Systematic Parasitology **28**: 125–144, 1994.

Life-cycle, delimitation and redescription of *Echinostoma revolutum* (Froelich, 1802) (Trematoda: Echinostomatidae)*

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Accepted for publication 7th January, 1993

Abstract

The life-cycle of *Echinostoma revolutum* (Froelich, 1802) Dietz, 1909 has been completed experimentally beginning with infected snails collected at the type-locality, near Erlangen, Germany. Based on the specimens obtained, each stage of the life-cycle has been redescribed. Important taxonomic features are discussed and hitherto unknown characteristics are described. Synonyms for *E. revolutum* are: *Fasciola revoluta* Froelich, 1802; *Echinostoma paraulum* Dietz, 1909; *E. audyi* Lie & Umathevy, 1965; and *E. ivaniosi* Mohandas, 1973. Adults and larvae described as *E. revolutum* in other works are found to be identical with *Echinostoma echinatum* (Zeder, 1803), *E. trivolvis* (Cort, 1914), *E. jurini* (Skvortsov, 1924), *E. caproni* Richard, 1964, *Moliniella anceps* (Molin, 1859), *Echinochasmus beleocephalus* (Linstow, 1873) and other echinostome species. For nearly a century, incorrect morphological, biological, life-cycle and host information has been attributed to *E. revolutum*, and at times these data have contributed to the diagnoses of the species. Occasionally, authors actually working with *E. revolutum* have ascribed their results to other species. Based on extensive experimental life-cycle studies beginning with infected snails from type-localities, it is shown that (1) the first intermediate host is a lymnaeid snail; (2) the second intermediate hosts are various pulmonate and prosobranch snails, mussels, frogs and freshwater turtles; (3) the final hosts are birds; (4) *E. revolutum* cercariae and adults have 37 collar spines; (5) the species occurs only in Europe and Asia; (6) *Cercaria echinata* Siebold, 1937, *Echinostoma echinatum* (Zeder, 1803) and *E. jurini* (Skvortsov, 1924) are the closely related 37-spined allies in Europe; and (7) species specific characteristics are expressed only in the larvae and the host-parasite relationships. The adults of *E. revolutum* cannot be identified using morphological criteria and it is proposed that worms with 37 collar spines belonging to the genus *Echinostoma* and occurring in naturally infected birds in Europe and Asia be referred to an "*E. revolutum* group."

Introduction

These studies are part of a programme involving the re-examination and redescription of members of the genus *Echinostoma* Zeder, 1800. *Echinostoma revolutum* (Froelich, 1802) Dietz, 1909 was re-examined first, as it is the type-species of genus *Echinostoma* and necessary as a standard for subsequent studies.

* Part of a Dissertation Thesis presented in Bulgarian (Kanev, 1985) and now additionally supplied with new data.

Materials and methods

Thirty-seven collar-spined cercariae being shed from naturally infected snails, *Lymnaea stagnalis*

(L.), collected near Erlangen in Germany, where Froelich (1802) found and described *Fasciola revoluta*, were used as a starting point for completing the life-cycle of *E. revolutum* from its type-locality. Metacercariae, obtained from the renopericardial sac of laboratory-bred, experimentally infected snails, *Physa acuta* (Draparnaud, 1801) and *Planorbarius corneus* (Dumeril, 1806) from Bulgaria, exposed to cercariae of *E. revolutum* from Germany, were fed to laboratory bred, uninfected chickens *Gallus gallus* dom. Moehring, pigeons *Columba livia* L. and ducks *Anas platyrhynchos* dom. L. Laboratory bred, uninfected snails, *L. stagnalis*, from Bulgaria were used as first intermediate hosts. Egg cultures for miracidia were obtained by washing the faeces of experimentally infected chickens. Techniques employed for collecting the parasite material and its fixation, staining and examination were the same as used in previous studies (Kanev, 1982a, 1985; Vassilev & Kanev, 1985; Kanev *et al.*, 1987).

The identity of *E. revolutum* is restored on re-examination of live material from its type-locality; on comparative studies of parasite specimens labelled as *E. revolutum* in private, Institute and Museum collections in Berlin, Vienna, Warsaw, Budapest, Prague, Moscow, Paris, Madrid, Alma-Atta, Hanoi, Vladivostok, Vilnius, Tbilisi and Sofia; on critical examination of both old and modern descriptions and illustrations published under the name of *E. revolutum*, including the original published (Fig. 1) by Froelich (1802); on comparative studies with adult and larval echinostomes collected in the same geographical regions and the same hosts from which Dietz (1909a,b, 1910), Johnson (1920), Lutz (1924), Beaver (1937), Supperer (1959), Zdarska (1964), Zajicek (1963), Vassilev & Kamburov (1972), Moravec *et al.* (1974), Rysavy *et al.* (1974), Nasincova (1986) and others have attributed their descriptions of adults and larvae to *E. revolutum*.

At least 100 specimens were measured for each stage of the life-cycle. All measurements in the text are in micrometres unless indicated otherwise. Figures were made with the aid of a camera lucida unless indicated otherwise.

The life-cycle of *Echinostoma revolutum* in its type-locality

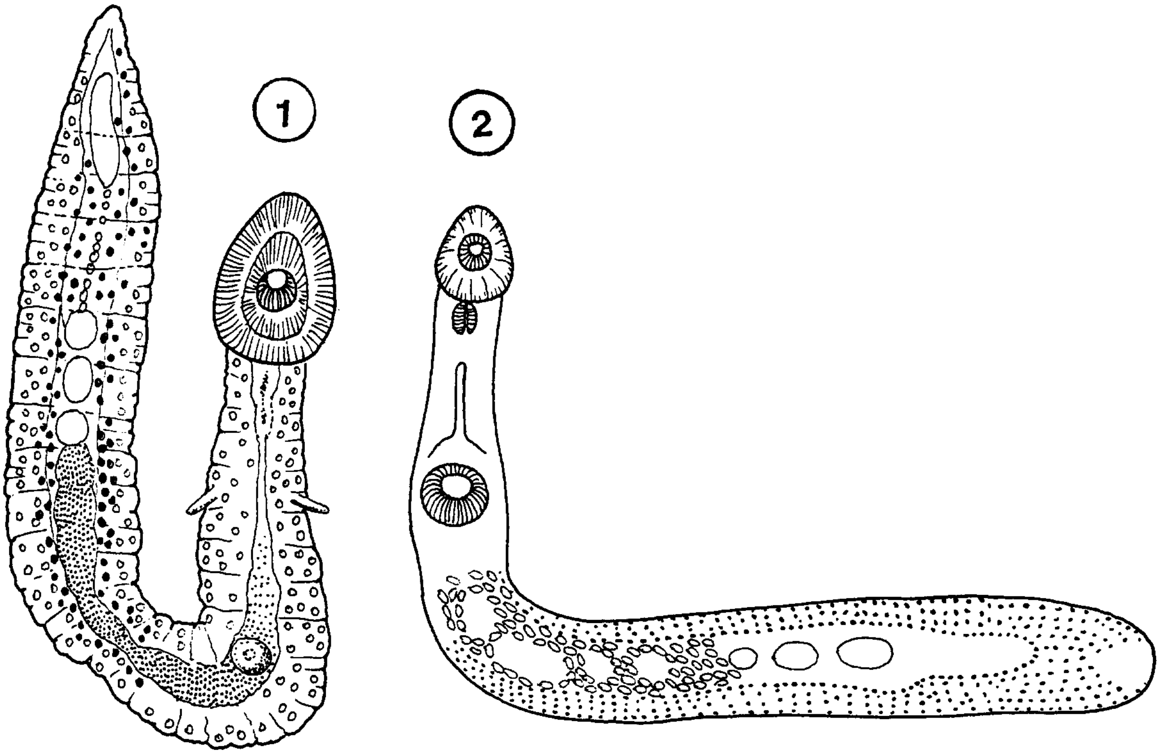
Egg (Fig. 3)

