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REPORTS ON THE COLLECTIONS OBTAINED BY THE HANCOCK PACIFIC EXPEDITIONS OF VELERO III OFF THE COAST OF MEXICO, CENTRAL AMERICA, SOUTH AMERICA, AND GALAPAGOS ISLANDS IN 1932, IN 1933, IN 1934, IN 1935, IN 1936, AND IN 1937.

A NEW GENUS OF DISTOMES (TREMATODA) WITH LYMPHATIC VESSELS

By H. W. MANTER
A NEW GENUS OF DISTOMES (TREMATODA) WITH LYMPHATIC VESSELS*

(With One Plate)

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The trematodes described in this paper are but two of over 100 species collected from marine fishes in 1934, during the third G. Allan Hancock Expedition to the Galapagos Islands. The author's presence on this expedition was sponsored in part by the Carnegie Institution of Washington. A brief preliminary report on the trematodes collected has been made (Manter, 1934) and a more complete report on the digenetic forms is in preparation. An early description of these two forms is felt justified in view of their significance in connection with the phylogeny of the Distomata. The author has already indicated (Manter, 1935) a relationship between certain allocreadiid-like distomes (Megasolena Linton and Hapladena Linton) and amphistomes. The new genus described below further substantiates such a view and indicates that the Anallocreadiinae in particular may be involved. A discussion of these relationships will follow a description of the new species.

Apocreadium mexicanum, new genus, new species
(Plate 2, figs. 1-3)

Host: Labrisomus xanti Gill
Position: Intestine
Locality: Tangola Tangola, Mexico
Incidence: 18 specimens from a single host

The body is elongate, tapering slightly and bluntly rounded at the anterior end, pointed at the posterior end, much flattened, especially posterior to midbody where the edges of the body become very thin and thrown into frill-like folds. The cuticula is scaled as far back as midbody. Mature specimens measure from 2.151 to 4.110 mm. in length by 0.757 to 1.096 mm. in greatest width. The body

* Studies from the Zoological Laboratories, the University of Nebraska, No. 191.
is approximately equally wide, except at the anterior and posterior fourth. The acetabulum is well anterior to midbody, the forebody being usually 1/4 to 1/5 total body length. Both suckers are subcircular with a tendency to be slightly longer than wide. The oral sucker is 0.225 to 0.315 mm. in diameter. The acetabulum is 0.352 to 0.502 mm. in diameter. Its aperture is transverse. The sucker ratio is approximately 2:3 or 3:5. Young specimens show a few pigment granules dorsally in the forebody but these are lacking in older specimens.

There is a short but distinct prepharynx. The pharynx is longer than wide, 0.142 to 0.202 by 0.112 to 0.165 mm. Its anterior fourth is modified as a sphincter region composed of circular muscles (suggesting the character of the pharynx in Gyliauchen) while the posterior region is composed of radial muscles. There is a distinct esophagus somewhat shorter than the pharynx. The intestinal bifurcation is approximately midway between the suckers. The ceca are narrow and extend to a point a short distance from the posterior end where the body begins its rather abrupt tapering to the posterior tip. Each cecum ends blindly.

The excretory vesicle is a long narrow tube extending anteriorly from the pore at the posterior tip of the body to the posterior testis where it spreads slightly to right and left and narrows to become a collecting tube on each side. Each collecting tube shortly after it leaves the vesicle forks into two tubules both extending forward, both at first median to the cecum, the larger tubule median to the smaller. Anterior to the acetabulum they are both lateral to the cecum. They seem to end near the level of the pharynx. Posterior to the level of the testes a very small excretory tubule can be seen on each side. These two posteriorly directed tubules arise at the same point where the anterior tubules unite. They extend to the posterior end of the body.

The lymphatic system consists of four longitudinal vessels close to the intestinal ceca, sometimes median, sometimes dorsal and ventral. Two of these lymphatic vessels extend anterior to the oral sucker to the extreme anterior end of the body where they end blindly. The longitudinal vessels do not give off side branches except in the posterior half of the body. Shortly behind the testes vesicle-like portions of the lymphatic system appear in the extreme lateral regions of the body. These are especially numerous near the
posterior end of the body where they are obvious in toto-mounts. Posterior to the testes each of the four vessels splits to form two making a total of four pairs. Each vessel is much branched, the ends of the branches extending to near the edge of the body. These tips are often swollen (plate 2, fig. 2).

