elongate; slender; with slight constriction before and behind ventrogenital sac. Oral sucker large; prepharynx short. Ventrogenital sac large, 32–36/100ths from anterior end; with large mass muscle fibres in wall antero-dextrally. Ventral sucker large, ratio o.s./v.s. (lengths) 0.8–1.0, bean-shaped, with anterior and posterior patches of minute spines. Gonotyl large, with variable lobing, not pierced by genital atrium. Seminal vesicle one-chambered, constricted. Vitellaria largely lateral, meet dorsally and ventrally, extend from level anterior testis to about ends of caeca. Eggs 21 (20–22) × 12 (11–14) μm. Excretory bladder short, reaches posterior testis.

(*s*) *Galactosomum yehi* (Dissanaike) n.comb.

Synonym

Heterophyopsis yehi Dissanaike, 1961, Figs. 1, 2; Pl. 1, Figs. A, B (dog; Colombo, Ceylon; descr.; types Colombo).

Dissanaike (1961) described *Heterophyopsis yehi* from three specimens, one of which has since been lost. Examination of the holotype and remaining paratype has revealed that *yehi* belongs in *Galactosomum.*



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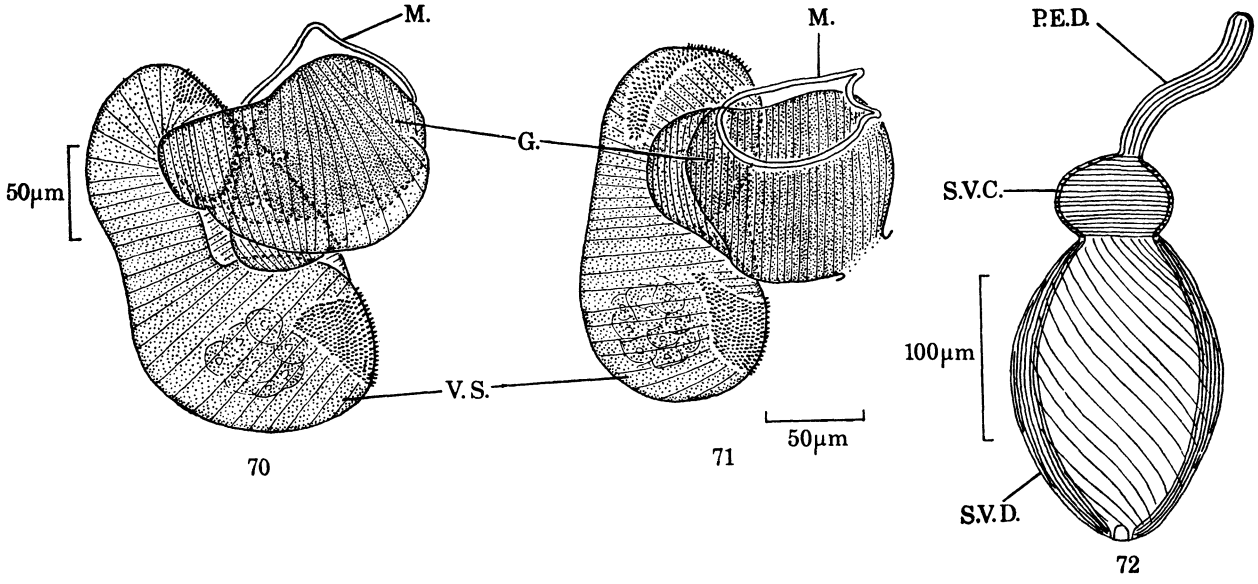

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FIGURE 69. *G. ussuriensis*. Ventrogenital complex.

FIGURE 70. *G. ussuriensis*. Ventral sucker contracted; gonotyl protracted through mouth of sac.

FIGURE 71. *G. ussuriensis*. Ventral sucker and gonotyl.

FIGURE 72. *G. ussuriensis*. Seminal vesicle distended with sperm.

Description (*figures* 73, 74, 94)

The following re-description is based on the type material (holotype (figure 73) and single paratype), together with 7 specimens collected by D. W. W. Kannangara from the type host and locality (figures 74, 94). All of the specimens were apparently dead when fixed and have been flattened; hence, size of organs and proportions are probably altered. Measurements (range) are given of six of Kannangara's specimens.

With the characters of the genus. Body fusiform 1.41–2.23 mm long, narrowing anteriorly, not constricted between fore- and hindbody; forebody shorter and narrower than hindbody, 290–443 μm wide, widest at level of ventrogenital sac; hindbody widest behind posterior testis, 500–628 μm wide.

Body closely covered with wide scales anteriorly, becoming smaller and narrower posteriorly, changing into spines about level of ovary, and continuing to posterior end. Some pigment granules scattered throughout forebody. Gland cells not seen.

Oral sucker subterminal, 80–89 × 89–107 μm. Prepharynx longer than pharynx, 150–180 μm. Pharynx 66–99 × 39–95 μm. Oesophagus very short. Caeca straight, extend more than half way between posterior testis and posterior end.

Ventrogenital sac small, without lateral pocket; 24–30/100ths from anterior end, and about three ventral-sucker lengths behind bifurcation of gut; mouth crescentic, with swollen, muscular antero-dextral lip. Muscle fibres associated with sac not clearly seen; dextral hemisphincter a wide band arising from base of gonotyl, encircling sac on right, and inserted anteriorly; fibres from antero-dextral lip appear to run dorsad. Ventral sucker symmetric, spherical, parenchymatous; 43–56 × 41–58 μm, ratio o.s./v.s. (lengths) 1.6–2.0; with shallow cavity bounded laterally by two elongate groups of minute spines up to 2.5 μm long. Gonotyl unarmed, solidly muscular, simple; 39–43 × 35–39 μm; arises sinistro-posteriorly, and bears genital pore dorsally. Genital atrium short, formed by union of ejaculatory duct and uterus at base of gonotyl, penetrates gonotyl and opens dorsally at inner end of longitudinal groove in gonotyl, opposite ventral sucker.

Testes diagonal, separated from each other and from ovary by coils of uterus; anterior testis 134–228 × 177–248 μm, posterior testis 100–234 × 181–268 μm; sperm ducts not seen. Seminal vesicle one-chambered, constricted; proximal part elongate, fusiform, 220–330 × 97–155 μm, extending to level of ovary, with thick layer of diagonal fibres; distal part rounded, 70–136 × 64–110 μm, with thinner layer of circular fibres; prostatic ejaculatory duct 46 μm long, thick walled, gland-cell bodies not seen; distinct ejaculatory duct absent, opens into genital atrium through short, conical papilla.