First eggs usually appeared in faeces 10 days after infection of birds. They are unembryonated, yellow-brown, with thickening at the anopercular end of the shell, and measure 88–113 × 61–74. Eggs kept in distilled water in a Petri dish at constant temperature of 28 °C, yielded fully-developed miracidia within 9 days.

Miracidium (Figs 4,5)

Hatching may start on 9th day, but usually miracidia hatch in greater numbers after 10–12 days. Exposure to light stimulates hatching which usually occurs after noon. Newly hatched miracidia swim rapidly, changing direction from time to time. They are positively phototactic and live for 6–8 h.

Fixed in hot 2% silver nitrate they measure 65–90 × 46–70. Refractile apical papilla 10 × 5 when protruded, with 2 pairs of setae. Body covered with 4 rows of ciliated epidermal plates: 1st (anterior) row with six triangular plates, 2 ventral, 2 dorsal and 2 lateral (one on each side), about 20 long and 13 wide at base; 2nd row with 6 square plates, 3 dorsal and 3 ventral, about 16 in diameter; 3rd row with 4 square plates, 2 lateral, one dorsal, and one ventral, about 25 in diameter; and 4th row with 2 subtriangular plates, one ventral and one dorsal, about 23 in diameter at anterior end. Cilia 15 long. Two lateral processes, 3.5 long, each situated posterior to lateral anterior epidermal plate, with short seta immediately anterior to each process. Primitive gut c. 25 long, filled with refractile granules, with opening at tip of apical papilla. Penetration gland cells not visible before or after vital staining with neutral red. Eye-spots consist of 2 pairs of dark-brown pigmented bodies side by side. Pigmented bodies consist of pair of oval discs measuring c. 5 in diameter and pair of rods situated posterior or



Figs 1–2. Fasciola revoluta Froelich, 1802. After Froelich (1802). 2. *Planaria latiuscula* Goeze, 1782. After Goeze (1782).

postero-lateral to oval discs. Two flame cells present; left one ventral and posterior; right dorsal and anterior. Two excretory ducts open between 3rd and 4th rows of epidermal plates; duct connecting right flame cell opening dorso-laterally, other ventro-laterally. Several germ-cells in middle and posterior parts of body.

Miracidia penetrate into snail host at mantle edge and along edges of foot, rarely through exposed parts, such as antennae and head region.

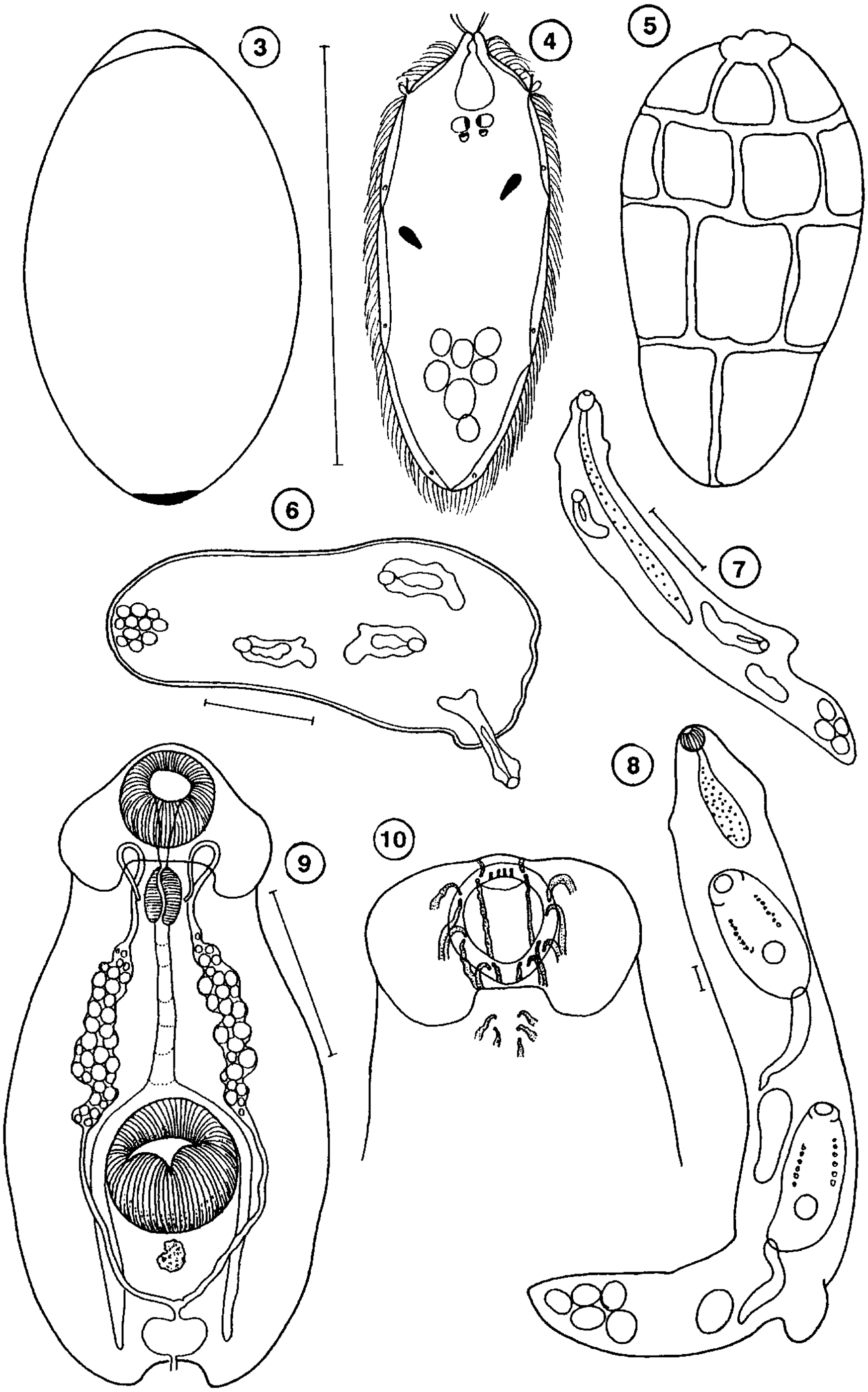
Sporocyst (Fig. 6)

