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Research Note

Taxonomy and Life Histories of Two North American Species of "Carneophallus" (=Microphallus) (Digenea: Microphallidae)

Digeneans from North American coastal waters referred to as Carneophallus spp. summon attention because they infect commercially important crustaceans, constitute potential public health hazards, and present taxonomic problems.

The nomenclature and taxonomy of worms placed into the genus Carneophallus Cable and Kuns, 1951 are not clearly defined. Bridgman (1969, Tulane Stud. Zool. Bot. 15:81–105) described the two species to which we direct most of our concern as C. basodactylophallus Bridgman, 1969 and C. choanophallus Bridgman, 1969. The type locality for both is the Mississippi River estuary. Later, Deblock (1971, Bull. Mus. Nat. Hist. Nat. 3ª Ser., Zool. 7:353–468) considered the former species as Microphallus basodactylophallus and the latter as a junior synonym of M. turgidus (Leigh, 1958). Even though he and Capron, Deblock, and Biguet (1957, Bull. Soc. Zool. Fr. 82:378–392) considered Carneophallus a junior synonym of Microphallus Ward, 1901, we regard the name valid for at least the type species, C. trilobatus Cable and Kuns, 1951, on the basis of the copulatory papilla being deeply lobed, partially banded by small papillae, and penetrated by the male duct, which opens through one of the lobes. Perhaps some or all of the several remaining species that have been placed in Carneophallus should be transferred to Spelotrema Jägerskiöld, 1901, with Spelophallus Jägerskiöld, 1908 as a junior synonym, rather than to Microphallus which, in fact, may be monotypic for M. opacus (Ward, 1894). No agreement concerning generic position of those species has been reached.

The range of Microphallus basodactylophallus extends at least from the coastal marshes of the Chesapeake Bay area to Louisiana and Texas. We have examined specimens of M. basodactylophallus from the Chesapeake Bay area, apparently conspecific with those referred to as Megalophallus sp. by Perkins (1971, J. Parasitol. 57:9–23) and Couch (1974, J. Invertebr. Pathol. 23:389–396), as well as specimens from Galveston, Texas, presumably conspecific with those reported as "similar to Spelotrema nicoli" by More (1969, Tex. Parks Wildl. Dep. Tech. Ser. 1:1–31). Actually, the species may extend to Costa Rica or further south and prove to be a junior synonym of M. skrjabini (Caballero, 1958).

Microphallus turgidus is known from New Jersey (Heard, 1970, Proc. Helminthol. Soc. Wash. 37:147–153) to Louisiana, and probably has a range similar to that of M. basodactylophallus. We follow Deblock (1971, loc. cit.) in considering M. choanophallus a junior synonym of M. turgidus because (1) the anatomy is similar for both taxa, (2) M. choanophallus uses several hydrobiid hosts, including Litterodinops monroensis (Frauenfeld), in common to both Gulf and Atlantic coasts, (3) Palaemonetes pugio is the principal crustacean hosts for both taxa, and (4) migratory birds serve as final hosts for both. Still, experimental cross-infection studies among and between Atlantic and Gulf of Mexico forms should be conducted to see if physiological races or sibling species occur.

Life histories of both digeneans include many more hosts than noted by Bridgman (1969, loc. cit.). He reported the cercaria of M. basodactylophallus to de-
velop in a spined form of *Lyrodes parvulus* Guilding (=*Pygophorus* p.), penetrate the blue crab, *Callinectes sapidus* Rathbun, and become a metacercaria infective to the raccoon, *Procyon lotor* (Linnaeus), and laboratory mice and rats. Heard (1967, M.S. Thesis, Univ. Georgia) noted *Hydrobia* sp. and *C. sapidus* as hosts for *Carneophallus* sp. (=*M. basodaetylophallus*) in coastal Georgia, and Kinsella (1974, Am. Mus. Novit. No. 2540. 12 pp.) listed *Uca* spp. as hosts from Cedar Key, Florida. We infected the blue crab with cercariae of *M. basodaetylophallus* from *Litterodinops palustris* Thompson from Jackson County, Mississippi, and Cedar Key in Levy County, Florida; from *Onobops jacksoni* (Bartsch) from Jackson County, Mississippi; and from two undescribed species of *Heleobops*, one from Horn Island, Mississippi, Little Dauphin, Alabama, and St. Marks Wildlife Refuge in Wakulla County, Florida, and the other from the same locality in Florida. Near Grand Isle, Louisiana, *Litterodinops monroensis* was infected. We additionally observed the presumed metacercariae in the digestive gland of *Uca longisignalis* Salmon and Atsaiades and *U. minax* (Le Conte) from Mississippi, Alabama, and Florida and of *U. minax* and *U. pugnax* (Smith) from Georgia. The marsh rice rat, *Oryzomys palustris* (Harlan), was as good a natural definitive host as the raccoon for *M. basodaetylophallus*. We successfully used the outbred albino mouse (COBS® CD®—1 stock) as the experimental host throughout our study.

