DESCRIPTION OF A NEW SPECIES OF MARITREMA NICOLL 1907, MARITREMA ARENARIA, WITH STUDIES OF THE LIFE HISTORY

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HISTORICAL

The genus *Maritrema*, established by Nicoll in 1907, includes a number of small distomes, most of them intestinal parasites of shore birds. The most characteristic morphological feature of the group is the ring-like arrangement of vitellaria, which almost completely encircle the body posterior to the testes. Other features of diagnostic value are the approximately equal size of the suckers; the exit of the male duct at a small papilla located near the acetabulum, and continuous with a well-developed cirrus sac; and restriction of the voluminous uterus to the posterior third of the body.

The species of Maritrema described to date are as follows:

M. gratiosum-Nicoll, 1907.

M. lepidum-Nicoll, 1907.

M. humile-Nicoll, 1907.

M. linguilla—Jägerskiöld, 1909.

M. subdolum-Jägerskiöld, 1909.

M. nicolli—Travassos, 1921.

M. pulcherrima—Travassos, 1929a, b.

M. sachalinicum—Schumakowitsch, 1932.

M. acadiae—Swales, 1933; Ciurea, 1933.

M. rhodanicum—Carrère, 1936.

M. ovata-Rankin, 1939b.

An apparently new species of *Maritrema* was recovered from the intestine of the black-headed gull by Rothschild (1938), who indicated in a footnote that a description of the form was forthcoming.

M. obstipum (Van Cleave and Mueller, 1932; Mueller, 1934—Syn. Microphallus obstipum), M. medium (Van Cleave and Mueller, 1932; Mueller, 1934—Syn. Microphallus medium), and M. nettae (Gower,

1938), previously in the genus *Maritrema*, were removed by Rankin (1939b) to a new genus, *Maritreminoides*.

DESCRIPTION OF MARITREMA ARENARIA, N. SP.

Examination of the intestines of a number of ruddy turnstones (Arenaria intrepres morinella) revealed a consistently heavy infection with small microphallid worms of an hitherto undescribed species of Maritrema. While other flukes have been found in the turnstone (Lebour, 1909; Rankin, 1939a), they occur in relatively small numbers. It seemed, therefore, appropriate to designate the new species of Maritrema as M. arenaria. Type and cotypes have been deposited in the United States National Museum, Washington, D. C., numbered 9293 and 9294 respectively.

 $M.\ arenaria$ has the characteristic tongue-shaped outline, measuring 0.858 mm. in length \times 0.380 mm. in greatest width in the living animal. These measurements were obtained from a well-developed adult worm under slight pressure of a cover glass. Like all flukes of this type, the animal exhibits considerable capacity for contraction and elongation. The body is sparsely covered with cuticular spines from its anterior end posteriorly to the level of the middle of the ovary. The acetabulum is well-developed, practically circular in outline, and located in the midbody region.

Excretory System

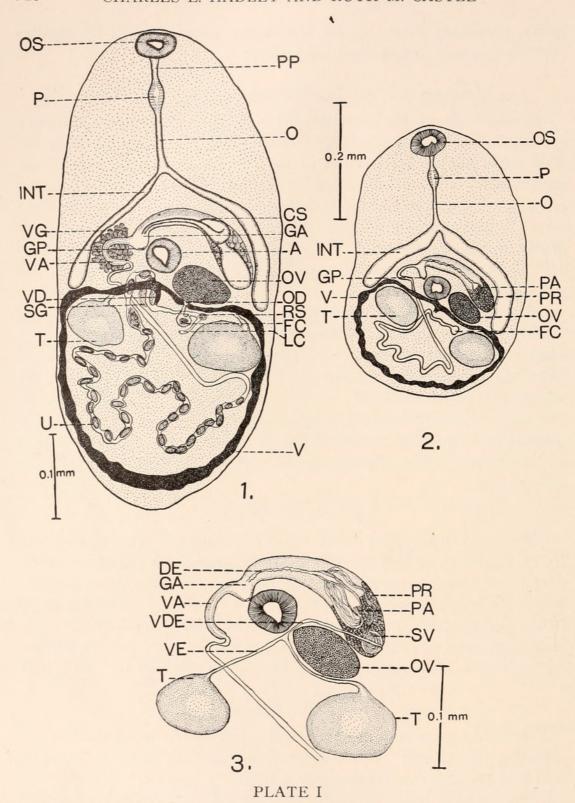
The excretory system is of the "Mesostoma" type (Rothschild, 1937) +, that is, each of the main collecting tubes divides into an anterolateral and a postero-lateral branch in the region of the ventral sucker—with a flame cell pattern of 2[(2+2)+(2+2)], conforming to the fundamental pattern for the family Microphallidae (Faust, 1932). The main collecting tubes are continuous posteriorly with a Y-shaped excretory vesicle, emptying through a posteriorly terminal excretary pore.