Ovary submedian on right, opposite proximal end of seminal vesicle; 84–147 × 117–188 μm. Seminal receptacle postero-dorsal to and contiguous with ovary; variable in size. Vitellaria cortical, follicular, in rosettes; anteriorly extend to or slightly beyond posterior border of ovary on right and to or beyond ovary on left; posteriorly exceed caeca and extend almost to posterior end; follicles may meet in mid-line, both dorsally and ventrally, between ovary and anterior testis, between testes and posterior to posterior testis. Uterus with typical course; with transverse loop ventral to seminal vesicle. Eggs (20, uterine) 26 (24–28) × 16 (15–17) μm.

Excretory pore subterminal, dorsal; excretory bladder tubular, short, does not reach posterior testis.

Comparison

Specimens examined

Ceylon	ex dog, holotype ex dog 18, paratype ex dog 9, Colombo	holotype and 1 paratype
	ex dog, coll. by Kannangara, Colombo, U.S.N.M. no. 72067; M.P.M. no. 19027; author's colln	7 specimens

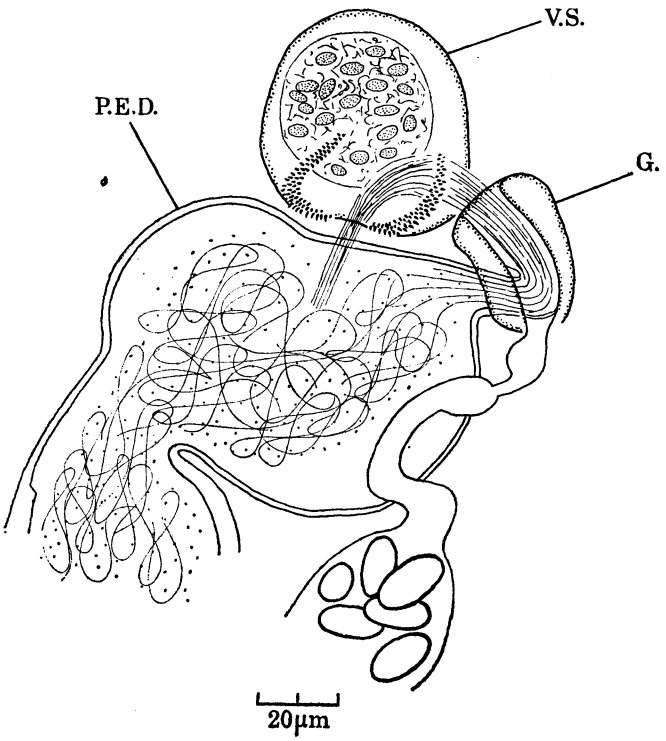


FIGURE 73. *Heterophyopsis yehi.* Holotype, ventrogenital complex.

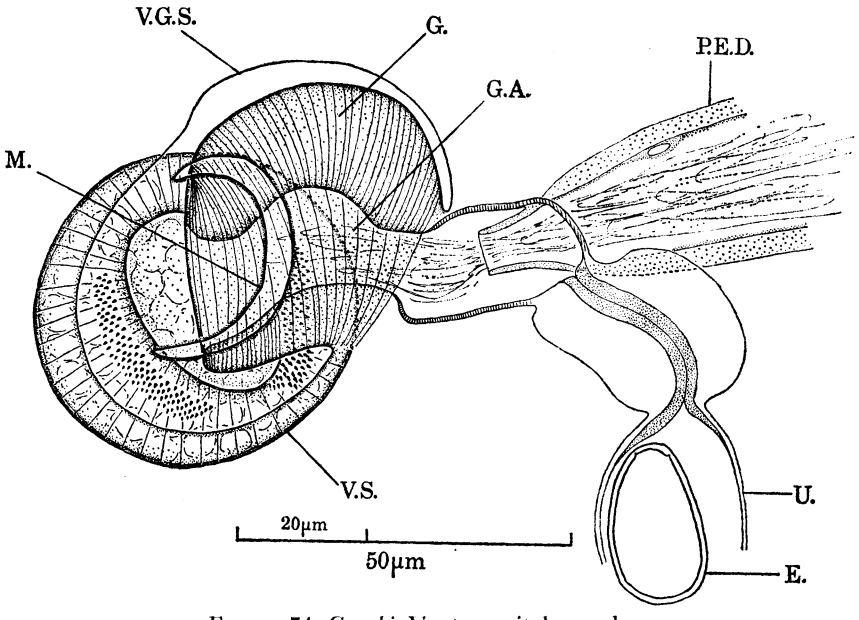


FIGURE 74. *G. yehi.* Ventrogenital complex.

Diagnosis

Body moderately elongate, forebody shorter and narrower than hindbody. Prepharynx longer than pharynx. Ventrogenital sac without lateral pocket, 24–30/100ths from anterior end and about three ventral-sucker lengths behind gut bifurcation, with crescentic mouth and thickened antero-dextral lip; ventral sucker distinctly smaller than oral, ratio o.s./v.s. (lengths) 1.6–2.0, symmetric, parenchymatous, with shallow cavity bounded laterally by elongate group of 2.5 μm spines; gonotyl simple; seminal vesicle one-chambered, constricted, proximal part thick walled and elongate, distal part thinner walled and rounded; prostatic ejaculatory duct short. Vitellaria extend anteriorly to or slightly beyond ovary, posteriorly almost to posterior end, meet mid-dorsally and mid-ventrally except over gonads. Eggs 26 (24–28) × 16 (15–17) μm. Excretory bladder short, does not reach posterior testis.

Galactosomum yehi is closest to *dollfusi* but differs distinctly in the form of the gonotyl, relative size of the ventral sucker, and shape of the mouth of the ventrogenital sac.

3. Species groups

The species of *Galactosomum* may be assigned to four groups on the basis of a combination of characters of ventral sucker, seminal vesicle and excretory bladder. *G. sanaensis* is too poorly described to be included in this discussion.

