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Revue critique
Renicolid Trematodes *(Digenea)* from the renal tubules of Birds.

by **Horace W. STUNKARD**

The American Museum of Natural History, Central Park West at 79th Street, New York 24, N.Y.

Résume

Le genre *Renicola* a été créé par Cohn en 1904 à partir de l'espèce *Monostoma pingue* (Mehlis in Creplin, 1846). Sa distribution est cosmopolite et les espèces connues ont été trouvées dans les reins d'Oiseaux appartenant à diverses familles.

Cercaria rhodometopa Pérez, 1924 possède un système excréteur très semblable, et les cercaires rhodométopes ont été considérées comme les formes larvaires des Rénicolides, bien que toutes les tentatives d'infestation expérimentale aient jusqu'à présent échoué.

Cable (1963) a signalé que certaines cercaires plagiorchides sont également des formes larvaires de Rénicolides, et il admet que les espèces de *Renicola* peuvent avoir deux types de cercaires, soit rhodométopes, soit plagiorchides.

Stunkard (1964) a décrit des cercaires plagiorchides de *Thais lapillus,* et il a obtenu leur développement en adultes appartenant à une espèce nouvelle, *Renicola thaidus,* dans les tubules rénaux du goëland, *Larus argentatus.* Il a observé que ces cercaires étaient semblables à d'autres provenant de *Littorina* spp., viz., *Cercaria parvicaudata* Stunkard et Shaw, 1931 et *Cercaria roscovita* Stunkard, 1932.

Werding (1969) rapporte que les métacercaires de *C. roscovita* se sont développées en adultes identifiés à *Renicola roscovita,* (Stunkard, 1932), dans les reins de *L. argentatus.* Il suggère l'éventuelle

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identité entre *C. roscovita* et *C. parvicaudata*. Robson et Williams (1970) désignent les cercaires de *Littorina littorea* sous le nom de *Cercaria A*. Ces cercaires ressemblent morphologiquement à *C. roscovita ;* mais les essais d'infestation de jeunes *L. argentatus*, de canetons, de poussins et de divers animaux de laboratoire se sont soldés par des échecs. Des tentatives répétées, effectuées par l'auteur, pour infester *L. argentatus* et d'autres oiseaux avec des métacercaires de *C. parvicaudata* ont donné des résultats négatifs.

La position systématique des cercaires rhodométopes est énigmatique ; toutefois, inclure dans le même genre des types morphologiquement aussi distincts que les cercaires plagiorchides et les cercaires rhodométopes est manifestement contraire au concept de l'unité générique.

Summary

The genus *Renicola* Cohn, 1904, was based on *Monostoma pingue* (Mehlis in Creplin, 1846) ; it is cosmopolitan in distribution and species have been found in the kidneys of birds belonging to various families. *Cercaria rhodometopa*, Pérez, 1924, has a similar excretory system and the rhodometopous cercariae have been regarded as renicolid larvae, although attempts at experimental infections have so far proved futile. Cable (1963) reported that certain plagiorchid cercariae are larvae of renicolid species and postulated that species of *Renicola* may have two types of cercariae, either rhodometopous or plagiorchid larvae. Stunkard (1964) described plagiorchid cercariae from *Thais lapillus* and their development in the renal tubules of gulls, *Larus argentatus*, to adults that were identified as a new species, *Renicola thaidus*. He noted that these cercariae are similar to others from *Littorina* spp., *viz., Cercaria parvicaudata*, Stunkard and Shaw, 1931, and *Cercaria roscovita*, Stunkard, 1932. Werding (1969) reported that metacercariae of *C. roscovita* developed in the kidneys of *L. argentatus* to adults identified as *Renicola roscovita* (Stunkard, 1932). He suggested the identity of *C. roscovita* and *C. parvicaudata*. Robson and Williams (1970) identified cercariae from *Littorina littorea* as *Cercaria A ;* the larvae agreed morphologically with *C. roscovita*, but attempts to infect juvenile *L. argentatus*, ducklings, chicks and various laboratory mammals failed. Repeated attempts by the writer to infect *L. argentatus* and other birds with metacercariae of *C. parvicauda* have given only negative results. The systematic position of the rhodometopodous cercariae is enigmatic, but the inclusion of such morphologically diverse types as the plagiorchid and rhodometopodous cercariae in a single genus controverts ideas of generic unity.