Sporocysts develop in ventricular cavity of snail heart where they arrived about 48 h after exposure of snail to miracidia. Newly-produced, live sporocysts measure 162 × 85. They developed into contractile, elongate sacs attached by their broader end to heart muscle and with narrow end free in heart cavity; contain germ-balls and one or 2 rediae.

Sporocysts of 8-days old measured 180–640 × 160–290; 10-day old sporocysts measure 790 × 416. Birth pore difficult to see, but rediae have been seen emerging from cleft opening near attached base of sporocyst. It is not clear if these rediae leave via birth pore or penetrate tegument. After the 3rd week sporocysts become smaller and more opaque, and production of rediae declines, until none are observed in sporocysts after 6 weeks. Empty sporocysts may persist in snail heart and remain active through 8th week post-exposure when they average 180 × 86 (maximum width). Old sporocysts are dark-grey, small and empty.

Redia (Figs 7–8)

Active first generation (mother) rediae were released 5 or more days after exposure. They are motile, colourless, with collar conspicuous when fixed with hot silver nitrate, locomotor organs c. 260 × 80, pharynx 15–33 wide, gut reaching al-



Figs 3–10. Echinostoma revolutum 3. Egg showing operculum and non-opercular thickening of the shell. 4. Miracidium, dorsal view, with apical papilla, gut, eye-spots, flame-cells and lateral processes. 5. Miracidium stained with silver nitrate, showing epidermal plates. 6. Sporocyst containing rediae. 7. First generation redia containing rediae, of about 11 days old. 8. Redia containing cercariae. 9. Cercaria, ventral view, showing collar, oral sucker, pharynx, oesophagus, caeca, acetabulum, main excretory ducts and genital primordia. 10. Free-hand drawing of cercaria stained with Nile blue sulphate, showing 21 duct outlets of the para-oesophageal gland cells. Camera lucida drawings, unless otherwise stated. *Scale-bars:* 100 μm.

most to locomotor organs, distance from anterior end to locomotor organs 207, and distance from anterior end to collar 46. Mother rediae usually remain in heart cavity, although some may migrate to haemolymph space surrounding viscera and albumin gland; they matured 16–22 days after exposure, producing daughter rediae. Mature rediae 10-days old measure 84–362 × 24–137, pharynx 17–33 in diameter, collar 30–60 from anterior end, birth pore dorsal and immediately posterior to collar, and gut length variable, reaching halfway to locomotor organs or further. Thirty 18-day old rediae fixed in hot water were c. 416–2,128 × 93–418, but when alive they may be much longer or shorter, depending on state of contraction. Redial production was soon replaced by production of cercariae, and 25–28 days post-exposure all or almost all rediae contained cercariae only. At this stage they measure 517–2,910 × 94–370, pharynx 30–60 in diameter, gut 120–540 long and ending far anterior to locomotor organs, and prominent collar 50–215 from anterior end. Young immature rediae of the 1st and 2nd generations are indistinguishable. Mature rediae differ in size, length of gut and larval content.

Second generation rediae are usually more than 1 mm long and may reach length of 3 mm. Second and 3rd generation rediae contain up to 30 cercariae, in addition to number of germ balls. In some rediae, along with cercariae there are also one or 2, rarely 3–4, rediae of next generation. Daughter rediae are concentrated in sinuses along columella adjacent to hepatopancreas and ovo-testis. Old rediae are shrivelled, with dark-grey bodies and orange gut.

Cercaria (Figs 9–12)

Cercariae may first escape from snail (maintained at room 18–20 °C) 28 days after exposure, but usually at 29–30 days. Emergence is most pronounced during morning hours. Cercariae are negatively phototactic, swimming easily through water while curving body ventrally. After swimming for 3–6 h, they sink to bottom and die several hours later. In half-strength saline they may live more than 12 h.

Measurements based on specimens fixed in 5% hot (70 °C) formalin: body 265–315 × 128–154. Collar distinct, 130–150 wide, with 37 spines 8–12 long, arranged as in adult. Body covered with minute spines in diagonal rows; longest spines, immediately posterior to collar, average 4 long, becoming sparse at posterior end. Oral sucker subterminal, 32–56 × 40–52. Prepharynx 14–25 long; pharynx 26–30 × 14–18. Oesophagus 50–109 long, consisting of approximately 6–7 indistinct cells. Caecal bifurcation anterior to acetabulum. Caeca reaching to posterior end of body. Acetabulum protuberant, 60–90 in diameter, posterior to mid-body. Cystogenous cells throughout body, numerous, oval to spherical, 18–25 long, few near oral sucker and pharynx, containing ovoid granules measure 2.5 × 1. Penetration gland cells occur along oesophagus with 4 inconspicuous gland ducts opening on dorsal lip of oral sucker. Para-oesophageal gland cells open via 16–20 outlets: 12–16 in oral sucker; 2–6, usually 4, in pharyngeal region. Genital primordia of 2 masses of cells, one at anterior margin of acetabulum, other between acetabulum and base of tail, connected by string of cells passing dorsally to acetabulum. Flame-cells inconspicuous, most probably 36, excretory bladder bipartite at posterior end of body; main collecting tubes distended between acetabular and pharyngeal levels, each containing numerous (27–120) excretory granules up to 12 in diameter in central portion and 8 at ends; caudal excretory tube extending 1/5th of tail length before bifurcating. Tail 414–430 × 39–50, with finger-like narrowing at tip. Seven fin folds, 2 dorsal, 2 ventral, 2 small ventro-lateral and one very small ventral just anterior to narrow tip.

Metacercarial cyst (Fig. 13)

Cyst spherical or subspherical, 132–152 in diameter. Cyst wall consisting of outer transparent layer, c. 12 thick, and inner opaque layer, c. 3 thick. Collar spines, excretory granules, oesophagus and caeca visible through cyst wall.