Bridgman reported the cercaria of *C. choanophallus* (=*M. turgidus*) from the "unspsined form of *Lyrodes parvula*" (=*Pygophorus* p.) to infect *Palaemonetes pugio* Holthuis and *Macrobrachium ohione* (Smith), which in turn infected the raccoon, Norwegian rat, and six experimental mammals. Previously, Heard (1967, loc. cit.) reported *Hydrobia* sp., *P. pugio*, *Rallus longirostris* Boddaert, and unnamed birds as hosts in Georgia. We observed developmental stages in *Litterodinops palustris* in Jackson County, Mississippi, Little Dauphin Island, Alabama, and Cedar Key, Florida; *L. monroensis* on Horn Island, Mississippi; and *L. tenuipes* (Couper) and *L. monroensis* from North Carolina to southeastern coasts of Florida. We observed the metacercaria in the abdominal musculature of *Palaemonetes pugio*, *P. vulgaris* (Say), *P. paludosus* (Gibbes), *Macrobrachium ohione*, and *Penaeus setiferus* (Linnaeus). Moreover, we experimentally infected *P. setiferus* with cercariae from *L. palustris* and *P. pugio* with cercariae from that snail and *L. monroensis*. Rather than mammals being the primary definitive hosts, our observations suggest that aquatic birds may be more important, supporting a hypothesis advanced by Yamaguti (1975, *A Synoptical Review of Life Histories of Digenetic Trematodes of Vertebrates*. Keigaku Publ. Co., Tokyo. 1029 pp.). In Mississippi, we found the digenean infecting the red-breasted merganser, *Mergus serrator* Linnaeus; bufflehead, *Bucephala albeola* (Linnaeus); common goldeneye, *B. clangula americana* (Bonaparte); eastern green heron, *Butorides virescens virescens* (Linnaeus); little blue heron, *Florida caerulea caerulea* (Linnaeus); willet, *Catoptrophorus semipalmatus* (Gmelin); and clapper rail, and it probably infects many other birds. It often occurs in large numbers; we found over 2,000 adults of *M. turgidus* in one merganser.

Flame cells and cephalic glands are often difficult to observe. Whereas Bridgman (1969, loc. cit.) reported a flame cell formula of \(2[(1+1) + (1+1)] = 8\) and two pairs of "penetration" glands in cercariae of both *M. basadoctylophallus* and *M. turgidus*, we observed a formula of \(2[(2+2) + (2+2)] = 16\) and four pairs
of glands of two types differing in size and location, as has become generally accepted as typical of microphallid cercariae (Fig. 1). Two pairs of larger glands posterolateral to the oral sucker narrow anteriorly as ducts that turn inward at about midlevel of the oral sucker and open at well-separated ventrolateral pores. Weak staining of these glands after forming a penetration cyst indicates their functioning in that process. Cercariae of both species form penetration cysts on the gills immediately after they attach and shed their tails (Figs. 2–3). If properly positioned, the penetration cyst allows rapid entrance into the lamellar sinus by the cercaria. Probably incorporated into the life history of many related microphallids, it is rarely reported (e.g., called pseudocyst by Prevot [1974, D.S. Thesis, Univ. Droit, Marseille] and penetration cyst by Helluy [1982, Ann. Parasitol. 57:263–270]). The other two pairs of glands lie slightly posterior to the midbody level, are smaller than the anterior glands, and take a much lighter stain with neutral red. Their ducts are narrower and extend anteriorly farther than those of the larger glands and open close together nearer the stylet. Because the posterior glands remain unchanged until encystment begins, they probably contribute to that process.