The genus *Renicola* was erected by Cohn (1904) to contain *Monostoma pingue* (Mehlis in Creplin, 1846), a parasite in the kidneys of the crested grebe, *Podiceps cristatus*, when he discovered that the species has a distinct acetabulum and could no longer be classed as a monostome. On the basis of this and similar observations Cohn advanced the idea that Trematodes which live in closed cavities have vestigial adhesive structures. The morphology of *Renicola* is peculiar and distinctive ; the genus was included by Odhner (1914) in the family *Troglotrematidae*, a heterogeneous assemblage of five genera, parasites of birds and mammals, that often occur in pairs in cyst-like cavities, but not in the intestine. Dollfus (1939) dismembered the artificial family and named *Renicola* as type of a new family. Dollfus (1946) presented a list of Trematodes from the renal organs of birds, revised the family *Renicolidae*, and devised a key for the identification of species. Since the account by Dollfus, the number of named species has increased from 9 to 39, and the distinctions between species have become increasingly equivocal.

DEVELOPMENTAL STAGES

It has been generally accepted that the rhodometopous cercariae are larvae of renicolid Trematodes but recent experiments cast doubt on the belief. Stunkard (1932) redescribed *Cercaria rhodometopa* Perez, 1924, a distinctive species from *Turritella communis*, a marine snail that lives at depths of twenty meters or more. *Cercaria rhodometopa* is very large, with a rose-colored anterior end ; flattened dorso-ventrally ; it has a long, powerful tail provided with lateral membranous fins ; no stylet ; an undeveloped digestive tract ; and a complex excretory system. The excretory vesicle almost fills the dorsal part of the body ; it is Y-shaped with branched diverticula from the stem and arms that extend to the anterior end of the larva and are filled with concretions. The flame-cell formula is 2[(5 + 5 + 5 + 5 + 5) + (5 + 5 + 5 + 5 + 5)]. Referring to the excretory pattern of *C. rhodometopa*, Stunkard stated, p. 326, « The system is so peculiar and characteristic that it will afford a quick and certain criterion for the identification of later stages in the life-history and may, indeed, lead to the correlation of this larva with an adult Trematode having the same excretory pattern. » Miriam Rothschild (1935) described new rhodometopous cercariae, four species from Plymouth, England and two species from Naples, Italy, all from *Turritella communis*. Infection experiments failed and search for metacercarial stages were fruitless until Rothschild and Sproston (1941) reported thick-walled cysts in the mesenteries around the pyloric caeca of *Gadus luscus* and *Gadus merlangus*. The cysts contained active metacercariae little changed from rhodometopous cercariae. Further evidence that fishes serve as intermediate hosts was supplied by Timon-David (1953), who reported similar metacercariae from the pyloric caeca and mesenteries of sardines, taken in the Mediterranean.

Yamaguti (1939) described *Renicola keimahuri* from the kidney of *Uria carbo* and *Renicola umigarasu* from *Uria aalge*, taken in Japan. Figures of those species

portray the branching excretory vesicle, characteristic of *C. rhodometopa.* Discussing the interrelationships and taxonomy of digenetic Trematodes, Stunkard (1946) cited the report of Yamaguti and stated, p. 153, « ...there is presumptive evidence that *Cercaria rhodometopa* is the larva of a species of *Renicola,* possibly the unnamed one reported by Dollfus (1939) ».

Wright (1954 *a*, 1954 *b*, 1956) presented data on renicolid Trematodes from birds that died in British zoos and from the large number of oiled birds washed up around the coast during the winter storms. He (1956) deplored the incomplete descriptions of many species, which renders recognition virtually impossible. He noted extensive morphological diversity and reported, (1956, p. 3), « During the course of the present work it has been found that variation between individual specimens from any batch of worms is so great that it must be accepted either that multiple infections with more than one species are common or that most previous workers have not taken into account the degree of variation within species. A study of the records of *Renicola* spp. together with their hosts shows that host-specificity in the sense of a group relationship does not apply in this genus. » After discussing hosts he concluded, p. 4, « The only feature in common, then, between most of the host species récorded is their fish-eating habit and for this reason the main search for *Renicola* was concentrated on fish-eating sea-birds. » He found that eggs of the parasite were fully embryonated when passed from the host but did not hatch in fresh, brackish or sea-water. When the eggs were ingested by snails, the miracidia emerged and were recovered from the stomach and intestine. But attempts to infect snails were inconclusive and no infections were found after feeding cysts to a duckling, a domestic chicken and a blackbacked gull. Morphological agreement indicates that the rhodometopotous cercariae are larvae of Renicolid Trematodes and the failure to obtain experimental infections of molluscan and avian hosts has been baffling.