Metacercariae occur in pericardial sac and posterior kidney region of freshwater snails (*Planorbarius corneus*, *Physa acuta*, *Lymnaea stagnalis* (L.)

and *L. truncatula* (L.)), in kidney and eye cavity of frogs (*Rana temporaria* (L.) and *R. ridibunda* (L.)) and fresh-water turtles (*Emys orbicularis* (Dumeril)). From time to time metacercariae were found in mantle and some soft tissues of snails already harbouring rediae and cercariae of same species; in some cases metacercariae have been found within their rediae. Within 1–2 days metacercariae become infective. Living metacercariae have been found in snails 18 months post-exposure to cercariae, and pigeons fed with these metacercariae successfully developed infection.

Adult (Figs 14–17)

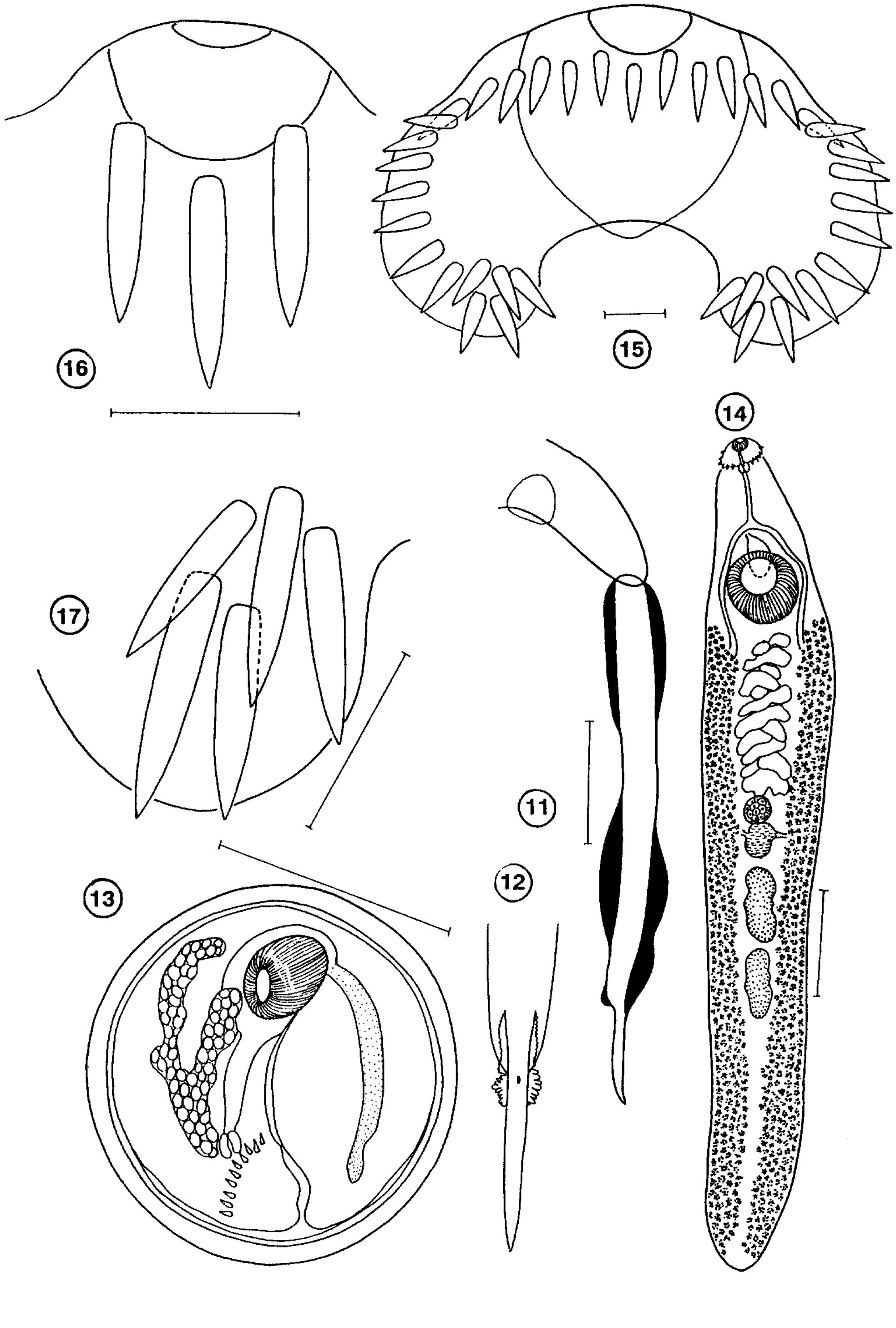
Adult worms live in posterior part of small intestine, caecum and rectum. Egg production begins c. 10 days after infection in young pigeons. Massive egg production starts several days later. Under laboratory conditions worms live between 4 and 8 weeks. Severe infections cause bloody diarrhoea, often followed by death in younger birds. Pigeons are more susceptible than ducklings. Rats, mice, hamsters and other mammals are refractory to infection under laboratory conditions.

Measurements based on 20–28 day-old worms, obtained from chicks. Body 6,460–30,000 × 620–1,630 attaining maximum width at about junction between 1st and 2nd thirds of body. Body spines posterior to collar, covering anterior 6th of body dorsally, all but posterior 6th laterally and almost all ventrally. Collar well developed, 500–600 wide with 37 conspicuous spines up to 112 long. Spine arrangement: 5 corner spines on each side, 3 oral and 2 aboral; 6 lateral on each side in single row; 15 dorsal, 3 oral and 3 aboral on each side, and 3 dorsomedian spines, 2 oral and one aboral, resulting in odd number of collar spines. Latero-aboral largest among corner spines; ventro-oral usually smallest. Oral sucker subterminal, 180–296 × 170–280. Prepharynx up to 250 long. Pharynx 130–240 × 100–180. Intestinal bifurcation anterior to acetabulum. Caeca extending almost to posterior end of body. Acetabulum in anterior 1/5th of body, 460–620 in diameter. Genital pore median, immediately pre-acetabular, followed by genital atrium. Testes tandem; in mid-hindbody, oval, entire or lobate; anterior testis 260–480 × 150–540; posterior testis 314–614 × 172–515. Small ovoid cirrus-sac extending postero-dorsally from genital atrium to middle of acetabulum, containing coiled internal seminal vesicle, pars prostatica and unspined cirrus. Ovary ovoid at or anterior to midbody, 130–460 in diameter. Oviduct with small dilated ovicapt near ovary. Seminal receptacle absent. Uterine seminal receptacle present. Laurer's canal opening medially on dorsal surface posterior to ovary, joining oviduct distally to ovicapt. Small vitelline reservoir present. Mehlis' gland diffuse. Uterus intercaecal, post-acetabular, pre-ovarian, with 8–16 coils, containing numerous eggs, opening into genital atrium through metraterm. Vitelline follicles lateral, dorsal and ventral to caeca, extending from near level of posterior margin of acetabulum to short distance from posterior end of body, rarely confluent posterior to testes (usually in larger worms found in small intestine). Excretory bladder Y-shaped; stem more or less coiled before opening at posterior extremity.