Digestive System

The oral sucker is subterminal and roughly circular in outline, surrounding the mouth. The contracted prepharynx is short, equal in length to the pharynx, leading into a relatively long oesophagus. One-third of the body length from the anterior end, the oesophagus branches to form intestinal crura which extend to the anterior border of the testis.

Male Reproductive System

The oval testes are entire, symmetrical, and approximately one-third of the body length from the posterior end. Their long axes are di-



All drawings made with camera lucida. Abbreviations used: A, acetabulum; CS, cirrus sac; CW, cyst wall; DE, ductus ejaculatorius; FC, fertilization chamber; GA, genital atrium; GP, genital pore; GPA, genital papilla; INT, intestine; LC, Laurer's canal; O, oesophagus; OD, oviduct; OS, oral sucker; OV, ovary; P, pharynx; PA, pars prostatica; PP, prepharynx; PR, prostate glands; RS, receptaculum seminis; SG, shell gland; SV, seminal vesicle; T, testis; V, vitellaria; VA, vagina; VD, vitelline duct; VDE, vas deferens; VE, vas efferens; VG, vaginal gland; U, uterus.

rected transversely. The vasa efferentia unite close to the left border of the ovary, to form the vas deferens, which extends dextrally along the anterior border of the ovary, crosses the cirrus sac obliquely near its proximal end, and enters the sac subterminally at its antero-lateral border. The cirrus sac is long and curved, extending from its enlarged proximal end, located at the right between the ovary and the right intestinal ramus, in the form of an arch applied closely to the anterior border of the acetabulum. Its distal end joins the genital atrium located on the left border of the acetabulum. The seminal vesicle is well-developed and coiled on itself in the bulbous proximal end of the cirrus sac, as indicated in Fig. 3. Prostate gland and pars prostatica are present, and associated with a slightly coiled ductus ejaculatorius, which empties into the genital atrium by a relatively small genital papilla.

Female Reproductive System

The ovoid ovary lies immediately anterior and slightly mesial to the right testis, with its long axis in a transverse plane, and its broader end toward the mid-line. The short oviduct, leading posteriorly from the caudal border of the ovary near its mesial end, widens to form a spherical chamber, commonly filled with mature sperms. This chamber we believe to be a fertilization chamber. It is joined to the proximal end of the oötype subterminally by a short duct. Dextrad to the point of union with the fertilization chamber, the ootype ends blindly in a slight enlargement, also commonly filled with sperms. This enlarged portion of the oötype we interpret as the receptaculum seminis. Laurer's canal arises from the caudal side of the receptaculum seminis, curving posteriorly toward the mid-line, and ending in a dorsal pore. From its point of union with the fertilization chamber, the oötype extends in a transverse plane dorsal to the oviduct, and receives the common vitelline duct in the mid-line of the body. The oötype then turns sharply anteriorly, and is seen to be surrounded by faintly staining glandular cells, apparently representing shell glands. Continuous with the oötype, the uterus arises near the posterior border of the acetabulum and then follows an undulating course posteriorly along the mesial border of the left testis. In the posterior region of a mature worm, the uterus forms nu-

PLATE I

Fig. 1. Adult Maritrema arenaria, dorsal aspect, whole mount, standard alum haematoxylin.

Fig. 2. Metacercaria of *M. arenaria*, dorsal aspect, whole mount, Lynch's precipitated borax carmine. (Slightly distorted specimen.)

