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## The identification and characteristics of *Echinoparyphium rubrum* (Cort, 1914) comb. new (Trematoda, Echinostomatidae) based on experimental evidence of the life cycle

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Abstract. The life cycle of Echinoparyphium rubrum (Cort, 1914) comb. n. has been completed experimentally. All of the developmental stages – egg, miracidium, sporocyst, mother and daughter rediae, cercaria, metacercaria, and adult – were examined and described. The miracidia infected freshwater snails of the genus Physa, P. gyrina and P. occidentalis. Attempts to infect snails of the genera Lymnaea, L. auricularis, L. peregra, L. truncatula and Bulinus, B. truncatus failed. Cercariae infected various pulmonate and prosobranch freshwater snails, mussels, frogs, water turtles and planarians. The adults developed in the small intestine of birds and mammals. The identity

and major characteristics of Echinoparyphium rubrum are discussed. Synonyms of E. rubrum are Cercaria rubra Cort, 1914; Cercaria biflexa Faust, 1917; Cercaria chisolenata Faust, 1918; Echinostoma callawayensis Barker et Noll, 1915; Echinostoma revolutum of Johnson (1920); Echinoparyphium elegans of Cannon (1938), of Bain and Trelfall (1977), of Mahoney and Trelfall (1977); and Echinoparyphium recurvatum of Jilek (1977), Harley (1972), Sankurathri and Holmes (1976). Comparisons are made between E. rubrum and its 43-collar-spined allies: E. flexum from North America, E. cinctum from Europe, E. dunni from Asia and E. elegans from Africa.

Key words: Echinoparyphium rubrum, Echinostomatidae, life cycle, identity

#### Introduction

Kanev 1990 published a checklist of the genus *Echinoparyphium* Dietz, 1909, containing a list of 151 species names. Approximately 45 names representing adult worms possessing 43-collar-spines, most of which are incompletely described and their life cycles are unknown. Only a few species are examined and described in detail. Among them are *Echinoparyphium elegans* (Looss, 1899), which is the type species of the genus *Echinoparyphium* 

and *Echinoparyphium cinctum* (Rudolphi, 1803), which is the oldest species within the genus.

Mouahid and Mone 1988 examined *E. elegans* (Looss, 1899) and found severe discrepancies and problems in the current interpretation of its identity, synonyms and characteristics. Similar discrepancies were found by Kanev et al. (1994) for *E. cinctum* (Rudolphi, 1803).

This paper presents the life cycle of a North American, 43-collar-spined *Echinoparyphium* trematode, as determined experimentally, and provides morphological de-

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scriptions for all the life cycle stages of this echinostome. Based upon these characteristics, synonymy among 43collar-spined echinostomes within North America is discussed.

#### Materials and methods

The Echinoparyphium life cycle stages used in this research were originally isolated from *Physa gyrina* snails collected from Douglas Lake, Michigan, and near Ann Arbor, Michigan. These snails shed cercariae possessing 43-collar-spines. Cercariae and metacercariae with 43-collar-spines were found in 29 of 975 physid snails from Necitah and Devil's Lake, Wisconsin. Metacercariae with 43-collar-spines were found in 2 of 206 naturally infected *Physa occidentalis* snails collected in Golden Gate Park, San Francisco, CA. In addition, metacercariae with 43-collar-spines were isolated from 8 of 16 Lymnaea elodes collected in northeastern Indiana. All sources were used for comparative examination and identification purposes. In this paper descriptions and measurements are based on materials from Michigan.

Adult worms were obtained by feeding the metacercariae to 9 laboratory-raised golden hamsters (*Mesocri*cetus auratus), 18 rats (10 Rattus rattus and 8 R. norvegicus), 10 mice (*Mus musculus*), 8 ducks (*Anas platyrhyn*chos dom.), 7 geese (*Anser anser* dom.), 12 chickens (*Gallus gallus* dom.), 4 pigeons (*Columba livia*), and 5 pheasants (*Phasianus colchicus*).