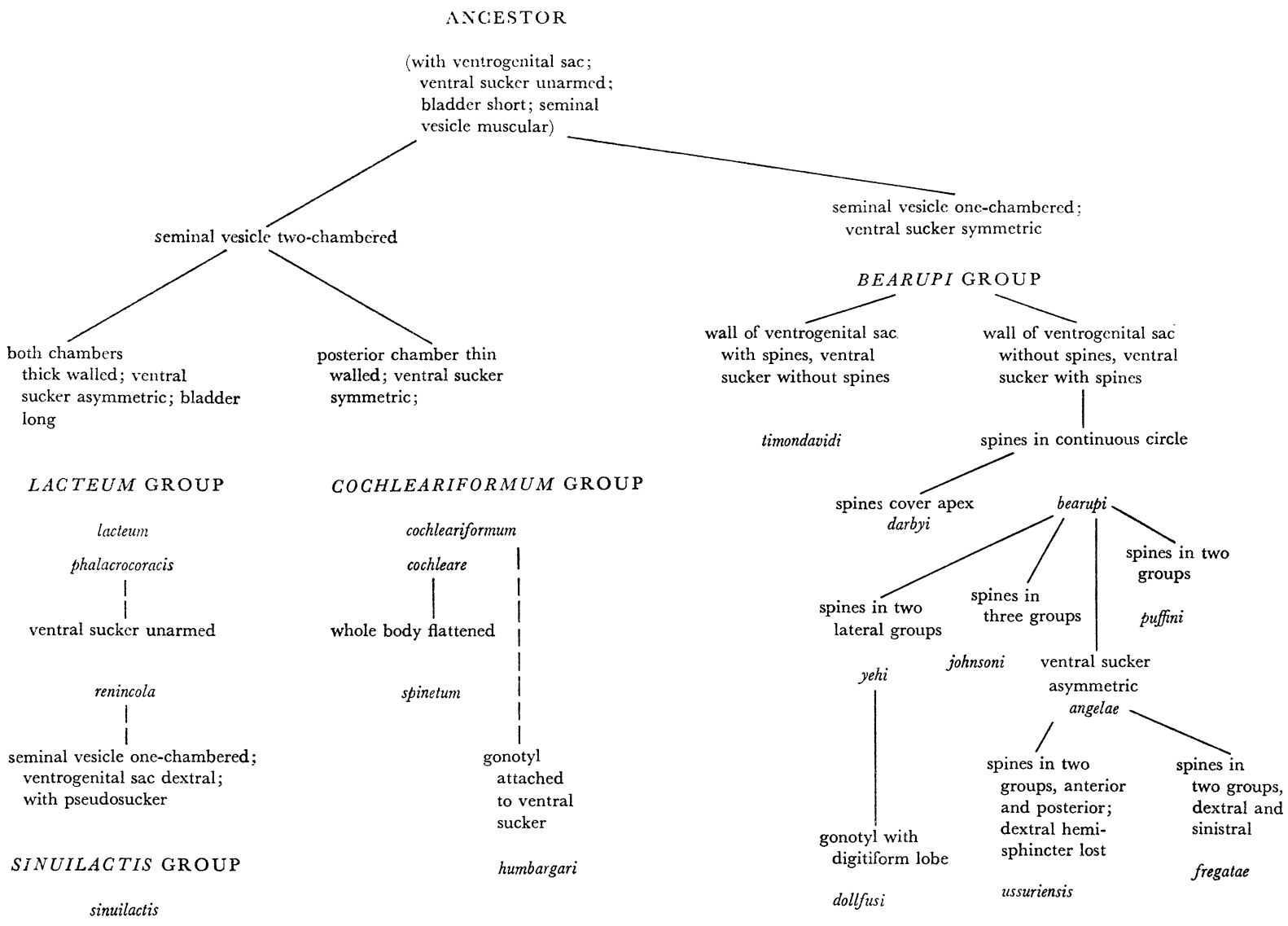
(1) The *lacteum*-group, containing the genotype and *phalacrocoracis*, is characterized by: (i) a two-chambered seminal vesicle, both chambers of which have a thick outer layer of diagonal fibres; (ii) a highly modified ventral sucker with spined knob and eversible, spiny cavity; and (iii) a long excretory bladder. Additionally, both species are known only from cormorants. In features of the ventrogenital sac, the two species differ markedly.

(2) The *sinuilactis*-group, containing a single species, is characterized by: (i) an undivided seminal vesicle with thick outer layer of circular fibres; (ii) a prostatic ejaculatory duct with thick outer layer of longitudinal fibres; (iii) a minute, simple, unarmed ventral sucker; (iv) a dextral ventrogenital sac containing a sinistral pseudosucker; (v) sinuous caeca; and (vi) a long excretory bladder. Additionally, *sinuilactis* is known only from cormorants.

It may seem odd to create a group for a single species, but *sinuilactis* is so distinctive that it is thought to be warranted.

The species *renincola* is in some features intermediate between the *lacteum*-group and the *sinuilactis*-group, although unlike them it has been found in terns and shearwaters, not in cormorants. It resembles the *lacteum*-group in having a knob, albeit unarmed, on the ventral sucker, and a two-chambered seminal vesicle, both chambers of which are thick walled, but with the difference that the outer layer of the anterior chamber is circular. It closely resembles *sinuilactis* in shape of body, size of oral sucker, blood-feeding habit, and unarmed ventral sucker, but differs in form of caeca, ventrogenital sac, and seminal vesicle.

(3) The largest group, here named the *bearupi*-group, contains *bearupi*, *angelae*, *fregatae*, *dollfusi*, *johnsoni*, *timondavidi*, *ussuriensis*, *yehi*, probably *darbyi*, and possibly *puffini*. It is characterized by: (i) one-chambered seminal vesicle with an additional layer of diagonal fibres over the major proximal portion and prominent circular fibres in the minor distal portion; and (ii) a short excretory bladder. In form, the seminal vesicle varies from essentially undivided, as in *timondavidi* (figure 92), to distinctly constricted, as in *fregatae* (figure 33). There is usually a single


ANCESTOR
(with ventrogenital sac; ventral sucker unarmed; bladder short; seminal vesicle muscular)
seminal vesicle two-chambered
seminal vesicle one-chambered; ventral sucker symmetric
both chambers thick walled; ventral sucker asymmetric; bladder long
posterior chamber thin walled; ventral sucker symmetric;
BEARUPI GROUP
wall of ventrogenital sac with spines, ventral sucker without spines
wall of ventrogenital sac without spines, ventral sucker with spines
timondavidi
spines in continuous circle
LACTEUM GROUP
COCHLEARIFORMUM GROUP
spines cover apex
darbyi
bearupi
lacteum
cochlearíformum
phalacrocoracis
cochleare
spines in two groups
puffini
spines in two lateral groups
spines in three groups
ventral sucker unarmed
whole body flattened
johnsoni
yehi
ventral sucker asymmetric
angelae
renincola
spinetum
seminal vesicle one-chambered; ventrogenital sac dextral; with pseudosucker
gonotyl attached to ventral sucker
spines in two groups, anterior and posterior; dextral hemisphincter lost
spines in two groups, dextral and sinistral
SINUILACTIS GROUP
humbargari
gonotyl with digitiform lobe
fregatae
sinuilactis
dollfusi
ussuriensis

longitudinal axis through both parts, less often two axes forming an obtuse angle, as in *puffin* (figure 87).

The ventral sucker varies from a simple radially symmetric form, with (*bearupi*) or without (*timondavidi*) spines, to a bilaterally symmetric (*fregatae*) or asymmetric form (*ussuriensis*); it is armed with a single group (*darbyi*), or a band (*angelae*, *bearupi*) of spines, which is, however, split into two or three groups of spines in the remaining species.