Delimitation of *Echinostoma revolutum*

In the original description and illustration of *E. revolutum*, Froelich (1802) described and illustrated (Fig. 1), as *Fasciola revoluta*, adult worms found in the large intestine of naturally infected wild ducks *Anas boschas fereae* (L.) dissected on July 20, 1798 in Germany. From this original description, it is known that *F. revoluta* is about 11 mm long, belongs to what is known today as the genus *Echinostoma*, has 37 collar spines, and develops in the intestines of ducks. These features serve as the main basis for further definitions of what is known today as *Echinostoma revolutum* (Froelich, 1802) Dietz, 1909.

Subsequently, the history of *F. revoluta* passed through two main periods. During the first one, Rudolphi (1809) selected *F. revoluta* as the type-species for the so-called group *Echinis* (*Echinostoma*) within the genus *Distoma* Retzius, 1786. After Rudolphi (1809), *F. revoluta* was out of use and its function as the type-species was performed



Figs 11–17. Echinostoma revolutum 11. Cercaria, lateral view, showing five dorso-ventral fin-folds on the tail. 12. Distal part of the tail, ventral view, showing ventro-lateral fin-folds with crenulate margins. 13. Metacercaria with some of the collar-spines, excretory granules, acetabulum and one intestinal caecum visible. 14. Adult worm, ventral view, general morphology. 15. Collar-spines in the adult worm, ventral view. 16. Three dorso-medial (central) spines which give the odd number for the whole crown. 17. Five corner spines. Camera lucida drawings. *Scale-bars:* 11–13, 15–17, 100 μm; 14, 1 μm.

by *Distoma echinatum* Zeder, 1803. Practically almost all collar-spined worms found in Europe from Rudolphi (1809) until Dietz (1909a,b) were diagnosed as *D. echinatum*. The second period is based on Dietz (1909a,b; 1910), who restored the validity of *Fasciola revoluta* and renamed it *Echinostoma revolutum* in his systematic reorganization of the collar-spined worms of the family Echinostomatidae. *Distoma echinatum* was declared to be invalid and a synonym of *E. revolutum*. A long list of adult worms and larval stages described originally as *D. echinatum* were transferred to *E. revolutum*. Following Dietz (1909a,b) adult worms and larval stages found in Europe, Asia, Africa, Australia, and North and South America have been described as *E. revolutum* in over 500 works. Of all the published descriptions, those considered the most important are by Johnson (1920), Lutz (1924), Beaver (1937), Mendheim (1940, 1943), Supperer (1959), Skrjabin (1947, 1956), Bisseru (1953, 1967), Yamaguti (1975), Odening (1964), Patnaik & Ray (1966), McDonald (1981), Kosupko (1972), Moravec *et al.* (1974) and Nasincova (1986). The present-day knowledge of *E. revolutum* is based mainly on descriptions and illustrations published by these authors. However, they give conflicting information about the validity, identity, synonymy, morphology, biology, ecology, life-history, hosts and distribution of adults and larvae described and illustrated by them as *E. revolutum*. The matter has been resolved by the extensive comparative experimental studies referred to in this paper.

Taxonomic features

Important taxonomic features of *E. revolutum* were fundamentally unknown because adults and larvae of different species and genera, possessing different morphological structures, were considered identical with *E. revolutum*. For this reason, its taxonomic features were described with numerous varying and conflicting forms. To illustrate this point, the following examples are presented.

Collar spines in cercariae and adults – number and arrangement. To date the number of collar spines of echinostomes considered by the authors to be identical with *E. revolutum* are reported as follows: 14 (Rudolphi, 1809; Bremser, 1824); 27 (Ercolani, 1881); 35 (Supperer, 1959); 36 (Linstow, 1873); 36–37 (Looss, 1899); 37 (Beaver, 1937); 37–38 (Yamaguti, 1971); 41 (La Valette, 1855); 43 (Johnson, 1920); and 40–45 (Wesenberg-Lund, 1934). According to Beaver (1937) spine number varies from 35 to 41; according to Bashkirova (1941) and Skrjabin (1956) it is strictly constant at 37; and Johnson (1920) and Iwata & Tamura (1933) believed that the adults have fewer spines than cercariae, due to the loss of some spines during adult development. Linstow (1873) assumed that spine number decreased not by loss but because of "corrosion and fusing" resembling tooth decay in vertebrates. Respectively, the collar spines arrangement was presented as: 1 row (La Valette, 1855); 2 rows (Looss, 1899); 27 spines in 2 rows plus 10 in 2 corner groups of 5 spines each (Bashkirova, 1941); in the formula(5 + 13 + 1 + 13 + 5) (Odening, 1970); and in the formula (3 + 2) + 6 + (7 + 8) + 6 + (2 + 3) (Patnaik & Ray, 1966).

Collar spines – shape and size. All spines have a similar size and shape (Yamaguti, 1958); certain spine groups considerably larger than the rest (Beaver, 1937; Kosupko, 1972).

The present study, based on material originating from the type locality, confirms that *E. revolutum* has 37 collar spines of similar size and shape that are arranged 2(5 + 6 + 6) + 3 (Fig. 15). For many years *Echinostoma* spp. were identified primarily on the basis of collar spine number, relative size and arrangement. We now know that there is an *E. revolutum* group of species that share the same number, size, and arrangement of collar spines.

Ducts of the para-oesophageal gland-cells in the cercariae. To date these morphological structures were described as follows: no para-oesophageal gland-cells or ducts (Moravec *et al.*, 1974); 8 ducts, all on the oral sucker (Patnaik & Ray, 1966); 10 ducts – 6 on the oral sucker and 4 in the pharyngeal region (Kosupko, 1972); 6 small ones on the ventral surface of the dorsal lip and 6 large ones on the oral sucker region of the ventral surface of the body (Beaver, 1937); 30–36 visible gland-cells in the body between the pharynx and acetabulum, plus 8 ducts and pores on the oral sucker (Nasincova, 1986). The present and previous studies (Kanev *et al.*, 1992a) found that in its type-locality in Germany the cercaria of *E. revolutum* possesses 16 ducts and pores arranged in a species specific pattern in which 12 are situated on the oral sucker and 4 on the ventral surface of the body at the level of pharynx.