Eggs were collected by washing the feces of infected hamsters. The eggs when incubated in tap water at 28°C yielded miracidia within 10 days. The miracidia were used to expose the following snails species: 100 *P. gyrina* and 86 *P. occidentalis* from USA, 20 Lymnaea auricularia, 80 L. peregra and 112 L. truncatula from Europe, and 120 Bulinus truncatus from Africa. All of the snails were laboratory-raised and uninfected at the time of exposure.

Several species of animals were tested as experimental, second-intermediate hosts. These included 30 specimens of the freshwater snails Helisoma trivolvis, 27 Physa gyrina, 15 P. heterostropha, 12 P. occidentalis, and 25 P. parkeri from the USA and 46 Planorbarius corneus, 30 Planorbis planorbis, 15 Physa acuta, 16 P. fontinalis, 30 Lymnaea stagnalis, 16 L. palustris, and 52 L. truncatula from Europe, along with 6 frogs, 2 Rana temporaria and 4 R. ridibunda, 2 water turtles, Emys orbicularis and 30 planarians (*Planaria* sp.).

For identification of parasites examined we used adults and larvae from the USA, which were described with features similar to these of *E. rubrum*. To avoid repetition, their names, hosts and places of collections are described in the Results, "Identification of parasites examined".

Methods employed throughout this study were similar to those described in Vassilev and Kanev (1984a, b). Figures were drawn with the aid of a camera lucida. All dimensions, except where noted otherwise, are measured in micrometers.

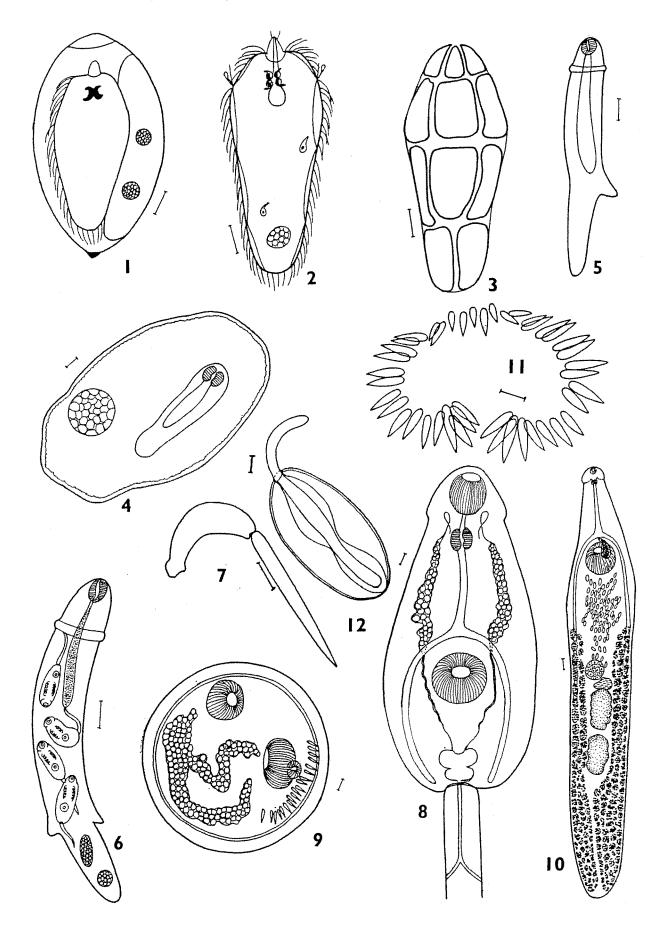
#### Results

#### The life cycle of parasite examined

Egg (Fig. 1). Eggs leave the mature worm in an uncleaved condition. They are oval, yellow-brown in color. Measurements, based on 50 eggs, 85-125 by 60-80 in size. The operculum is 30-40 broad and a thickened area is present at the non-operculate end of the egg shell. Fully developed miracidia appear within 10-11 days when eggs are kept at  $28^{\circ}$ C in tap water.