Taxonomic Relations

Knowledge of life-cycles and larval stages has made it possible to relate certain cercarial types to particular families. Accordingly, La Rue (1957) proposed a new system of classification based on correlation of larval stages, cercarial development, and adult morphology. It recognized two distinct types of cercariae : those in which the excretory vesicle is simple and membranous, formed by the medial fusion of the primary collecting ducts, and those in which the primary vesicle is enclosed and replaced by mesodermal cells that form a thick-walled bladder. In the first group, the excretory pores are on the tail which is often forked, and there is no stylet. In the second group, the primary pores are at the body-tail furrow or a stylet is present. Species in the first category were included in a superorder, *Anepitheliocystidia,* which contained three orders : *Strigeatoidea, Echinostomida,* and *Renicolida.* The second category, *Epitheliocystidia,* contained two orders : *Plagiorchiida* and *Opisthorchiida.* The rhodometopous cercariae did not closely resemble any other cercarial type and since none had been described with an epithelial excretory vesicle, La Rue proposed a separate

order, *Renicolida ;* suborder, *Renicolata* and superfamily, *Renicoloidea* to receive the family *Renicolidae*. It should be noted that Rothschild (1935) had reported the primary excretory pores of *Cercaria pythonike*, a rhodometopous species, at the body-tail furrow and not on the tail.

Odening (1962) made no reference to life-cycles or cercariae but attempted a revision of the family *Renicolidae*, based on adult morphology. He reviewed earlier studies and noted that Wright (1957) had assigned the named species to four groups, listed as *pelecani, mediovitellata, pinguis* and *goliath*. He discussed the value of different features for taxonomic determination and the difficulty of evaluation since features vary with age, degree of sexual maturity, and other factors. He proposed a new genus, *Neorenicola*, to receive *Renicola monorchis*, Dollfus and Capron, 1958 and another, *Pseudorenicola*, to receive *Renicola nana* Bykhovskaia-Pavlovskaia, 1954. He listed thirty species in the genus *Renicola*, analyzed the descriptions of several unnamed species and provisionally allocated certain of them to new species. He recognized the groups of Wright (1957) and proposed three new subgenera : *Renicola* to contain the *pinguis* and *pelecani* groups ; *Wrightrenicola* to contain the *goliath* group, and *Anatirenicola* to contain the *mediovitellata* group. The erection of the new genera has doubtful validity and the revision adds nothing of importance to knowledge of the family.

La Rue's taxonomic disposition of the *Renicolidae* was questioned by Cable (1963). He (1956) had described three « Troglotrematid » cercariae from Puerto Rico : *Cercaria caribbea VII, Cercaria caribbea VIII*, and *Cercaria caribbea IX*. All of them had branched excretory vesicles of the rhodometopous type and in the first of these species the primary excretory pores were at the body-tail furrow. The flame-cell pattern of the mature cercaria was not determined but six flame-cell groups were indicated on each side, three in the anterior and three in the posterior portion of the body. All three species were flat, with long tails, and the flame-cell formula of *C. caribbea VIII* was given as probably $2[(3 + 3 + 3) + (3 + 3 + 3)]$. *Cercaria caribbea IX*, from *Cerithium variable*, was found only once, in a crushed snail. The cercariae appeared fully developed but did not swim. However, the livers of Gobiid fishes from the lagoon at Punta Arenas where the snail was taken contained « encysted metacercariae of a larva that could hardly be other than of this type ».

In the same publication, Cable (1956) described « Plagiorchioid » cercariae and in particular *Cercaria caribbea XXXII* from *Cerithidea costata* and *Cercaria caribbea XXXIII* from *C. costata* and *Batillaria minima*. These two species are very similar to *Cercaria parvicaudata*, Stunkard and Shaw, 1931 from *Littorina* spp. at Woods Hole, Massachusetts and *Cercaria roscovita* Stunkard, 1932, from *Littorina saxatilis nigrolineata* at Roscoff, France. The family status of these xiphidiocercariae remained totally unresolved until Schiller (1959) reported two types of cercariae, an « early stage » and a « completely developed » larva in the life-cycle of a Microphallid Trematode in Alaska. Cable (1963) recognized the « early stage » as a typical Microphallid and the « completely developed » stage as a distinct species related to *C. caribbea XXXII* and *C. caribbea XXXIII*. On geographical and other grounds he eliminated

hosts other than birds and of the known Trematodes of birds, he predicated, p. 454, « it seemed possible that only renicolids could be adults of this widely distributed type of xiphidiocercaria ». Furthermore, he knew that Stunkard had found a similar cercaria in *Thais lapillus* on the New England coast and had obtained sexually mature specimens of *Renicola* by feeding encysted metacercariae of this species to herring gulls, *Larus argentatus*. Accordingly, the order *Renicolida*, suborder *Renicolata* and superfamily *Renicoloidea* were suppressed and the family *Renicolidae* was transferred to the order *Plagiorchiida*, superfamily *Plagiorchioidea*.