Cercarial tail size, shape and fin-folds. So far these structures have been described with different characteristics as follows: *size*: 284–384 long (Johnston & Angel, 1941); 540–750 (Tsuchimochi, 1924); *shape*: cylindrical, with very specific uni-lateral pinch in the tip (Beaver, 1937); cylindrical with conical tip (Siebold, 1837, 1842; Johnson, 1920); *fin-folds*: no fin-folds on the tail surface (Johnson, 1920); only one very short fold, located dorsally on the posterior half of the tail (Beaver, 1937), 2 small dorso-ventral fin-folds in the second half of the tail (Kosupko, 1972); one long and one short fold (Odening, 1964); 2 long folds, which cover all dorsal and ventral surface of the tail, except the tip (Balusek & Vojtek, 1973); 2 very long fin-folds, which cover the tail tip (Zdarska, 1963); and 4 fin-folds variable in size and position (Moravec *et al.*, 1974). The present and previous studies (Kanev *et al.*, 1992b) on the tail and fin-folds of the cercaria of *E. revolutum* based on materials from its type-locality showed a cylindrical tail with a finger-like process at its distal end and 7 independent fin-folds arranged in 3 pairs plus a single small one. The same characteristics were found in *Cercaria spinifera* La Valette, 1855, *C. trivolvis* Cort, 1914, and other 37 collar-spined cercariae of the genus *Echinostoma* (see Kanev & Fried, 1982; Kanev, 1985), so *E. revolutum* and its closely related allies cannot be distinguished on the basis of their tail morphology.

Metacercarial cyst. Characteristics reported: *size*: 117–125 in diameter (Johnston & Angel, 1941); 147–220 (Tubangui, 1932; Zdarska, 1964); 360–380 in diameter (Supperer, 1959); *cyst wall thickness*: 10–12 (Beaver, 1937); 40–45 (Supperer, 1959); *Shape*: round or oval (Johnson, 1920; Beaver, 1937); elliptical (Johnston & Angel, 1941). According to our results the metacercarial cyst of *E. revolutum* is spherical or subspherical, 132–152 in diameter with a wall 15 thick.

Species now considered identical to Echinostoma revolutum

Echinostoma audyi Lie & Umathevy, 1965 was described from Southeast Asia by Lie and his co-workers in nearly 40 papers published between Lie (1965) and Lie & Kanev (1983) and by Kanev and his co-workers, from Europe and Asia, in approximately 40 studies published between Kanev (1977) and (1987). The identity of *E. revolutum* and *E. audyi* was confirmed in different comparative experimental studies on materials from Europe and Asia, including Germany and Malaysia, where *E. revolutum* and *E. audyi* were originally described (Lie & Kanev, 1983; Dimitrov *et al.*, 1985; Kanev, 1985). The results obtained, that *E. audyi* corresponded completely with *E. revolutum* in both the adult and larval morphology and biology, were supported by Odening (1986), Dimitrov (1987), Christensen *et al.* (1990) and Huffman & Fried (1990).

E. paraulum Dietz, 1909 was reported in Europe and Asia in approximately 60 papers published from Dietz (1909a,b) to Iskova (1985). Its identity was confirmed in experimental studies on the complete life-history of parasites from Europe, including from Austria where *E. paraulum* was originally described (Kanev, 1985). The results obtained showed that *E. paraulum* corresponded completely with *E. revolutum*.

E. ivaniosi Mohandas, 1973, was described from India by Mohandas and his co-workers in three papers published between Mohandas (1973) and Mohandas (1981). This species is considered identical with *E. revolutum* because its adult worms and larval stages completely correspond in morphology and biology to our studies on *E. audyi* (=*E. revolutum*).

Closely related species in Europe

In Europe, where *E. revolutum* was originally described, there are three closely related echinostome species with 37 collar-spines as follows:

Cercaria echinata Siebold, 1837. Siebold (1837) described *C. echinata* on material from Germany. Later its adults and larvae were presented with different generic and specific names such as *Distoma echinatum* Zeder, 1803, *D. herise* Railliet, 1895, *Echinoparyphium aconiatum* Dietz, 1909, *Echinostoma revolutum* (Froelich, 1802), *C. nudicaudata* Nasir, 1960, *C. deficipinnata* Khan, 1960, and others. The identity, validity and life-history will be discussed in another paper. Here it should be said only that *C. echinata* resembles *E. revolutum* both in its type-locality in Central Europe and in having 37 collar-spines, based on which Dietz (1909a), Dawes (1968) and others presented *C. echinata* as the larva of *E. revolutum*. Many workers considered *C. echinata* to be identical with *E. revolutum* of Beaver (1937) in America. All these conclusions are incorrect. In its type-locality, *C. echinata* belongs to the 37-spined adults which Dietz (1909a) described as *Echinoparyphium aconiatum*. *C. echinata* differs from *Echinostoma revolutum* in its: bigger body size; presence of hundreds conspicuous bodies in the oesophagus and caeca; flame-cell formula composed of nearly 100 cells; number ($2n = 20$) and morphology of chromosomes; cone-like tail form; absence of fin-folds on the tail surface; number and arrangement of argentophilic structures; absence of para-oesophageal gland-cells and ducts; and 8 to 12 ducts and pores of penetration gland-cells. The metacercariae of *C. echinata* are larger (about 200 μm), have developed ovary and testes, and become infective after three weeks. The adults of *Echinoparyphium aconiatum* differ from *Echinostoma revolutum* in their smaller (1–3 mm) body size, localization in the duodenum and jejunum, short uterus containing 1–10 eggs, anterior limit of the vitellarium is between the ovary and the acetabulum, and the presence of four larger corner spires.

Echinostoma jurini (Skvortsov, 1924). The original material was named *Cercaria jurini*, but subsequently its adults and larvae were described with different names, such as *Echinoparyphium sisjakovi* Skvortsov, 1934, *Cercaria bolschevensis* Kotova, 1934, *Echinostoma sisjakovi* (Skvortsov, 1934) Yamaguti, 1971, *E. revolutum* (Froelich, 1802), *E. armigerum* Barker & Irwine, 1915, *E. bolschevensis* (Kotova, 1934) Nasincova, 1991, and others, of which the identity will be discussed in a separate paper. Here, it should be said that adult *E. jurini* resemble *E. revolutum* but cannot be identical because adult *E. jurini* do not develop in ducks or other birds. They develop easily in golden hamsters *Mesocricetus auratus* Mehring and rats *Rattus rattus* Lamarck, but attempts to infect wild and domestic ducks *Anas platyrhynchos* have failed. Ducks from the same stocks fed with metacercariae of *E. revolutum* developed an infection. The cercaria of *E. jurini* is different to that of *E. revolutum* in its: first intermediate prosobranch viviparid snail host; number and arrangement of argentophilic structures; number and position of penetration gland cell pores (6) on the ventral surface of the dorsal lip of the oral sucker; number and position of para-oesophageal gland-cells pores on the oral sucker and body surface (O); and chromosome morphology.