Miracidia (Figs. 2 and 3). Hatching may begin as early as the tenth day but usually occurs around the 12th day. Light stimulates hatching. Miracidia penetrate any exposed part of Physa gyrina and P. occidentalis snails from the USA. Attempts to infect Lymnaea auricularia, L. peregra and L. truncatula from Europe and Bulinus truncatus from Africa with large numbers of miracidia were unsuccessful. Measurements based on 50 specimens, fixed in hot  $(70^{\circ}C)$  2% silver nitrate showed 80–110 by 50–65; whereas, those alive in egg albumen were 95-115 by 38-60. Apical papilla 12 by 6, with two pairs of setae being present. The body was covered with four rows of ciliated epidermal plates. The anterior (first) row contains six triangular plates: two ventral, two dorsal, and two lateral (one on each side). The second row consists of six square plates: three dorsal and three ventral. A third row possesses four rectangular plates: two lateral, one dorsal and one ventral. The posterior row has two subtriangular plates.

Figs. 1-12. Echinoparyphium rubrum: 1 - egg with fully developed miracidium, showing operculum and thickening at the opposite end of the shell; scale bar = 10 µm. 2 - miracidium dorsal view, showing cilia, lateral processes, apical papilla, eyespots, and flame cells; scale bar = 10 µm. 3 - miracidium, showing epidermal plates; scale bar = 10 µm. 4 - sporocyst containing one redia and germ ball; scale bar = 5 µm. 5 - first generation redia, about 12 days post infection, showing pharynx, gut, collar, and locomotor organs; scale bar = 50 µm. 6 - redia 33 days post infection, showing cercariae and germ balls, pharynx, gut, collar, locomotor organs; scale bar = 200 µm. 7 - cercaria, lateral view of body and long cylindrical tail with conical tip; scale bar = 100 µm. 8 - cercaria, ventral view, showing structures of oral and ventral suckers, head collar, pharynx, oesophagus, caeca, main excretory ducts, bladder, and caudal excretory tube and its bifurcation; scale bar = 20 µm. 9 - metacercarial cyst, with visible parts of ventral and oral suckers, collar spines, excretory granules, and pharynx; scale bar = 10 µm. 10 - adult worm, showing general morphology in ventral view; scale bar = 150 µm. 11 - collar spines in the adult worm; scale bar = 75 µm. 12 - cirrus pouch; scale bar = 50 µm



Body covered with cilia 15 long. Two lateral processes are 5 long. The penetration gland is pyriform, 2. Two eyespots are composed of dark-brown pigmented bodies about 5 in diameter. Two flame cells are present; the right one is dorsal and anterior, the left one being ventral and posterior. Two excretory pores are visible between the third and fourth rows of epidermal plates. Germinal cells are located in the posterior half of the body.

Sporocyst (Fig. 4). After 24 hours sporocysts are 85 long by 50 wide, resembling miracidia but lacking plates. After 2-3 days, they migrate to their permanent location, generally in the mantle ridge or occasionally the atrium and ventricle of the heart. Young sporocysts, 3-8 days old, are sac-like, elongated and colorless. Measurements, based on 30 sporocysts, 9-15 days old, are 110-180 by 60-110 and sporocysts contain from one to three rediae and numerous germ balls. Old sporocysts beyond 30 days were empty, shriveled and gray or yellowish-gray in color.

Redia (Figs. 5 and 6). The first rediae were found 8 days after infection of the snails. They were located along the renal and pulmonary veins flanking the kidney and occasionally along the venous sinuses in the dorsal ridge. The young rediae are colorless and possess a conspicuous collar and locomotor organs. Measurements, based on 50 rediae, 10-12 days old, fixed in a hot (70°C) 2% silver nitrate solution showed: body 160-720 long by 60-110 wide; pharynx 30-60 wide; gut 50-90 long; collar 80-90 from the anterior end of the body; locomotor processes 100-150 from the posterior end of the body. Fifty rediae, obtained from the hepatopancreas of snails 30 days after infection, fixed in hot water and measured under the cover glass showed: body 970-3900 long by 120-390 wide; pharynx 60-80 in diameter; collar 120-240 from the anterior end; birth pore dorsal and immediately posterior to collar; gut short and about two or three times larger than the pharynx. Each redia contained from 1 to 25 fully developed cercariae. Old rediae with dark gray bodies and orange-colored intestines were found 25 days post infection.