Cable (1963) accepted the possibility that certain species of *Renicola* may have xiphidiocercariae and others may have rhodometopous larvae. Citing evidence from other groups, especially a series of new species, *Cercaria opaca*, *Cercaria nubeculata* and *Cercaria ingentis* described by Holliman (1961), Cable recognized loss of the stylet and progressive increase in the extent of the excretory vesicle. Accordingly, he devised a diagnosis of the renicolid cercariae. It presumes that the family embraces cercariae with stylets ; short, simple tails ; simple excretory vesicles and diverse flame-cell formulas ; together with magnicercous, even zygocercous cercariae, without stylets ; and complex excretory systems in which the vesicles exténd the length of the body and in which the stem and arms bear branched diverticula. It admits that cercariae with stylets encyst in Mollusks and mature in shore-birds while those of the rhodometopous type lack stylets, encyst in Fishes, and mature in Birds that feed off-shore.

LIFE CYCLES

Stunkard (1964) published the results of a five-year investigation of the genus *Renicola*. The plagiorchid cercariae from *Thais lapillus* encysted in the gills, walls of the suprabranchial chambers, mantle and foot of bivalve Mollusks, especially *Mytilus edulis*, *Aequipecten irradians*, and *Gemma gemma*. Metacercariae of this species matured in the renal tubules of *L. argentatus* and were described as a new species, *Renicola thaidus*. This was the first experimentally proved life-cycle in the family and confirmed the transfer of the *Renicolidae* to the *Plagiorchiida*.

After the description of the successive stages in the life-history of *Renicola thaidus*, Stunkard (1964) reported, p. 486, « The cercariae from *Thais lapillus* and *Thais lamellosa* are very similar to *Cercaria parvicaudata* Stunkard and Shaw, 1931 from *Littorina littorea*, *Littorina saxatilis* and *Littorina obtusata* taken at Woods Hole, Massachusetts and *Cercaria roscovita* Stunkard, 1932 from *Littorina saxatilis nigrolineata* taken on the Brittany coast near Roscoff, France. The resemblance is striking, particularly in the development and structure of the excretory system as reported for *C. parvicaudata* by Stunkard (1950). » This similarity suggested the possibility that *C. parvicaudata* may be the larval stage of a renal parasite. Accordingly, in the summer of 1965 the study of *C. parvicaudata* was resumed. The cercariae were found in all three species of *Littorina ;* they encysted in the snails from which they had emerged, in other snails of the same genus, and in the bivalves, *Mytilus edulis* and *Pecten irra-*

dians. On June 25, a small gull was fed two *L. saxatilis* and two *M. edulis* that had been exposed since June 18 to the cercariae from two shedding *L. saxatilis.* The bird was autopsied on July 6, and no worms were recovered from the kidneys. A second gull was fed on July 20, three *M. edulis* that had been exposed to *C. parvicaudata* from three *L. saxatilis* since July 2. This bird was autopsied on August 9, and no worms were recovered. A third gull, fed August 6 on three *L. saxatilis,* one *L. littorea* and two *M. edulis* that had been exposed since July 19 in a bowl with two shedding snails, was dissected on August 18 and no worms were found in the kidneys. These negative results indicated that *C. parvicaudata* is not the larva of a renal parasite and attention was directed to other species, especially to members of the family *Notocotylidae.*

Other Plagiorchid cercariae have been identified as larvae of Renicolid Trematodes. Stunkard and Shaw (1931) described *Cercaria parvicaudata* from *Littorina littorea* taken at Woods Hole, Massachusetts. Stunkard (1950) published a further study of *C. parvicaudata* and reported the close resemblance between this species and *Cercaria roscovita,* a species he (1932) had described from *Littorina saxatilis nigrolineata* at Roscoff on the Brittany coast of France. The cercariae are very similar morphologically, have the same excretory pattern and Stunkard predicated, p. 142, « Except for the difference in color of the sporocysts, the two species are almost identical. ...The general structure of the two species, and especially the details of the excretory system, suggest that they are not only closely related but that they are probably members of the family *Plagiorchiidae.* Since the members of this family are rare or unknown in marine fishes, and occur frequently in Birds and Mammals, it is probable that some Bird or Mammal which frequents the seashore is the final host of *Cercaria parvicaudata.* » As noted, after the elucidation of the life-cycles of *Renicola thaidus,* thousands of metacercariae of *C. parvicaudata,* were fed during the summer of 1965 to gulls, with only negative results. Failures are ordinarily not reported, which in this instance was fortunate.