In characters of the ventral sucker and the seminal vesicle, *puffini* fits into the *bearupi*-group somewhere between *angelae* and *fregatae*; however, Yamaguti (1941) says that the excretory bladder in *puffini* reaches the ovary. If this is so, then *puffini* would be excluded from the *bearupi*-group. Unfortunately the extent of the bladder could not be determined in the types of *puffini*. For the present, *puffini* is tentatively included in the *bearupi*-group.

The extent of the excretory bladder in *darbyi* is not known; nevertheless, it is tentatively assigned to the *bearupi*-group on the form of the seminal vesicle.

(4) The *cochleariformum* group, containing *cochleariformum*, *cochleare*, and *spinetum*, is characterized by: (i) a two-chambered seminal vesicle, the anterior chamber with thick layer of circular fibres and the posterior chamber thin walled and either short and straight (*cochleariformum*) or long and sinuous (*cochleare* and *spinetum*); (ii) a symmetric ventral sucker with eversible spined cavity; and (iii) a short excretory bladder.

The last species to be placed, *humbargari*, is singular in form of ventral sucker and attached gonotyl, although sharing with the *cochleariformum* group a short excretory bladder and a similar seminal vesicle.

It will be evident, on comparing the composition of the species groups with the sketches of whole worms (figures 75–94), that little or no weight has been given to shape of body, size of oral sucker, length of prepharynx, or distribution of vitellaria.

The suggested inter-relationships of members of the various groups are shown on p. 435.

4. Key to species

(1)	Caeca simple, straight; ventrogenital sac median.	2
	Caceca loop forward beside pharynx, sinuous; ventrogenital sac dextral.	*sinuilactis* (figure 90)
(2)	Ventrogenital sac armed with spines; ventral sucker unarmed.	*timondavidi* (figure 92)
	Ventrogenital sac unarmed; ventral sucker armed or not.	3
(3)	Forebody spatulate, distinctly wider than hindbody.	4
	Forebody not distinctly wider than hindbody.	7
(4)	Forebody with dorsal pit; ventral sucker unarmed.	*renincola* (figure 88)
	Forebody without dorsal pit; ventral sucker armed with spines.	5
(5)	Seminal vesicle two-chambered, with thin-walled proximal chamber shorter than thick-walled distal chamber.	6
	Seminal vesicle otherwise.	7
(6)	Ventral sucker asymmetric, with spiny cavity and knob.	*lacteum* (figure 76)
	Ventral sucker symmetric, without knob.	*cochleariformum* (figure 80)
(7)	Ventral sucker symmetric, sucker like.	8
	Ventral sucker asymmetric, or not sucker like.	16
(8)	Uterus extends anterior to ventrogenital sac.	*spinetum* (figure 91)
	Uterus does not extend anterior to ventrogenital sac.	9
(9)	Ventral sucker armed with single group of spines.	14
	Ventral sucker otherwise (2 or 3 groups of spines).	10
(10)	Ventral sucker with two groups of spines; body elongate.	11
	Ventral sucker with three groups of spines; body short and wide.	*johnsoni* (figure 85)

(11)	Two groups of spines symmetric.	12
	Two groups of spines asymmetric, that on right larger.	*puffini* (figure 87)
(12)	Excretory bladder exceeds anterior testis.	*sanaensis* (figure 89)
	Excretory bladder does not reach posterior testis.	13
(13)	Gonotyl with accessory finger-like lobe.	*dollfusi* (figure 82)
	Gonotyl without accessory lobe.	*yehi* (figure 94)
(14)	Seminal vesicle one-chambered; o.s. > v.s.	15
	Seminal vesicle two-chambered; o.s. ≈ v.s.	*cochleare* (figure 79)
(15)	Prepharynx ≈ pharynx; spines in narrow band on rim.	*bearupi* (figure 78)
	Prepharynx ⩾ pharynx; spines in circular patch.	*darbyi* (figure 81)
(16)	Seminal vesicle two-chambered, both chambers thick-walled, ventrogenital sac > 40/100ths from anterior end.	17
	Seminal vesicle otherwise; ventrogenital sac < 40/100ths from anterior end.	18
(17)	Ventrogenital sac inflated.	*phalacrocoracis* (figure 86)
	Ventrogenital sac not inflated.	*lacteum* (figure 75)
(18)	Ventral sucker pyriform; seminal vesicle two-chambered, proximal thin walled, distal thick walled.	*humbargari* (figure 84)
	Ventral sucker elliptical; seminal vesicle one-chambered.	19
(19)	Ventral sucker with band of spines; seminal vesicle not or slightly constricted.	*angelae* (figure 77)
	Ventral sucker with two groups of spines; seminal vesicle strongly constricted.	20
(20)	Long axis of ventral sucker diagonal; lateral pocket present.	*fregatae* (figure 83)
	Long axis of ventral sucker parallel to body axis; lateral pocket absent.	*ussuriensis* (figure 93)

IV. Functional morphology of the ventrogenital complex

The following account, although based on the study of many species of heterophyids, is entirely speculative as no one has examined any heterophyid *in copula*.

Attempts at explaining the possible functioning of the ventrogenital complex are few. Jägerskiöld (1904, Fig. 3) made the plausible suggestion that in *Scaphanocephalus expansus*, worms paired head to tail and that the protracted 'Zunge' (ventral sucker) of each worm was inserted into the 'Bauchsaugnapf' (anterior pocket of ventrogenital sac) of the other, thus approximating the genital pores. Pratt (1911) suggested that the 'gonotyl' (ventral sucker) of *Galactosomum cochleariforme* acted like a penis, and was received by the 'tongue-like body' (gonotyl), but did not explain how it could so function when in fact, the genital pore would be occluded by the 'gonotyl'.

It is argued above (see § I), that heterophyids are cross-fertilizing. If, then, one looks on the ventrogenital complex in *Galactosomum* as a copulatory apparatus and attempts to postulate how it may function, it will be seen that there are two common forms of complex, those with and those without a lateral pocket. As an example of the first group *angelae* will be considered, as the musculature of the ventrogenital sac is known in some detail. As an example, of the second group, *lacteum* will be considered. In both cases it is assumed that the shift of the genital pore from pre-acetabular to para-acetabular allows flukes to copulate head-to-head, rather than head-to-tail as suggested for *Scaphanocephalus*, and that insemination is mutual, that is each member of a pair acts as male and female during copulation.

In *angelae* (figure 9), the ventral sucker is solidly muscular and its cavity apparently not eversible. It is considered that copulation is probably effected by protrusion and interlocking of the two gonotyls, each held in place by the ventral sucker of the partner (figure 95). The manner in which this may be accomplished is as follows (figures 12–15). Opening of the mouth of the sac would be accomplished by the fibres dextral (S.D.F.) and antero-sinistral (S.A.S.F.) to the mouth and both opening and depression of the mouth by fibres antero-sinistrally (D.A.S.F.)