Cercaria (Figs. 7 and 8). Measurements, based on 50 specimens following fixation in hot (70°C) 5% formalin showed: body 380-550 long by 100-180 wide; head collar 80-150 wide armed with 43-collar-spines, about 11 long. The arrangement of collar spines is as in the adult worms. The body surface was covered with minute tegumentary spines averaging 3-5 long. At the anterior part of the body these spines are bigger and conspicuous and became less prominent toward the posterior end. Oral sucker oval, subterminal, 35-52 long and 30-50 wide; prepharvnx up to 30 long. Pharynx 15-28 long by 15-25 wide. Oesophagus 100-190 long, consisting of approximately 12 to 16 poorly visible cells; bifurcation anterior to the ventral sucker; caeca blind, extend to the posterior of the body. Ventral sucker oval, postequatorial 56-90 long by 60-90 wide. Cystogenous cells oval to spherical in shape, 15-20 in diameter, were found throughout the body; only a few

were proximal to the oral sucker and pharynx. These cells contained ovoid granules 2.5 long by 1 wide. Many gland cells were located round the oesophagus. They were connected to weakly visible ducts and outlets on the ventral surface of the dorsal lip region of the oral sucker. Genital primordia consist of two cell masses, one at the anterior margin of the ventral sucker and the other between the ventral sucker and excretory bladder, both connected by a string of cells passing dorsally to the acetabulum. The stenostome excretory system possessed approximately 90 flame cells. Their exact number was difficult to count because they are covered by numerous cystogenous cells. A large excretory bladder, 25-45 long and 30-50 wide was located in the posterior region of the body. The main collecting channels were located between the ventral sucker and the pharyngeal levels. They contained numerous excretory granules that were up to 5 in diameter around the central portions and 2-3 at the ends. A caudal excretory tube extends one-fifth of the tail-length before bifurcating into two lateral branches. Tail cylindrical, with a conical tip, 390-560 long and 30-65 wide. No finfolds on the tail surface. In laboratory infections, the first cercariae were obtained 28-30 days after snails were exposed to miracidia.

Metacercaria (Fig. 9). Measurements, based on 50 specimens showed: cysts, spherical and subspherical in shape, 142-170 in diameter; cyst wall of two layers - an inner, opaque, layer about 3-4 thick and outer, transparent, layer about 12 thick. Various morphological structures, such as parts of the collar spines, excretory granules, oesophagus, and caeca are visible through the cyst wall. In experimental infections, cercariae penetrated and developed into metacercarial cysts in various second-intermediate hosts. Metacercariae were found in the pericardial sac and posterior kidney region of freshwater snails Helisoma trivolvis, Planorbarius corneus, Planorbis planorbis, Physa gyrina, P. fontinalis, P. acuta, P. heterostropa, P. occidentalis, P. parkeri, Lymnaea stagnalis, L. palustris, and L. truncatula freshwater snails, as well as, the kidney and eye cavity of frogs Rana temporaria and R. ridibunda, turtles Emys orbicularis and planarians (Planaria sp.).

Adult (Figs. 10, 11 and 12). Examination of 30 specimens ranging in age from 20–25 days, obtained from golden hamsters, showed: body 3800-6800 long and 450-970 wide; body spines up to 30 long; collar reniform, 350-520 broad, armed with 43 conspicuous collar spines arranged as follows: 4 corner spines (measuring 76–121 long and 12–18 wide) located on each ventro-lateral side of the head collar; 4 single spines of similar size (50–96 long and 10–14 wide) and shape are located on each lateral surface; 12 spines (6 oral – 46–87 long and 8–12 wide and 6 aboral – 60–100 long and 10–16 wide) extending on each dorso-lateral surface; and 3 remaining dorso-median spines (2 oral – 44–84 long and 8–12 wide and 1 aboral – 64–108 long and 10–16 wide) produce the odd number of collar spines; oral sucker subterminal, 125–180 in diame-