The genital pore is median close to the anterior edge of the acetabulum. The testes are more or less rectangular in outline, slightly lobed, tandem, close together, approximately in the middle of the body. Except in young individuals (where the testes are of about equal size) there is a distinct tendency for the anterior testis to be wider than long, smaller and less lobed while the posterior testis tends to be longer than wide, larger and more deeply lobed. The posttesticular space is very long, sometimes more than ½ body length. A large, elongated sac-like seminal vesicle occurs immediately posterior to the acetabulum and overlapping the ovary. Anteriorly it narrows into a fine tube which continues without modification to near the anterior edge of the acetabulum where it joins the uterus to form a simple tubular genital sinus. Prostate gland cells are lacking unless represented by a few scattered cells around the male duct. A cirrus and cirrus sac are lacking. The narrow straight tube from seminal vesicle to genital pore is not muscular and since the pars prostatica cannot be distinguished from a cirrus portion, the tube might be termed the ejaculatory duct. It seems to have the same structure after its union with the uterus to form the ductus hermaphroditicus or genital sinus.

The ovary is spherical, midway between the anterior testis and the acetabulum, slightly to the right, just median to the right cecum. Mehlis' gland is well-developed, lying between ovary and anterior testis. A large flask-shaped seminal receptacle extends anterior to the ovary almost to the acetabulum. Laurer's canal is well-developed, coiled, and opens dorsally at mid-ovary level. The uterus is pretesticular filling most of the area between testes and acetabulum, wholly to the left of the ovary and largely to the left of midbody axis. It becomes a straight tube dorsal to the acetabulum and joins the male duct near the anterior edge of the acetabulum. The eggs are fairly thin-shelled, 61 to 67 by 31 to 34 μ. The vitelline follicles extend from the level of the ovary to near the posterior end of the body. In 13 specimens studied the follicles reached the posterior border of the acetabulum in 2 (in which the ovary also was far for-
ward) and in none did they reach the extreme posterior tip of the body. The vitellaria largely fill the body posterior to the testes and form two longitudinal intercecal, posttesticular areas.

**GENERIC DIAGNOSIS OF APOCREADIUM**

Elongate disomes with body much flattened posterior to mid-body where the edges are very thin. Acetabulum anterior to mid-body, larger than oral sucker. Pharynx well developed with an anterior region of circular muscles. Ceca extending not very far apart to near posterior end. Testes in midbody region, tandem, intercecal, close together. Seminal vesicle large, undivided, sac-like. Cirrus and cirrus sac lacking. Prostate cells poorly developed. A tubular genital sinus present. Genital pore median at anterior edge of acetabulum. Ovary spherical, pretesticular, slightly to the right. Mehlis' gland large, postovarian; Laurer's canal and seminal receptacle present. Uterus pretesticular, largely to the left. Vitellaria follicular in sides of body, confluent posterior to testes. Excretory vesicle I-shaped with 2 pairs of anterior and 1 pair of posterior tubules. Lymphatic system of 4 large longitudinal vessels branching at least in posterior half of body. Type species: *Apocreadium mexicanum*.

**SPECIFIC DIAGNOSIS OF *Apocreadium mexicanum***

(Measurements in mms.)

Body rounded anteriorly, pointed posteriorly; scaled to mid-body; 2.151 to 4.110 by 0.757 to 1.096. Acetabulum 1/4 to 1/5 from anterior end, 0.352 to 0.502 in diameter, with transverse aperture; oral sucker 0.225 to 0.315 in diameter. Prepharynx and esophagus present; intestinal bifurcation midway between suckers. Four longitudinal vessels branched in posterior half of body. Genital pore median at anterior edge of acetabulum. Seminal vesicle just posterior to acetabulum, overlapping ovary; genital sinus tubular, shorter than ejaculatory duct. Ovary spherical; seminal receptacle extending anterior to ovary; uterus to left of ovary; eggs 61 to 67 by 31 to 34 μ; vitellaria from near posterior edge of acetabulum to near posterior edge of body.