James (1968) described ten species of Trematode larvae from intertidal Prosobranch Mollusks in Cardigan Bay on the Welsh coast. A species from *Littorina neritoides* and *L. saxatilis* was identified as *C. roscovita.*

Werding (1969) reported *C. roscovita* from *Littorina littorea* taken on the North Sea coast near Helgoland. He found the cercariae encysted in the same host and in other Mollusks of the area. When fed to gulls, *L. argentatus,* the metacercariae developed in the kidneys to mature worms that were described as *Renicola roscovita* (Stunkard, 1932) n. comb. Descriptions of the sporocysts, cercariae, metacercariae and adults supported the taxonomic determination. Agreement with the description of *C. roscovita* confirmed the specific identity. Werding noted that Stunkard (1950) had published a redescription of *C. parvicaudata* and compared that species with *C. roscovita.* Commenting on the general agreement Werding stated, p. 321. « Da sich in der Morphologie und im Verhalten der von mir gefunden Cercarien keine Unterschiede zu den von Stunkard (1950) beschriebenen Arten finden lassen, die Farbe der Sporocysten aber ein äusserst variables Merkmal ist, ist nicht auszuschliessen, dass es sich bei allen erwähnten Funden um ein und dieselbe Art handelt. In diesem Falle wäre

Cercaria roscovita ein Synonym für *C. parvicaudata.* ». Werding also referred to possible identity between *R. roscovita* and *R. thaidus.*

Robson and Williams (1970) reported a plagiorchid cercaria from *Littorina littorea* collected from Scalby Rocks, Scarborough, on the Yorkshire coast of England. It was described and designated *Cercaria A.* They noted close resemblance to *C. parvicaudata* and *C. roscovita* but until a definite identification with one of these or with an adult stage has been made, preferred to refer to the xiphidiocercaria as *Cercaria A.* They noted, p. 163, « The cercaria encyts readily in species of *Littorina* and *Carcinus maenas* but attempts by us to infect juvenile herring gulls, ducklings, chicks and various laboratory mammals failed. »

The account of Werding made renewed study of *C. parvicaudata* imperative. Accordingly, infected *L. littorea* were collected beginning in June 1970 from the Wee Pecket Islands in Buzzards Bay, which harbor rookeries of cormorants and gulls. These snails, shedding *C. parvicaudata,* were placed three in each finger bowl with specimens of *Mytilus edulis* or *Aequipecten irradians* for several days. The bivalves were then replaced by others, so a large number of metacercariae become available for experimental feeding of birds. Six newly hatched gulls, *L. argentatus,* and three cormorants, *Phalacrocorax auritus,* were taken from the Wee Pecket rookery and two « white egrets », (juvenile phase of the little blue heron, *Florida caerulea*), and one black-crowned night heron, *Nycticorax nycticorax,* were collected from the rookery on Martha's Vineyard Island. All were fed thousands of metacercariae at intervals during the summer in the attempt to obtain a sequence of developmental stages in the renal tubules. The birds were autopsied at different times, the herons and the last two gulls in late September, some three months after the first feeding of metacercariae. No Renicolid eggs were recovered from droppings during the summer and no worms were found at autopsy. Possibly some other bird, one of the sand pipers, may be the natural host.

The cercariae of *R. thaidus* and *R. roscovita* are very similar to *C. parvicaudata,* but the three are probably distinct. All are referable to the plagiorchid type ; they are small, with simple tails ; small stylets ; well developed digestive tracts ; simple Y-shaped excretory bladders with short arms ; and with the flame-cell formula 2[(3 + 3 + 3) + (3 + 3 + 3)]. The rhodometopous cercariae have long been regarded as larvae of the Renicolid Trematodes but they are very different from the cercariae of *R. thaidus* and *R. roscovita.* The characteristic features of *C. rhodometopa* are listed earlier in this report. The inclusion of such utterly diverse types in a single genus is not in accord with present concepts of genetic unity and only further information can resolve the dilemma. Discovery of the life-cycle of the type species, *R. pinguis,* would aid in resolution of the problem.

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