ter; prepharynx 180 long; pharynx 100-160 long by 70-120 wide; oesophagus 450-800 long; bifurcates anterior to the acetabulum; caeca blind, extend almost to the posterior end of the body; ventral sucker spherical, in anterior half of the body, 320-650 in diameter; genital pore median, preacetabular, followed by the genital atrium; testes, oval smooth or only slightly irregular in contour, located tandem at the mid-hindbody; the anterior testis 240-600 long and 150-410 wide; the posterior testis is slightly smaller 220-540 long by 130-350 wide; cirrus sac oval in shape, 280-660 long, extends postero-dorsally from the genital atrium to the middle of the ventral sucker; seminal vesicle and poorly developed pars prostatica present; cirrus cylindrical, unspined up to 350 when protruded; ovary spherical, or somewhat ovoid, 130-280 long by 120-250 wide, located pretesticular and intercaecal at the midbody region; a true seminal receptacle is absent; however, the uterine seminal receptacle was found to contain numerous spermatozoa; Laurer's canal opens medially on dorsal surface posterior to the ovary; a small vitelline reservoir and a diffuse Mehlis' gland are present; uterus short, intercaecal, postacetabular, preovarian, containing between 10 and 80 eggs; vitelline follicles exist lateral, dorsal, and ventral to the caeca and run from about halfway between the ventral sucker and the ovary to near the posterior end of the worm, although sometimes they coalesce dorsally posterior to the testes; excretory bladder uncoiled, Y-shaped with an excretory pore terminating at the posterior extremity. In experimental infections adult worms were obtained from various birds: Gallus gallus dom., Anas platyrhynchos dom., Anser anser, Columba livia, and Phasianus colchicus, and mammals, Mus musculus, Rattus norvegicus, R. rattus, and Mesocricetus auratus. Worms were located in the small intestine-duodenum and jejunum. Specimens are available at HWML Helm., Col. slides Nos. 35349, 39462-39465, and at the Institute of Experimental Pathology and Parasitology, Bulgarian Academy of Sciences, Sofia, slides Nos. 1862-1864.

#### Identification of parasites examined

The parasite examined in this paper could be described in two different ways: in one way it could be considered to be a new species. In the second way, it could be considered to be a member of a preexisting species with adults and larvae that have already been found in North America but were misidentified. It seems to us that the second way is most likely true, because both adult and larval echinostomes have been examined and described in North America repeatedly over the last 100 years. Based on this suggestion we have conducted numerous comparative studies comparing this echinostome species with previously reported adult and larval echinostomes in the United States and Canada. The results are as follows:

Cercaria rubra. Cort (1914) described C. rubra from metacercariae found in naturally infected Campeloma sub-

solidum, collected in Connecticut. In its original description C. rubra is the first 43-collar-spined echinostomes found in North America. Therefore, C. rubra is the first and the original name given for 43-collar-spined echinostomes from North America. This suggested that in this study we have worked with adults and larvae that are identical with those described by Cort (1914) as C. rubra. In support of this suggestion is the fact that the original descriptions, measurements and illustrations of C. rubra by Cort (1914, 1915) show features that correspond to those described here for E. rubrum. Because of these similarities we prefer to consider the 43-collar-spined echinostomes described in this paper as E. rubra, instead of a new species.

Cercaria biflexa. Faust (1917a) described C. biflexa from naturally infected Physa gyrina and Planorbis trivolvis snails collected in Montana. In the original description, C. biflexa is presented with 42-collar-spines. We have counted 43-collar-spines in echinostome cercariae found in the same snail host (P. gyrina) collected in Michigan and Illinois. In their morphology, including the excretory system, the cercariae completely correspond to E. rubrum described herein. The adult worms obtained experimentally from rats infected with metacercariae from P. gyrina snails from Michigan correspond in morphology to those of E. rubrum. Therefore, C. biflexa is considered identical to E. rubrum.