Host: *Labrisomus xanti* Gill

The name Apocreadium is from *apo*: away from and *creadium* and implies the fundamental differences between this trematode and the Allocreadiidae. The name *mexicanum* is for the locality.
Apocreadium longisinosum, new species
(Plate 2, figs. 4-7)

Hosts: Cheilichthys annulatus (Jenyns)
Albermarle Island and Charles Island, Galapagos Islands
Spheroide s angusticeps (Jenyns)
Charles Island, Galapagos

Position: rectum
Incidence: 2 to 10 in a host, total of 15 collected from 3 hosts.

The body is orange-yellow in its posterior half, unspined, more or less flattened, 6.57 to 9.65 by 1.552 to 2.403 mm., widest about at midbody, tapering toward each end. A 4.650 mm. specimen was immature. The posterior third of the body is thin and flexible with numerous lateral folds. It tapers sharply to a pointed posterior end. The anterior half of the body is more plump, smooth, and tapers gradually. A small, fleshy preoral lobe is present. The oral sucker is subcircular but usually slightly longer than wide, 0.375 to 0.532 mm. in transverse diameter. The acetabulum is about \( \frac{1}{4} \) body length from the anterior end, is longer than wide, 0.675 to 0.885 mm. in transverse diameter. Its aperture is longitudinal. The sucker ratio is approximately 5:8. The forebody measures 1.360 to 2.430 mm.

There is a fairly short prepharynx (about \( \frac{1}{2} \) pharynx length). The pharynx is usually somewhat pyriform in shape. The anterior third is more narrow, provided with a larger number of circular muscles, and separated from the posterior region by a very slight constriction. Muscles extend from the oral sucker to the pharynx outside the prepharynx. The esophagus is approximately the same length as the prepharynx. The intestinal bifurcation is usually a little nearer the oral sucker than the acetabulum but it may be approximately midway between the suckers. The narrow ceca extend some distance in from the body margins to within a short distance of the posterior end. They do not reach the posterior end and may fail to do so by some distance. One curious abnormality involved the left cecum which was almost completely degenerate except for a short normal-appearing stub barely reaching beyond the bifurcation and ending abruptly. The remainder of the cecum was represented by a few strands of fine fibrous tissue.
The genital pore is median very closely anterior to the acetabulum. It may even be directly ventral to the anterior edge of the acetabulum. The testes are immediately posterior to midbody, tandem, close together, lobed, squarish in shape. The posterior testis is usually slightly longer. The posttesticular space varies from 2.497 to 4.455 mm. being always considerably longer than the forebody. The seminal vesicle is a large, elongate, thin-walled sac, free in the parenchyma, extending backward from near the posterior edge of the acetabulum almost to the ovary from which it is separated by the seminal receptacle. The pars prostatica is about the same length as the seminal vesicle. It extends uncoiled diagonally forward dorsal to the acetabulum or, rarely, along the right side of the acetabulum. Its lumen is narrow and smooth, its wall fairly thick and cellular, surrounded by a few prostatic gland cells. These flattened and granular gland cells lie free in the parenchyma and are most numerous near the vesicle. The uterus enters the pars prostatica dorsal to the acetabulum to form a long tubular slightly muscular ductus hermaphroditicus or genital sinus. This tube bends ventrally toward the genital pore at the anterior edge of the acetabulum or may seem to bend back to reach the genital pore from an anterior direction (plate 2, fig. 5) but this appearance may be due to flattening of the specimen. The genital sinus is approximately the same length as the pars prostatica. Its lumen is wide, its wall fairly thin but muscular and surrounded by a few rounded non-granular cells.

The ovary is globular, pretesticular, to the right near the right cecum. It is separated from the anterior testis by a short space occupied by Mehlis' gland and the yolk reservoir. The uterus arises from the posterior side of the ovary and extends back as far as the anterior testis whence it coils forward to occupy the intercecal space to the left and anterior to the ovary. It joins the pars prostatica dorsal to the acetabulum as noted. A large seminal receptacle is present anterior to the ovary adjacent to the seminal vesicle. It connects to the oviduct posterior to the ovary. Laurer's canal is well developed, coiled, opening on the dorsal surface just anterior to the ovary. Eggs measure 88 to 102 by 48 to 60 μ, usually about 95 by 54 μ. The vitelline follicles extend from the level of the ovary to the posterior end of the body. At first extracecal, they become confluent posterior to the testes.
The excretory system is like that of *Apocreadium mexicanum*. The narrow excretory vesicle gives rise near the posterior testis to 2 pairs of anteriorly directed tubules, one pair larger than the other. Both pairs extend forward at least as far as the acetabulum but only one pair seems to reach as far as the oral sucker. From the common stem of each pair near the median vesicle a single sinuous tubule passes posteriorly on each side.