E. echinatum (Zeder, 1803). In its type-locality, *E. echinatum* was found (Kanev, 1985) to be identical with *E. lindoense* Sandground & Bonne, 1940, which was described as a species infecting 200 ethnically segregated native people of Toradja stock living in the villages on a narrow shore between the jungle and Lake Lindoe, Celebes Island, Indonesia. Its adults and larvae have been described as *Distoma anatis* Zeder, 1800, *D. echi-

natum, *D. herise*, *Echinostoma revolutum*, *E. lindoense*, *E. miyagawai* Ishii, 1932, *E. robustum* Yamaguti, 1935, *E. londonensis* Khan, 1960, *Cercaria spinifera*, and others whose identity will be discussed in a separate paper. The identity of *E. echinatum* and *E. lindoense* was confirmed in comparative experimental studies on materials from different geographical regions of Asia, South America and Europe, including Germany where *E. echinatum* and its larva *Cercaria spinifera* were originally described (Kanev, 1985; Kanev & Odening, 1983; Lie & Kanev, 1983; Vassilev *et al.*, 1982a, b; Vassilev & Kanev, 1985). The adult *E. echinatum* resembles *E. revolutum* in its type-locality in Germany, in having 37 collar-spines, in its avian hosts, and overlapping morphological features. Based on these similarities, Dietz (1909a,b, 1910), Beaver (1937), Mendheim (1940, 1943), Skrjabin (1947, 1956), Yamaguti (1958, 1971) and others considered *D. echinatum* a synonym of *E. revolutum*. I consider *E. echinatum* a valid species because its adults and larvae differ from *E. revolutum* in: its use of mammals including man as definitive hosts; its use of planorbid snails as its first intermediate host; the number and arrangement of protein fraction of homogenates of adult worms; the cirrus surface and shape; the number and position of penetration gland-cells opening on the ventral surface of the dorsal lip of oral sucker (6); the number and position of para-oesphageal glands-cell pores (total number 60–64, 14–16 being located on the oral sucker and 36–42 on the body); the number and arrangement of argentophilic structures; and chromosome morphology. The validity of *E. echinatum* was supported by Odening (1986), Schuster (1986), Dimitrov (1987), Christensen *et al.* (1990) and Huffman & Fried (1990).

Planaria latiuscula Goeze, 1782. This species, described from the adult worms found in naturally infected *Falco milvus* from Germany, is described and illustrated with exactly the same morphological structures which Froelich (1802) presented for the original material of *E. revolutum* (see Figs 1,2). For many years both species have been considered valid, mainly because their adults have been found in birds belonging to two different families and orders. Now this difference is not regarded as sound because the adult worms of *E. revolutum* easily infect birds of different families and orders. Nevertheless, I do not consider *E. revolutum* and *P. latiuscula* identical because of the lack of proof. Others (Lie & Umathevy, 1965) and my own studies (Kanev, 1985; this paper) have shown that the closely related 37 collar-spined worms of genus *Echinostoma* possess very similar and overlapping morphology and cannot be recognised on the basis of adult morphology only.

Invalid descriptions of Echinostoma revolutum

The following reports are considered invalid descriptions of *E. revolutum*.

E. revolutum of Dietz (1909a,b) is a composite of adult worms and larval stages described in the original as *Distoma echinatum* by Zeder (1800, 1803), Rudolphi (1809, 1819), Bremser (1824), Diesing (1850, 1858), Linstow (1873, 1884, 1894), Looss (1899) and 33 other workers. Dietz (1909a,b) considered this parasite identical to *E. revolutum* because he believed that *D. echinatum* and *Fasciola revoluta* were identical. In support of this concept, he presented a long list of parasite specimens, original descriptions and illustrations which he had studied in four museums in Europe: Vienna, Berlin, Greifswald and Königsberg. The last two Museums were destroyed during World War II. Kanev (1985) re-examined available material in Vienna and Berlin, showing that many specimens are adults and larvae belonging to different species and genera such as *Echinostoma echinatum*, *E. jurini*, *E. trivolvis* (Cort, 1914) Kanev, 1985, *E. caproni* Richard, 1964, *Echinoparyphium aconiatum* Dietz, 1909, *E. recurvatum* (Linstow, 1873) Lühe, 1909, *Neoacanthoparyphium echinatoides* (Filippi, 1954) Odening, 1962, *Paryphostomum radiatum* (Dujardin, 1845) Dietz, 1909, *Hypoderaeum conoideum* (Bloch, 1782) Dietz, 1909, *Isthmiophora melis* (Schrank, 1788) Lühe, 1909, *Cathaemasia hians* (Rudolphi, 1809) Looss, 1899 and *Echinochasmus beleocephalus* (Linstow, 1873) Dietz, 1909. The exact identity of these parasites is fully discussed in a separate revision of *E. echinatum*. For example, Dietz (1909a) identified as *E. revolutum* an adult worm from fish-eating birds having 14 collar-spines arranged in a single row interrupted dorsally. This is typical for the genus *Echinochasmus* Dietz, 1909. Thus, the general morphology of the adults and the nature of their hosts show that they belong to *Echinochasmus* and not *Echinostoma revolutum* as Dietz (1909a) assumed.

E. revolutum of Johnson (1920) is a composite of 43-spined larvae from naturally infected freshwater snails, *Physa occidentalis* Dall, collected in the Golden Gate Park, San Francisco, California and the 37-spined adult worms found in naturally infected birds, *Marila marila* (L.), shot in the same park. Yamaguti (1971) and others have used Johnson's (1920) illustrations to present *E. revolutum* cercariae. Kanev (1985) examined new 43-spined echinostomes obtained from the same snail host and locality as Johnson's (1920) material, and showed experimentally that they were larval stages of 43-spined adults of the genus *Echinoparyphium*. We had no permission to shoot birds in the Golden Gate Park and thus no opportunity to confirm the 37 collar-spined adult worms described by Johnson as identical with *E. revolutum*. These adults belong to *Echinostoma*, but are probably the same species which Beaver (1937) described as *E. revolutum* and Kanev (1985) renamed *E. trivolvis*. The latter is very common and widely distributed in North America. No snails have been found so far in North and South America to harbour rediae and cercariae of the real *E. revolutum* from Europe.