*Cercaria chisolenata.* Faust (1917b, 1918) described *C. chisolenata* from cercariae from naturally infected *Physa gyrina* snails collected in Illinois. Faust counted about 40-collar-spines; however, our study on cercariae from the same snail host (*P. gyrina*) and the same state (Illinois) showed 43-collar-spines. In its morphology and biology, *C. chisolenata* corresponded to *E. rubrum*; therefore, we consider them identical.

Echinostoma callawayensis. Barker and Noll (1915) described E. callawayensis from a collection of adults from the muskrat Ondatra (Fiber) zibethicus from Nebraska. Beaver (1937) considered E. callawayensis identical with E. revolutum. In the same paper, Beaver (1937) concluded that the original descriptions and illustrations of E. callawayensis were made on a mixture of small adults of the genus Echinostoma, E. revolutum and Echinoparyphium sp. According to Beaver (1937) this explains why the collar spine numbers of Echinostoma callawavensis range from 37 to 41. Later, the validity of E. callawayensis was restored by Macy (1942) on adults experimentally obtained from rats fed with metacercariae from planarians Planaria sp. collected from a lake in Minnesota, where muskrats are abundant. Physa gyrina from the same locality were shown to be the first intermediate host. Based on Macy's (1942) descriptions, E. callawayensis was considered a valid species by Skryabin (1947, 1956) and Yamaguti (1958, 1971, 1975). Four slides of E. callawayensis deposited by Prof. R. Macy at the HWML Helm. Col., No. 23423 were examined by us.

These specimens possessed the same morphological features as those of E. rubrum and we consider them identical.

Echinoparyphium contiguum. Barker and Bastron (1915) described E. contiguum from a collection of adults found in muskrats also from Nebraska. In its original description E. contiguum has 37-collar-spines, but Beaver (1937) found that in the U.S. all specimens of the genus Echinoparyphium examined by him have more than 37collar-spines. The same results were found by one of us (I. Kanev) from adult worms of the genus Echinoparyphium from naturally infected birds and mammals from the U.S., including specimens from muskrats. Some of these worms possessed 43-collar-spines and morphological features corresponding to those of E. rubrum. We consider these worms identical. Some worms contained collars with from none to 43 spines, but the presence of a scar or empty space between the spines clearly indicated that some of the spines were lost or missing. Loss of one or more collar spines in adult echinostomes, including in the genus Echinoparyphium and Echinostoma were described by Lie (1963), Kanev (1985) and Kanev and Busta (1992).

Echinostoma revolutum. Johnson (1920) described as E. revolutum a 43-collar-spined cercariae and metacercariae found in naturally infected Physa occidentalis snails collected in California and 37-collar-spined adult worms from naturally infected birds in the same locality. These trematodes consisted of larvae of the genus Echinoparyphium and adults of the genus Echinostoma. This was discussed in detail by Kanev (1985, 1994). In addition, the larval stages described and illustrated by Johnson (1920) as E. revolutum are morphologically identical to those from E. rubrum described in this paper. Also, adults obtained experimentally by one of us (I. Kanev) from the 43-collar-spined cercariae from California were compared with E. rubrum described in this paper. No differences were found, and we consider them identical.

*Echinoparyphium* sp., collected by S. J. Taft from a naturally infected broad-winged hawk (*Buteo platypterus platypterus*) examined in Wisconsin and sent to HWML for identification (Col. Nos. 35569, 36314) contained specimens with morphological features that correspond with those of *E. rubrum*. We consider them to be identical.

Echinoparyphium sp., collected by one of us (M. Sterner) from red-tailed hawks (Buteo jamaicensis bornealis) and from a broad-winged hawk (Buteo platypterus platypterus) in Nebraska presented 53 specimens with 43-collar-spines and morphology that completely corresponded with that of *E. rubrum*, and we consider them to be identical.