The lymph vessels are well developed. They are considerably branched in the posterior half of the body as in *A. mexicanum*. The branches run almost parallel with the stems, diverging gradually toward the body surface. They are not swollen at their tips as are such branches in *A. mexicanum*. The lymph vessels of the forebody also branch but here the branches are shorter and may extend in any direction. Because of the courses taken by the branches, the number of main stems of the lymph system is very difficult to determine. For some distance posterior to the testes there seem to be 4 pairs of longitudinal tubes, although 2 pairs extend farther back than the others. In the region of the acetabulum there seem to be 2 pairs. An accurate count was not possible in the forebody. In most specimens one pair extended into the preoral lobe. Evidently the lymph system is very similar to that of *A. mexicanum*.

Lymphocytes or at least large cells of some kind (plate 2, fig. 7) are not infrequent within the lymph vessels. These cells seem to have been amoeboid. They measure 14 to 19 μ in diameter which is as great as the diameter of most of the lymph vessels. The cytoplasm of these cells is finely granular, the nucleus staining very deeply, much more deeply than those of other cells.

**SPECIFIC DIAGNOSIS OF Apocreadium longisinosum**

(Measurements in mms.)

Body tapering toward each end, pointed at posterior end, widest at midbody, 6.57 to 9.65 by 1.552 to 2.403, in life orange-yellow in color. Oral sucker 0.375 to 0.532 in diameter; acetabulum ⅗ from anterior end, 0.675 to 0.885 in diameter, with longitudinal aperture. Genital pore median close in front of acetabulum. Short prepharynx, pharynx 0.210 to 0.292 (length) by 0.225 to 0.315 (width), anterior third slightly modified; esophagus short; bifurcation about midway between suckers; ceca narrow extending to near posterior end. Testes tandem, close together, slightly lobed, squarish, just poster-
ior to midbody. Seminal vesicle elongated sac-like from acetabulum to near ovary; pars prostatica about as long as vesicle, straight; ductus hermaphroditicus a simple muscular tube as long as pars prostatica. Ovary globular; Mehlis' gland posterior to ovary; seminal receptacle anterior to ovary; uterus between testes and acetabulum; eggs 88 to 102 by 48 to 60 μ; vitellaria from ovary to posterior end, confluent behind testes. Excretory vesicle extending to testes; 2 pairs of anterior and 1 pair posterior collecting tubules. Lymph vessels well developed, much branched, apparently fundamentally 2 pairs of longitudinal stems forking to form 4 pairs along much of body length. Type host: *Cheilichthys annulatus*. Other host: *Spheroides angusticeps*, a related fish. Type locality: Galapagos Islands.

The name *longisinosum* refers to the long genital sinus.

Comparisons. *A. longisinosum* is more than twice larger than *A. mexicanum* and the body is relatively wider. The aperture of the acetabulum is longitudinal rather than transverse. The vitellaria do not nearly reach the acetabulum as they do in *A. mexicanum*, a difference correlated with the larger uterus in *A. longisinosum*. In *A. longisinosum* the genital sinus is much longer; the eggs much larger (maximum length 102 μ compared with 67 μ); the lymph vessels more branched anteriorly. In spite of these differences the species are very similar and clearly congeneric.

There are genera of the Allocreadiidae with the cirrus sac weakly developed or lacking, for example the Anallocaudini and Opecoeliinae, but Apocreadium differs from most in its tubular genital sinus and from all in its lymphatic system. It is probably significant that the Anallocaudini which lack a cirrus sac also possess a tubular genital sinus described as “a common tube” in the form of an “unspecialized cloacal invagination” by Simer (1929, p. 564) for *Anallocaudium armatum*; as a “long genital sinus” by Manter (1926, p. 87) for *Homalometron pallidum*; as “an invaginated cloaca” by Hunter & Bangham (1932, p. 138) for *Anallocaudium pearsei*; but as a “genital atrium” by Manter (1936, p. 34) for *Crassicutis cichlasomae*. In this latter case however, the “atrium” may be tubular in form.