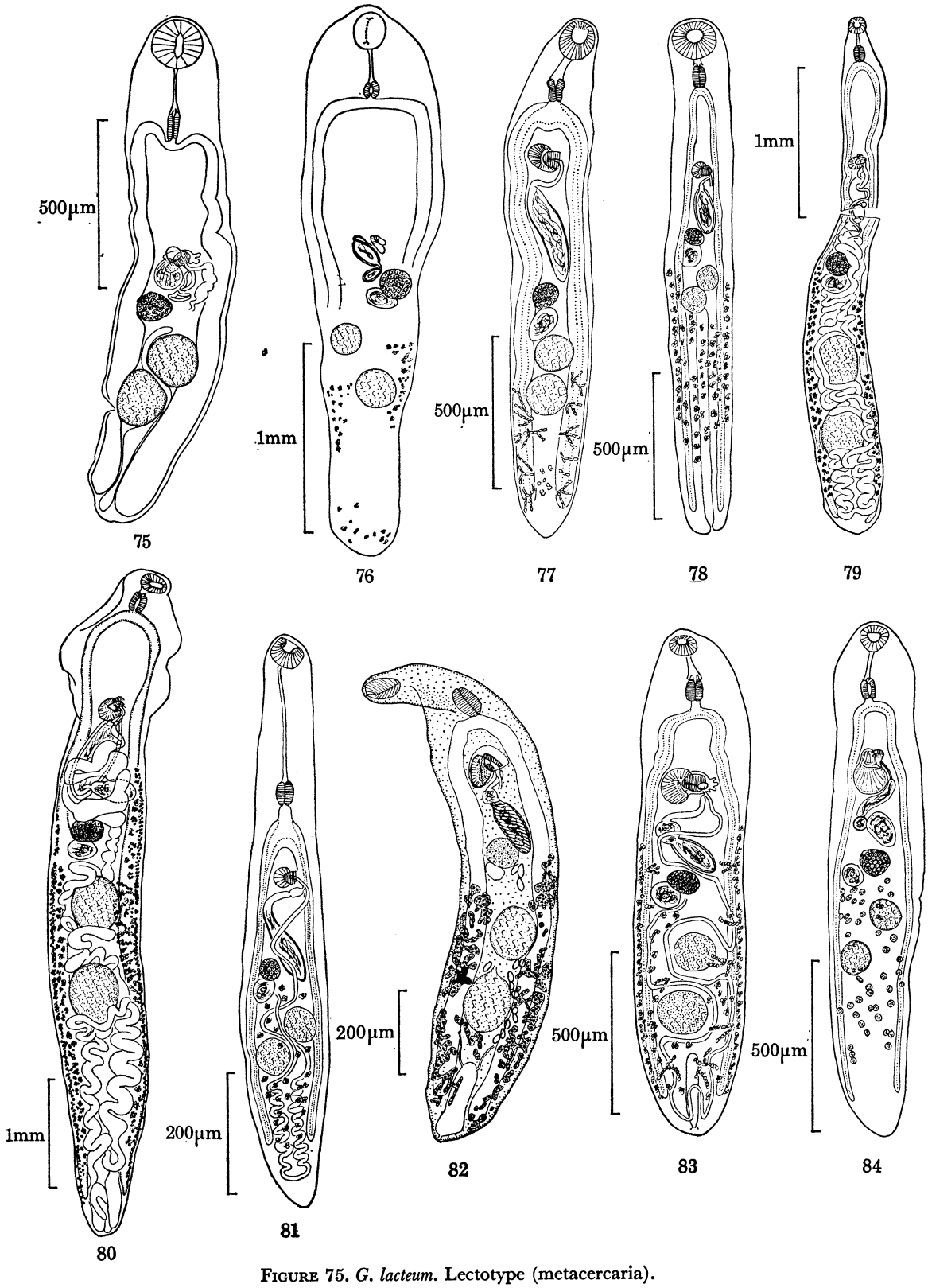


FIGURE 75. *G. lacteum.* Lectotype (metacercaria).
FIGURE 76. *G. lacteum.* Adult (flattened).
FIGURE 77. *G. angelae.* Holotype.
FIGURE 78. *G. bearupi.* Paratype.
FIGURE 79. *G. cochleare.* Syntype.
FIGURE 80. *G. cochleariformum.* Syntype.
FIGURE 81. *G. darbyi.*
FIGURE 82. *G. dollfusi.* Holotype (flattened).
FIGURE 83. *G. fregatae.*
FIGURE 84. *G. humbargari.*