Fig. 3. Male genital organs and associated structures of an adult M. arenaria, dorsal aspect.

merous egg-filled coils, which eventually extend around the caudal edge of the right testis, and then continue diagonally to a point anterior to the lateral end of the left testis, where it joins the metraterm. The metraterm, or vagina, is curved, has unusually thick walls, and is surrounded by a dense mass of deeply staining cells which appear to be glandular. These cells we interpret as vaginal glands (Figs. 1, 7). Anteriorly the vagina leads into the genital atrium. The vitellaria, characteristic of this genus, form an almost complete circle, lying just inside the borders of the posterior end of the body, and inclosing both testes. The left and right vitelline ducts unite a short distance posterior to the acetabulum in the mid-line of the body.

COMPARISON WITH PREVIOUSLY DESCRIBED SPECIES

The species known and described up to 1939 were reviewed by Rankin in his paper of that year. The eleven forms of *Maritrema* listed by him may be distinguished from *M. arenaria* by the following easily noticeable differences:

M. lepidum, M. humile, M. linguilla, M. nicolli, and M. pulcherrima—by their shorter intestinal crura; M. gratiosum and M. acadiae—by the median to slightly dextral position of their ovary; M. ovata—by the more median position of ovary and testes; and M. subdolum, M. sachalinicum, and M. rhodanicum—by disparity in the size of the two suckers.

THE METACERCARIA

The metacercarial stage occurs in the common barnacle, *Balanus balanoides*. These cysts are found in practically all barnacles on rocky shores visited by ruddy turnstones. In regions where the surf is heavy, it is noticeable that turnstones are absent, and the barnacles consistently small and uninfected. Barnacles from Norman's Woe and Chebeague Island, Maine, were found to be heavily infected, which fact makes it seem probable that the barnacles all along this coast are parasitized.

The thin-walled, spherical cysts occur most numerously around the gut of the host, but in cases of heavy infection—that is, 600–1,000 cysts in a single barnacle—they are found in every part of the body except the appendages and the interior of the gut.

The cysts are yellow in color, and show clearly the curled-up meta-cercaria, with gut crura and oesophagus. A large cyst measures ca. $0.328 \text{ mm.} \times 0.343 \text{ mm.}$, and when opened by dissection with fine needles, liberates a metacercaria ca. $0.576 \text{ mm.} \log \times 0.360 \text{ mm.}$ in greatest diameter, with anterior and posterior suckers of about the same diameter, 0.055 mm.

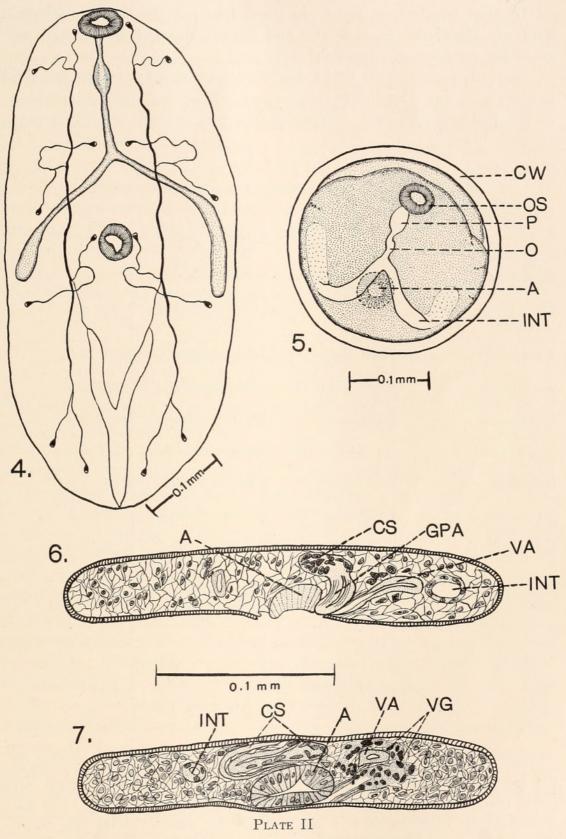


Fig. 4. Excretory system of an adult M. arenaria.

- Fig. 5. Mature, encysted metacercaria of M. arenaria.
- Fig. 6. Transverse section, M. arenaria, through region of genital papilla.