The genus Apocreadium then shows evidence of relationship to the Anallocaudini. On the other hand, however, its lymphatic vessels, the structure of the pharynx and the excretory system sug-
gest the genera Megasolena and Hapladena for which Manter (1935, p. 438) named the subfamily Megasoleninae. The essential difference is the presence of an hermaphroditic sac in the Megasoleninae. Apocreadium seems to stand almost midway between these two subfamilies. If included in the Megasoleninae, the subfamily (and family) description must be altered to include forms with neither hermaphroditic nor cirrus sac; if included in the Anallocreadiinae the subfamily must be extended to include forms with a lymphatic system. For the present, the writer prefers to recognize the lymphatic vessels as of fundamental significance, especially since their presence is again associated with pharyngeal modifications and to classify Apocreadium in the Megasoleninae.

Discussion. For many years it has been the custom to classify digenetic trematodes into three groups, the Amphistomata, Monostomata, and Distomata. But it has been increasingly apparent that these divisions are heterogeneous and not natural. Some monostomes (e.g. the Angiodictyidae) are actually amphistomes which have lost their posterior sucker. Other monostomes are evidently distomes which have lost the ventral sucker. In other words, members of these groups may show closer relationship to one of the other groups than to members of its own group. Amphistomes are generally considered as the most primitive. Little study has been made of possible relationship between amphistomes and distomes. Dawes (1936, p. 177) remarks: "Nous savons vraiment peu de chose sur les relations qui existent entre les Distomata et les Paramphistomida; c'est un point qui est visiblement négligé par les zoologistes." The author, however (Manter, 1935), has found strong evidence of such relationship exactly where it would be most expected, namely among trematodes of fish. It even seemed necessary to classify two distome genera (Megasolena and Hapladena) among the Paramphistomida. These two genera showed certain features suggesting the family Allocreadiidae where Megasolena at least was once classified.

Apocreadium is still more evidently allocreadiid-like. It serves to link the Paramphistomida not only to the Allocreadiidae but to the Anallocreadiinae. But Apocreadium can be included in the Megasoleninae especially if the lymphatic system is to be emphasized. There is, in fact, a fairly well graded series of forms between the amphistomes such as Gyliauchen and Opistholebes through Paragyliauchen, Apocreadium and the Anallocreadiinae to the Lepo-
creadiiinae. Even the position of the acetabulum is intermediate in some forms such as *Paragyliauchen chaetodontis* Yamaguti. Megasolen a and Hapladena are definitely associated with such a series but differ from the others in their peculiar hermaphroditic sac. There results a plausible conclusion that the large distome family Allocreadiidae probably evolved from amphistome ancestors. Or the amphistomes may have evolved from allocreadiid ancestry.

Type specimens of the new species described in this paper are deposited in the United States National Museum. Paratypes are deposited at The University of Southern California and in the author’s collection.
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EXPLANATION OF PLATE 2

All figures were drawn with the aid of a camera lucida. The projected scale has the value (in mms.) indicated for each figure. Abbreviations: \(ac\), acetabulum; \(ce\), intestinal cecum; \(ex\), excretory vesicle; \(gp\), genital pore; \(gs\), genital sinus; \(l\), lymphatic vessel; \(pp\), pars prostatica; \(sr\), seminal receptacle; \(sv\), seminal vesicle; \(ut\), uterus.

Fig. 1. *Apocreadium mexicanum*. Dorsal view.

Fig. 2. *A. mexicanum*. Frontal section through posterior half of the body, showing the branching lymphatic vessels.

Fig. 3. *A. mexicanum*. Cross-section through the region of the seminal receptacle.

Fig. 4. *A. longisinosum*. Ventral view.

Fig. 5. *A. longisinosum*. Terminal reproductive organs.

Fig. 6. *A. longisinosum*. Cross-section through anterior portion of the pharynx.

Fig. 7. *A. longisinosum*. Portion of two lymphatic vessels showing lymphocytes.