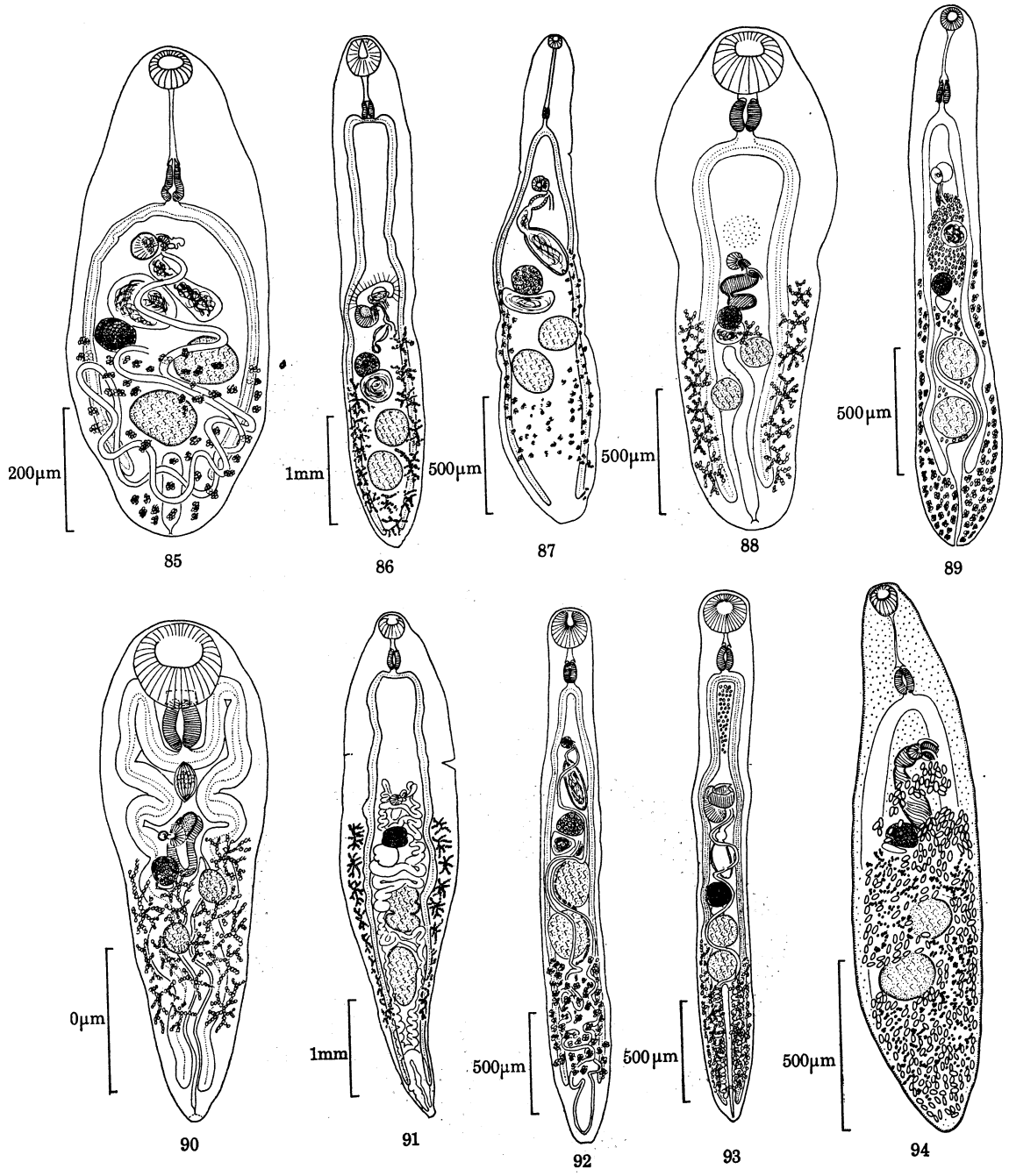
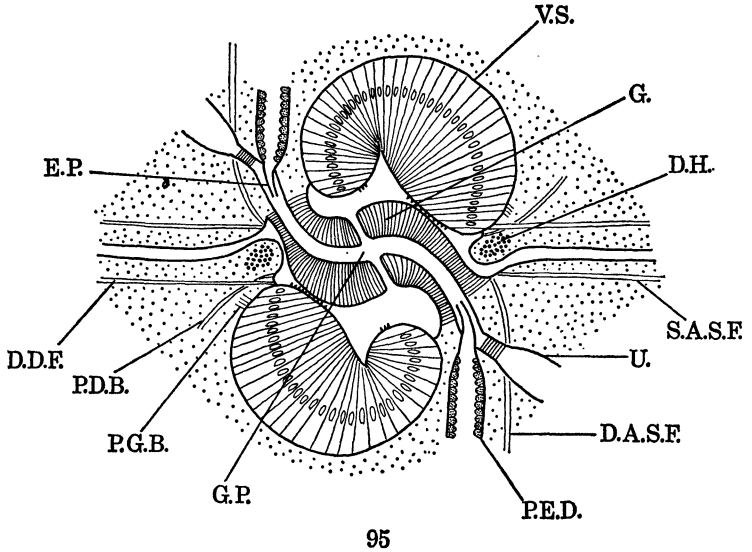


FIGURE 85. *G. johnsoni.*
FIGURE 86. *G. phalacrocoracis.* Paratype.
FIGURE 87. *G. puffini.* Holotype.
FIGURE 88. *G. renincola.* Holotype.
FIGURE 89. *G. sanaensis* (after Kobayasi 1942).
FIGURE 90. *G. sinuilactis.* Paratype.
FIGURE 91. *G. spinetum.* Syntype.
FIGURE 92. *G. timondavidi.*
FIGURE 93. *G. ussuriensis.*
FIGURE 94. *G. yehi.*

and posteriorly (D.P.F.) (figure 12). Dilation of the sac posteriorly may be effected by the postero-dextral band (P.D.B.). Elevation of the gonotyl may be aided by the anterior (A.G.B.) and posterior (P.G.B.) bands running from the root of the gonotyl to the ventral sucker, in addition to being effected by the musculature of the gonotyl itself. The intrinsic muscle-fibres of the gonotyl are largely radial, an arrangement that allows the gonotyl to lengthen without constricting the genital atrium.



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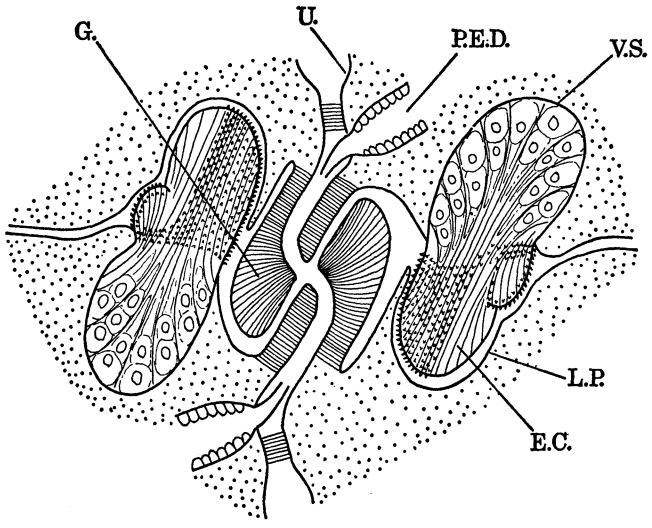

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FIGURE 95. Hypothetical transverse section of *G. angelae in copula.*

FIGURE 96. Hypothetical transverse section of *G. lacteum in copula.*

Following mutual insertion of the gonotyls (figure 95), their ventral faces would be lodged in the cavity of the partner's ventral sucker and held in place by the band of spines, especially those on the raised dextral lip. The dorsal faces of the two gonotyls would then be opposed and the genital pores opposite each other. The large, semicircular bundles (D.H.) may act together to form a sphincter about the two appressed gonotyls.

Fibres from the point of attachment of the sac to the sucker (D.D.F.) and from the sucker anteriorly (D.A.F.) and posteriorly (D.P.F.) run to the ventral surface. These appear to be suspensory, but perhaps may act to elevate the ventral sucker. The loop of fibres about the uterus (L.U.) also appears to be suspensory.

The probable function of the postero-dextral fibres (P.D.F.) arising from the dextral hemisphincter (D.H.) is not clear, unless perhaps they aid in dilating the posterior wall of the sac, or act to open out the semicircular bundle.

Apposition of the dorsal faces of the gonotyls would result in approximation of the two genital pores, or of the grooves into which they open. Given the high degree of mobility of the fluke body, one can imagine the papilla on the ejaculatory duct so elongated that it can be inserted into the uterus of the partner as an intromittent organ, thus eliminating the chance of self-fertilization.