Fig. 7. Transverse section, M. arenaria, through region of vagina and vaginal glands.

In most respects, as shown in Figs. 1 and 2, the metacercaria and adult are identical. Smaller size and absence of eggs, however, distinguish the metacercaria from the adult.

Marie Lebour (1908, 1911) described a trematode cyst occurring in barnacles of the Northumberland coast. This cyst was described as thin-walled and spherical, measuring 0.04 mm. across, and liberating a

Table I

Measurements of adult and metacercaria of Maritrema arenaria.

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	Living adult (under No. 2 cover slip)	Preserved adult stained whole mount (range in 10 specimens)	Living metacercaria (under No. 2 cover slip)
Body length	0.858 mm.	0.303-0.566 mm.	0.576 mm.
Body width (region of testes)	0.380 mm.	0.192-0.266 mm.	0.360 mm.
Acetabulum	0.055 mm.	0.038-0.050 mm.	0.055 mm.
Oral sucker	0.055 mm.	0.038-0.054 mm.	0.055 mm.
Prepharynx	0.034 mm.	0.010-0.014 mm.	0.019 mm.
Pharynx	0.034 mm.	0.020-0.030 mm.	0.028 mm.
Oesophagus	0.153 mm.	0.064-0.10 mm.	0.150 mm.
Intestinal crura	0.239 mm.	0.142-0.208 mm.	0.220 mm.
Left testis	0.087×0.112 mm.	$0.036 \times 0.064 - 0.076 \times 0.088 \text{ mm}.$	0.080 × 0.110 mm
Right testis	$0.087 \times 0.112 \text{ mm}.$	$0.040 \times 0.060 - 0.070 \times 0.10 \text{ mm}.$	0.074 × 0.110 mm
Ovary	$0.068 \times 0.146 \text{ mm}.$	$0.030 \times 0.054 - 0.062 \times 0.084$ mm.	$0.050 \times 0.070 \text{ mm}$
Egg	$0.010 \times 0.020 \text{ mm}.$	$0.006 \times 0.016 - 0.007 \times 0.020 \text{ mm}.$	none

[&]quot;cercaria" 1.0 mm. long. We suspect that 0.4 mm. is the correct figure for the diameter, as it seems unlikely that a metacercaria 1 mm. long could be contained in a cyst measuring only 0.04 mm. across. The cyst described by Miss Lebour is larger than the metacercarial cyst of *M. arenaria*, and *C. balani* Lebour, 1 mm. long, is longer than any metacercaria or adult which we have obtained. In *C. balani* Lebour, the prepharynx is very long, longer than the oesophagus, while in the meta-

cercaria of *M. arenaria* the prepharynx is markedly shorter than the oesophagus. In the former, the body of the animal is covered with spines even at the posterior end, while in the latter the spines do not extend posterior to the level of the middle of the ovary. Miss Lebour states that the animals were badly preserved, and that measurements of the organs were not made from the living animal. Unfortunately it seems impossible with the amount of information available to state definitely that *Cercaria balani* Lebour and the metacercaria we have found are the same form—or that they are different. Lebour suggested (1908) that *C. balani* might be the larval form of *Spelotrema excellens* Nicoll, but later (1911) retracted this suggestion. Nicoll and Small (1909) found *C. balani* Lebour to bear more resemblance to *Levinseniella brachysoma*. Since *Spelotrema* and *Levinseniella* are also members of the *Microphallidae*, it seems probable that the two metacercariae must be, if not the same form, closely related ones.