Our attempts to obtain *P. parvulus* from near the mouth of the Mississippi River where Bridgman collected snails proved unsuccessful, not allowing us to compare cercariae from those snails with the cercariae we describe. We, however, did collect infected *L. monroensis* and *L. palustris* from that area.

Behavior of the two species differs. The cercaria of *M. turgidus* swims faster
Figures 2–3. Penetration cysts. 2. Cysts of *Microphallus basodactylophallus* attached to a glass slide, showing encased larva and detached cercarial tail. 3. Cyst of *M. turgidus* on gill lamella of *Palaemonetes pugio* with underlying cercaria (arrow).

and more erratically than the larva of *M. basodactylophallus*, which stops periodically. Both species, however, stop if disturbed, such as when encountering respiratory currents of potential hosts, thereby allowing them to be swept into the branchial chamber of the host to penetrate the gills.

In heat-killed cercariae of *M. basodactylophallus* from *Litterodinops monroensis* near Grand Isle, Louisiana, the body measured 86–92 μm long by 38–40 μm wide, the tail 80–92 μm long, and the stylet 17 μm long. The entire stylet is easy to see in living specimens, but only the more heavily sclerotized portion 15 μm long is distinct in heat-killed specimens. The thin-walled metacercarial cysts averaged 233 (220–245) μm across at both 40 and 67 days. The metacercariae became infective at 25–30 days. Specimens in the blue crab for 40 days developed in mice and started discharging eggs within 48 hr.

In heat-killed cercariae of *M. turgidus* shed by *L. palustris* from Ocean Springs, Mississippi, the body measured 76–80 μm by 38–44 μm, the tail measured 80–90 μm long, and the stylet length appeared 15 μm in fixed material and 18 μm in fresh specimens. The tail detached when the cercaria attached to the gill lamella and produced the penetration cysts. The cyst averaged 62(53–75) μm long by 41(39–43) μm wide by 36(34–40) μm high. After entering the circulatory system, the body could be seen rotating irregularly along the major vessels. By 18 hr postexposure, most of the worms lodged in the hepatopancreas and abdominal musculature and started developing a cyst wall. By 21 days, the metacercaria was infective, and after 30 days, its vitelline follicles became more compact and its cyst wall thicker. A 30-day-old metacercaria placed in 0.85% saline at 39–40°C began to produce eggs within 8 hr. In grass shrimps, the cyst had a thick, laminated, outer layer of host origin. The cyst from *Palaemonetes pugio* measured 278–420 μm long by 222–333 μm wide including that outer layer; without it, the cyst measured 247–290 μm by 203–222 μm. The relatively thin-walled cyst in the white shrimp at 46 days measured 320 by 220 μm.

Limited data on blue crab infections with *M. basodactylophallus* suggest that the cercaria from *Litterodinops palustris* encysts only in the thoracic ganglion. The cercaria of *M. basodactylophallus* from other snails encysts mostly in the hepatopancreas, but it often passes through the circulatory system and lodges within the somatic musculature. Because of the potential harm to the blue crab fishery from neurological infections, we recognize the need to see if different forms exist by infecting a variety of snails with eggs from adults originating both
from *L. palustris* and crab nervous tissue and from other snails and crab hepatopancreas. In any event, a heavy infection with metacercariae of either species from any source can kill the crab or shrimp hosts.

In addition to possibly harming the crustacean host, either digenean might also be able to harm man. *Microphallus brevicaeca* (Africa and Garcia, 1935) (syn. *Carneophallus b.*) has been implicated in adverse and fatal involvement of the heart, spinal cord, and other vital organs of people in the Philippines (e.g., Africa, Leon, and Garcia, 1937, Philipp. J. Sci. 62:393–399). Even though crustaceans have not been eaten raw historically in the United States as they have in the Philippines, recent innovations in cuisines give Americans the opportunity to eat more raw or minimally cooked shrimps and crabs.

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