In *lacteum* (figures 5, 6), the ventral sucker is not solidly muscular and its spined cavity can be everted (figure 7) to form a large knob. The essential difference between copulation here and that ascribed to *angelae*, is that the spined knob (everted cavity) of the ventral sucker is protracted into the lateral pocket of the partner and is thus not as closely associated with the gonotyl of the partner. Again, the gonotyls are opposed, and gonotyls and ventral suckers together are held by the two hemisphincters (figure 96).

An outpocketing of the ventrogenital sac, presumably for the reception of the ventral sucker, has apparently been formed separately in a number of heterophyids, as it is found in *Cryptocotyle* and *Scaphanocephalus* (muscular anterior pocket, cf. *sinuilactis*, also with unarmed ventral sucker); in *Haplorchis* (dorsal pocket), but not in *Euhaplorchis*, *Stellantchasmus* and *Procerovum*, in the *Haplorchis* group; and in *Stictodora* and *Acanthotrema*.

V. Remarks on the life-cycle

To date, there is no complete life-cycle known for any member of the genus *Galactosomum*. That the second intermediate host is a fish, has been known since Jägerskiöld (1896) described *lacteum* from metacercariae, and has been substantiated by several authors for a number of species (*angelae*, *bearupi*, *humbargari*, *sinuilactis*, *spinetum* and *timondavidi*), but there has been no experimental link established between a cercaria and a metacercaria.

Cercaria

Hutton & Sogandares-Bernal (1960) ascribed to *spinetum* a magnacercous opisthorchioid cercaria, and Cable (1956, 1963) has suggested on ecological grounds that members of this magnacercous group belong to members of *Galactosomum*. Dr G. Prévot, of Marseille, is at present prosecuting research on the life-cycles of magnacercous opisthorchioid cercariae and, hopefully, will demonstrate one or more life-cycles in *Galactosomum* and related genera.

As cercariae show promise of being useful taxonomically, a brief account is given of cercarial types within the family Heterophyidae. But before doing so, it would be as well to look at the origin and changing definitions of two descriptive terms commonly employed, namely pleurolophocercous and parapleurolophocercous.

In recent papers (Rothschild 1938*b*, Martin 1950, Cable 1956) the two terms have been used to differentiate between cercariae with (parapleurolophocercous) and without (pleurolophocercous) lateral finfolds at the base of the tail. However, as originally proposed by Sewell

(1923), the two terms call attention not to lateral finfolds but to differences in state of development of the ventral sucker. His Parapleurolophocerca group is defined as distomate, with oral sucker not modified into a penetrating organ, and his Pleurolophocerca group as monostomate, with oral sucker modified into a penetrating organ. Sewell does refer finfolds, but does not differentiate between the two groups in this respect. Rothschild (1938*b*) has proposed uniting the two groups, largely, it would seem, on the basis of a gradation in development of fins. Earlier, Vogel (1934) had proposed uniting the two groups as the ventral sucker varies from an indistinct rudiment to a well-developed sucker. But, the descriptions on which this series is based are far from convincing.

Unless and until Sewell's parapleurolophocercous cercariae (Cercariae indicae XXXI and L) are found to be not distomate, his distinction must be accepted.

Cercariae showing undoubted affinities with the families Heterophyidae and Opisthorchiidae, have the following features in common: (i) small, usually pigmented bodies; with or without eyespots; oral sucker a penetrating organ; penetration glands typically seven pairs, with ducts opening in four groups; ventral sucker rudimentary; excretory bladder epithelial, sac like to broadly V-shaped; tail with dorso-ventral finfold. Cercariae in this common group cannot be assigned to family on cercarial morphology as Vogel (1934) said many years ago, although they may be on snail host.

Among heterophyids in general there is some variation, such as absence of eyespots (*Eurychelmis monorchis* by Ameel 1938); presence of lateral fin-fold (*Ascocotyle pachycystis* by Schroeder & Leigh 1965), absence of dorso-ventral finfold (*Centrocestus formosanus* by Martin 1958), or absence of the finfold dorsally (*Metagonimoides* sp. by Ingles 1935), and variation in the number of penetration glands, from four pairs in *Ascocotyle pachycystis* as described by Schroeder & Leigh (1965) to 10 pairs in *Opisthorchis felineus*, as described by Vogel (1934).

Among haplorchines, the penetration glands are constant in number, but their arrangement varies. They may, as first pointed out by Price (1940), be in front of the excretory bladder (pre-vesicular) as in opisthorchids and other heterophyids, or may extend, lateral to the bladder, to the posterior end (para-vesicular), as in the *Haplorchis* group and magnacercous forms. The tail may be long and without finfolds, or short, with dorso-ventral finfold, and sometimes with lateral finfolds.

A tentative sorting of haplorchine genera and cercarial types follows:

(i) Cercaria with pre-vesicular penetration glands; tail with lateral finfolds *Stictodora*, *Acathotrema*.

(ii) Cercaria with para-vesicular penetration glands; tail with lateral finfolds *Haplorchis*, *Euhaplorchis*, *Procerovum* (in part).

(iii) Cercaria with para-vesicular penetration gland; tail without lateral finfolds *Stellantchasmus*, *Procerovum* (in part).

(iv) Cercaria with para-vesicular penetration glands; tail magnacercous ?*Galactosomum*, ? *Cercarioides*, ? *Knipowitschiatrema*.

Recent studies by Holliman (1961) suggest that there may be forms intermediate between groups (i) and (ii) above (consider his *Cercaria cursitans*, *C. vivata*, and *C. coruscantis*, in which the penetration glands extend progressively farther posteriorly) and possibly between groups (i) and (iv) (consider *Cercaria komiyai* Ito, 1956, a magnacercous form with pre-vesicular penetration glands).

The relationships between cercarial types and genera may be further complicated if it is

found, as seems likely, that not all cercariae in *Galactosomum* are magnacercous. Such cercariae, with large and pigmented tails, are adapted to infecting free-swimming or plankton-feeding fish, and so becoming available as metacercariae to surface-feeding birds, such as terns, shearwaters and frigate birds, common hosts of species of *Galactosomum*. But consider the genotype, *lacteum*. The metacercaria of this is found in bottom-dwelling fish of the genus *Cottus*, and the only definitive hosts are cormorants as Jägerskiöld (1908) found after a long search through many kinds of piscivorous birds. Is it probable that *lacteum* has a magnacercous cercaria? Unfortunately, the host ranges of species of *Galactosomum* are not sufficiently well known to attempt seriously to prognosticate cercarial types.

Metacercaria

The metacercaria is now known for seven species: *lacteum* (figure 4), described by Jägerskiöld (1896); *timondavidi*, to be described presently by G. Prévot; *spinetum* (figure 67), briefly mentioned by Hutton & Sogandares-Bernal (1960) and described herein; and *angelae* (figure 16), *bearupi* (figure 23), *humbargari* and *sinuilactis* (figure 65) described herein.