LIFE HISTORY OF MARITREMA ARENARIA

The metacercariae found in barnacles of the Woods Hole region and the adult fluke found in the gut of the ruddy turnstone, Arenaria interpres, resemble each other very closely, the chief difference being a greater development of the reproductive system and a greater body size in the adult. On this basis alone, it would be possible to state that the form encysted in Balanus is the metacercaria of M. arenaria. Corroboration is furnished by study of the feeding habits of Arenaria, and examination of the gut of freshly-killed birds. The turnstone is found most frequently on rocky shores, where it obtains food by turning over small stones with its bill, and by searching the surface of the larger rocks, which are usually covered with barnacles. Observations on the feeding habits of Arenaria led us to consider it as a possible adult host for our metacercaria, which we had found before the host of the mature worm was known. The gut of the first bird killed and examined contained bits of barnacle shell, whole and partially digested barnacles, partially and freshly excysted metacercariae, and 10,000-12,000 adult M. arenaria. A similar condition was found in a dozen turnstones subsequently investigated. It was impossible to obtain an uninfected bird for experimental excystment of metacercariae, as Arenaria breeds within the Arctic circle, and is heavily infected before reaching this region. While we have not been able to secure excystment after experimental feeding of the following animals—young gulls (Larus argentatus), young terns (Sterna hirundo hirundo), spotted sandpiper (Tringoides macularius), white mouse, white rat, kitten, and domestic fowl—we feel certain that the metacercaria from Balanus is an immature form of M. arenaria.

Extensive surveys in the Woods Hole region showed the incidence of infection to be very high in Balanus balanoides, except for surf-swept shores, where rocks bear only small barnacles. Indeed, so extensive is this infection that uninfected barnacles proved to be a notable exception in one region after another. The number of metacercarial cysts per barnacle, ranging from 1 cyst to upwards of 1,000 cysts, and predominantly averaging between 30 and 100 cysts per individual, indicated either an abundance of cercariae, or retention of the encysted parasites over long periods of time. Studies of a number of authors, including Faust (1932) and Rothschild (1937), make it seem probable that the cercaria is a Xiphidiocercaria of the Ubiquita type (Sewell, 1922), and therefore a minute, feebly-swimming form. With the two above facts in mind, it was natural to expect to find the cercariae of this fluke developing in a molluscan host living in close proximity to barnacle-covered rocks. Mollusks common to such a habitat near Woods Hole are Littorina littorea, L. rudis, L. palliata, Urosalpinx cinereus, Mitrella lunata, Mytilus edulis, Modiolus demissus, Mya arenaria, Petricola pholadiformis, Anomia simplex, and Crepidula fornicata. Over a period of two summers, hundreds of individuals of each of the above-mentioned mollusks were carefully observed, both in living and crushed condition. Aside from cercariae of known life cycles, but two cercariae were found as possible suspects, Cercaria parvicaudata (Stunkard and Shaw, 1931) and a form tentatively identified as C. ubiquitoides (Stunkard, 1932). Repeatedly, uninfected or lightly infected Balanus individuals were exposed to free cercariae of these two types with completely negative results.

Rees (1936) reports an ubiquitous cercaria found in *Littorina*. In February and March, 20 out of 50 specimens of *L. rudis*, 4 out of 40 specimens of *L. palliata* (obtusata), and 2 out of 2,000 specimens of *L. littorea* were infected. The cercaria closely resembles *C. ubiquitoides* Stunkard (1932), and is also similar to *C. ubiquita* Lebour (1907). We have been unable to identify any cercaria found in the Woods Hole region during the summer as the form reported by Rees, or by Lebour. Cable and Hunninen recently described (1938) an ubiquitous cercaria, *C. nassicola*, as yet unconnected with any known life history.

All species of snails common to shores with heavily infected barnacles were repeatedly exposed to the mature eggs of M. arenaria for weeks, following which these snails proved to be devoid of cercariae.

In the light of this evidence, it is suggested by the authors that the completion of this life cycle may resolve itself into a careful study of the mechanics or chemistry of the infection process, or a study of the possibilities that the period of infection is limited seasonally. The

migration dates of the turnstone, the adult host, are such that fresh infections of the molluscan hosts of this region must fall between May 1 and June 8 (June 24), and between (July 4) July 24 and October 16. Allowing for a period of development of cercariae, and assuming that the period of cercaria production, once begun, may be limited, it appears possible that the cercariae are not present in the Woods Hole region during the summer months.

SUMMARY

A new species of the trematode genus Maritrema, Maritrema arenaria, is described as to morphology, adult host (Arenaria interpres), and metacercarial host (Balanus balanoides). Negative results are reported from a search for the sporocyst and cercarial stages of this fluke, and the suggestion is made that the cercaria may not be present during the summer months in the Woods Hole region.

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