*Echinoparyphium* sp., from North Carolina described by Fried et al. (1998) completely corresponded with that of *E. rubrum*, and we consider them to be identical. Fried et al. (1998) described ways of distinguishing species of *Echinoparyphium* from *Echinostoma trivolvis* based on cercarial and metacercarial characteristics. Other reported *Echinoparyphium* trematodes that show similarities and perhaps synonymy with *E. rubrum* include: *Echinoparyphium elegans* of Cannon (1938), of Bain and Threlfall (1977) and of Mahoney and Threlfall (1977) collected from naturally infected birds and mammals in Canada and the United States; and *Echinoparyphium recurvatum* as described by Jilek (1977), Harley (1972), Sankurathri and Holmes (1976), and from echinostome cercariae found in naturally infected *Physa gyrina* snails collected in Alberta, Canada.

#### Discussion

There are at least two species of the genus Echinoparyphium found in the United States. One, E. flexum (Linton, 1892), is a 45-collar-spined echinostome that uses lymnaeid snails as its first intermediate hosts. The life cycle of E. flexum has been completed experimentally by Najarian (1953, 1954). The second species is represented by adults and larvae possessing 43-collar-spines, uses physid snails as first intermediate hosts, and develops into adults within the intestinal tract of a variety of birds and mammals. The life cycle of this echinostome has been completed experimentally and is described in this paper. We named this species Echinoparyphium rubrum since the original description of Cercaria rubra by Cort (1914) takes precedence. E. rubrum differs from E. flexum in the number of collar spines and in the first intermediate snail host. Adult worms of both species are found in birds, but only those of E. rubrum develop in mammals.

Outside the United States, the genus Echinoparyphium is represented by several other species with 43-collarspines (Kanev 1990). One of them, E. cinctum (Rudolphi, 1803) is distributed in Europe and Asia. This species uses lymnaeid snails as first intermediate hosts. The adult worms develop only in birds, and the cirrus pouch possesses a long, coiled, seminal vesicle. Based on these features E. cinctum is easy to distinguish from E. rubrum and allied species (Kanev et al. 1994). The second species, E. elegans (Looss, 1899), is found in Africa and Sardinia and its larvae use bulinid snails as first intermediate hosts. Morphologically, E. rubrum is very similar to E. elegans suggesting that these echinostomes are closely related or may even be members of the same species. However, our inability to infect Bulinus truncatus snails from Africa with E. rubrum miracidia or conversely, physid snails with E. elegans miracidia suggest they are different species. For this reason, until more information is obtained, E. rubrum and E. elegans will be considered as distinct species. In Egypt two other echinostome species possessing 43-collarspines, named by Moravec et al. (1974) Echinoparyphium recurvatum and by Lie et al. (1975) E. ralphaudyi have been examined and their life cycles reported. Both are considered by Mouahid and Mone (1988) as synonyms of E. elegans, and for this reason they will not be discussed here. Another echinostome species with 43-collar-spines,

Echinoparyphium rubrum life cycle and identity

Echinoparyphium dunni, has been described from material in Malaya by Lie and Umathevy (1965). Kanev et al. (1994) considered *E. dunni* as a synonym of *E. cinctum*. *E. rubrum* differs from *E. dunni* in features similar to those discussed above for *E. cinctum*.

In this paper, the life cycle, the morphological details and host use patterns for *E. rubrum* in the United States has been worked out. The results obtained were used to compare this species with previously reported species in the USA and Canada.

According to similarities observed above among E. rubrum and earlier descriptions of other echinostomes from North America, the synonyms of E. rubrum are considered: Cercaria rubra Cort, 1914; Cercaria biflexa Faust, 1917; Cercaria chisolenata Faust, 1918; Echinostoma callawayensis Barker et Noll, 1915; Echinostoma revolutum of Johnson (1920); Echinoparyphium elegans of Cannon (1938), of Bain and Threlfall (1977), of Mahoney and Threlfall (1977); and Echinoparyphium recurvatum of Jilek (1977), Harley (1972), Sankurathri and Holmes (1976). Their final and intermediate hosts are considered to be hosts of E. rubrum.

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