Enough has been seen in all of these to generalize as follows. The metacercaria in *Galactosomum* attains an advanced stage of development not far short of sexual maturity. In size, it may be as large or larger than small ovigerous adults. In characters of the ventrogenital complex, it attains the full adult condition, and so may be identified to species, using the key given above, while bearing in mind the ways in which the seminal vesicle may alter when distended with sperm.

The relative sizes of metacercaria and adult vary among species. Thus, the metacercaria is as large as ovigerous adults in *lacteum*, *angelae*, *bearupi*, *humbargari* and *sinuilactis*, whereas it is half as large as the adult in *spinetum*, and may be even smaller in *phalacrocoracis*, judging by the range in size of adults.

Adult

Accurate records of the exact location of sexually mature worms in the definitive host are few, but from these few it does appear that the location may vary with the species. Thus, *cochleare*, *darbyi*, *johnsoni*, *timondavidi* and *ussuriensis* are recorded from the small intestine only, and I have found *bearupi* and *ussuriensis* only in the small intestine. The species *fregatae* is recorded from both the large intestine and the bursa. Two species occur in the bursa, *sinuilactis* and *renincola*, and the latter also occurs in the renal ureter.

It may be noted that of the species examined alive (*bearupi*, *renincola*, *sinuilactis*, and *ussuriensis*), the two in the bursa (*renincola* and *sinuilactis*) had blood-filled caeca, whereas the two in the small intestine (*bearupi*, *ussuriensis*) did not. In *renincola* from the kidneys, the caeca were filled with blood.

The definitive hosts of species of *Galactosomum* are fish-eating birds, although two species, *fregatae* and *yehi*, have been found in the dog (*fregatae* by Yamaguti (1941), as *G. canis* in Japan, and both species by Kannangara in Ceylon) and a third species, *sanaensis*, was recovered from a dog fed experimentally (Kobayasi 1942).

Although the host range is but imperfectly known for all species, it is perhaps of interest to note (i) that *lacteum*, *phalacrocoracis* and *sinuilactis* are known only from cormorants; (ii) that *darbyi* is known only from pelicans; (iii) that *bearupi*, *cochleare*, *cochleariformum*, *dollfusi*, *renincola*, *spinetum*, and *ussuriensis* are known only from birds that feed at the surface, such as terns,

shearwaters, and frigate birds; and (iv) that *angelae*, *fregatae*, and *humbargari* have wide host-ranges.

Indeed, comparably wide host-ranges may be discovered for additional species, invalidating the above groupings. Against this, it may be pointed out that in a large series of birds examined by the late Professor T. H. Johnston and his students, *angelae* was found in gulls, terns and penguins, but *sinuilactis* in cormorants only.

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List of abbreviations

A.D.B.	antero-dextral band
A.D.F.	antero-dextral fibres
A.D.M.	antero-dextral mass
A.D.L.	antero-dorsal lobe of gonotyl
A.F.	anterior fibres
A.G.B.	anterior band from gonotyl
A.K.	apical knob of ventral sucker
A.V.F.	antero-ventral fibres
B.F.G.	bodies of frontal-gland cells
B.P.G.	bodies of prostatic-gland cells
C.	cavity of ventral sucker
Ca.	caecum
C.F.	circular fibres
D.A.F.	deep anterior fibres
D.A.S.F.	deep antero-sinistral fibres
D.C.	dorsal chamber of ventrogenital sac
D.D.F.	deep dextral fibres
D.F.	diagonal fibres
D.G.	dorsal groove of gonotyl
D.H.	dextral hemisphincter
D.H.1	dextral branch
D.H.2	deep anterior branch
D.H.3	sinistral branch
D.L.	dorsal lobe of gonotyl
De.L.	dextral lobe of gonotyl
D.P.	dorsal pit
De.P.	dextral digitiform projection of gonotyl
D.P.F.	deep posterior fibres
D.P.F.M.	deep posterior fibres to mouth of ventrogenital sac
D.R.F.	deep radial fibres
D.S.V.	distal chamber of seminal vesicle
D.V.S.	dextral lobe of ventral sucker
E.	egg
E.C.	everted cavity of ventral sucker
E.D.P.	externo-dorsal prominence
E.P.	papilla on ejaculatory duct
E.S.P.	eversible spined pocket of ventral sucker
F.	fornix in prepharynx
F.D.P.	fibres of dorsal pit
F.L.	finger-like lobe of gonotyl
F.W.	folds in wall of ventrogenital sac
G.	gonotyl
G.A.	genital atrium
G.P.	genital pore
G.S.	genital sac
L.C.	Laurer's canal
L.P.	lateral pocket
L.U.	loop about uterus
L.V.S.	swollen lip of ventral sucker
M.	mouth of ventrogenital sac
O.	opening between dorsal and ventral chambers of ventrogenital sac
Oe.	oesophagus
O.F.G.	openings of frontal glands
Ov.	ovary
P.	papilla at entrance of sperm ducts
P.B.	papillary band
P.D.B.	postero-dextral band
P.D.F.	postero-dextral fibres
P.E.D.	prostatic ejaculatory duct
P.F.	posterior fibres
P.G.B.	posterior band from gonotyl
P.L.	posterior lip of mouth of ventrogenital sac
P.M.	parenchymatous medulla of ventral sucker
P.M.V.	papilla in mouth of ventrogenital sac
P.P.	protractors of pharynx
Ps.	pseudosucker in wall of ventrogenital sac
P.S.F.	postero-sinistral fibres
P.S.V.	proximal chamber of seminal vesicle
R.F.	radial fibres
R.F.1	radial fibres from spined pocket
R.F.2	radial fibres of dextral lobe of ventral sucker
R.P.	retractors of pharynx
S.	spines on wall of ventrogenital sac
S.A.F.	superficial anterior fibres
S.A.S.F.	superficial antero-sinistral fibres
S.D.F.	superficial dextral fibres
S.H.	sinistral hemisphincter
S.L.	sinistral lobe of gonotyl
S.P.	sensory papilla
Sp.	sphincter
S.P.F.	superficial posterior fibres
S.R.	seminal receptacle
S.R.F.	superficial radial fibres
S.S.F.	superficial sinistral fibres
S.V.	seminal vesicle
S.V.C.	portion of seminal vesicle with prominent circular fibres
S.V.D.	portion of seminal vesicle with prominent diagonal fibres
S.V.S.	sinistral lobe of ventral sucker
T.	testis
T.B.	transverse band of fibres
T.B.1	transverse band on apex
T.B.2	transverse band dorsal to spined pocket
U.	uterus
V.C.	ventral chamber of ventrogenital sac
V.D.	single vitelline duct
V.G.S.	ventrogenital sac
V.L.	ventral lobe of gonotyl
V.L.L.	ventro-lateral lobe of gonotyl
V.P.	ventral pit
V.R.	vitelline reservoir
V.S.	ventral sucker