E. revolutum of Lutz (1924) is unlikely to be identical with the real *E. revolutum*, which has not yet been found in America (Lie & Kanev, 1983). Lutz (1924) based his description on echinostomes found in naturally infected snails, *Physa rivalis* (Maton & Rickett), collected in Brazil. Later, Lie & Basch (1967) and Hsu *et al.* (1968) found *P. rivalis* from the same region of Brazil to be the first intermediate host of two different 37-spined species, *E. paraensei* Lie & Basch, 1967 and *E. rodriguesi* Hsu *et al.*, 1968.

Cercaria trivolvis Cort, 1914 is based on the 37 collar-spined cercaria found in naturally infected snails, *Helisoma trivolvis*, collected in north, central and north-eastern USA. Beaver (1937) and other authors have presented *C. trivolvis* as the larva of *E. revolutum*. We re-examined *C. trivolvis* material from its type-locality in the USA (Kanev & Fried, 1982; Kanev, 1985; Kanev *et al.*, 1988b; Vassilev *et al.*, 1984) and established that *C. trivolvis* and its adults are not identical with *E. revolutum*, but differ in the features listed below.

E. revolutum described by Beaver (1937) is based on *Cercaria trivolvis*. Beaver (1937) completed the life-history of *C. trivolvis*, finding that its adults are morphologically similar to adult worms from Europe described as *E. revolutum*. Based on that similarity, Beaver (1937) considered *C. trivolvis* and its adult worms identical to *E. revolutum*. However, in spite of the similarities, *E. revolutum* of Beaver (1937) described from material from North America is not identical with European *E. revolutum*. Kanev (1985) recognised *E. revolutum* of Beaver (1937) as an independent species, now known as *E. trivolvis* (Cort, 1914) based on its original name. This identity of *E. trivolvis* is based on comparative studies of material from Europe and the USA (Kanev & Fried, 1982; Kanev, 1985; Vassilev *et al.*, 1984) and has been confirmed by Odening (1986), Christensen *et al.* (1990) and Huffman & Fried (1990). *E. trivolvis*, differs from *E. revolutum* in its: (i) first intermediate planorbid snail host; (ii) use of mammals as final host; (iii) number and arrangement of protein fractions in the homogenates of adult worms; (iv) number and distribution of argentophilic structures; (v) number of penetration gland-cell ducts on the ventral surface of the dorsal lip of the oral sucker (6); (vi) number and position of para-oesphageal gland-cells ducts (total number 4–6, all on oral sucker); and (vii) geographical distribution (North America).

E. revolutum described by Fried and his co-workers in more than 50 articles published between Fried & Fink (1968) and Donovick & Fried (1988) is identical with *E. revolutum* of Beaver (1937), which was renamed by Kanev (1985) as *E. trivolvis* (Cort, 1914). This identity was confirmed after numerous joint studies (Kanev & Fried, 1982; Vassilev *et al.*, 1984; Kanev *et al.*, 1988).

E. revolutum of Sprehn (1930, 1932) is a mixture of *E. revolutum*, *E. echinatum*, *E. jurini* and *Echinoparyphium* sp. compiled from the descriptions by Dietz (1909a,b), Johnson (1920), Looss (1899) and others.

E. revolutum of Mendheim (1940, 1943) is based on descriptions by Looss (1899), Dietz (1909a,b), Johnson (1920), Beaver (1937) and others. As discussed above, these authors confused species currently regarded as *E. echinatum*, *E. jurini*, *E. trivolvis*, *E. caproni* and *Echinoparyphium* sp. but not *E. revolutum*.

E. revolutum of Bashkirova (1941) is based on adults collected from naturally infected birds in Europe and Asia, where both *E. revolutum* and *E. echinatum* occur. Bashkirova (1941) considered most of the 37-spined adults to be *E. revolutum* and her description may include both species.

E. revolutum of Bonne *et al.* (1947, 1953) from humans in southeastern Asia is unlikely to be identical with *E. revolutum* which does not develop in humans. They are probably *E. lindoense*, described in humans from Indonesia and synonymized by Kanev (1985) with *E. echinatum*.

E. revolutum of Skrjabin (1947, 1956) is a mixture of adults and larvae of *E. revolutum*, *E. echinatum*, *E. jurini*, *E. caproni*, *Echinoparyphium* sp. of Johnson (1920), described as *E. revolutum* by Looss (1899), Dietz (1909a,b), Lutz (1924), Johnson (1920), Beaver (1937) and Bashkirova (1941).

E. revolutum described by Bisseru (1953, 1967) is identical with *E. caproni*. His material was obtained from the same snail hosts *Biomphalaria glabrata* [=*B. alexandrina* (Ehrenberg)] and *Bulinus truncatus* (Audouin) collected in the same regions of Africa where *E. caproni* is known to be very common (Kanev, 1985). *E. caproni* differs from *E. revolutum* in: (i) its first intermediate planorbid snail host; (ii) using mammals as final host; (iii) the number and arrangement of argentophilic structures; (iv) the number of penetration gland-cell ducts on the ventral surface of the dorsal lip of the oral sucker (6–8); (v) the absence of para-oesophageal gland-cells; and (vi) its geographical distribution (Africa).

E. revolutum of Yamaguti (1958, 1971, 1975) is a mixture of adults and larvae of *E. revolutum*, *E. echinatum*, *E. jurini*, *E. trivolvis*, *E. caproni*, *Moliniella anceps* (Molin, 1858) Hubner, 1939, *Echinoparyphium* sp. of Johnson (1920), and others described as *E. revolutum* by Dietz (1909a,b), Johnson (1920), Lutz (1924), Beaver (1937), Supperer (1959), and others.

E. revolutum of Supperer (1959) is identical with *Moliniella anceps*. This identity was established experimentally using 35 collar-spined echinostomes from Austria which were collected from the same snail hosts and the same biotopes as Supperer's (1959) material (Kanev, 1982, 1985).

E. revolutum of Zdarska (1963, 1964) is a mixture of *E. revolutum* and *E. echinatum*, based on larvae in both lymnaeid and planorbid snails from Czechoslovakia. However, as shown above, *E. revolutum* does not develop in planorbid snails. Our experimental studies (Vassilev *et al.*, 1982a; Kanev, 1985), with the same larvae obtained from the same planorbid snails and regions in Czechoslovakia as Zdarska's (1963, 1964) material, showed infection with *E. echinatum*.

E. revolutum of Zajicek (1963) is a mixture of *E. revolutum* and *E. echinatum*. Like Zdarska (1963, 1964), he has presented, as *E. revolutum*, 37 collar-spined echinostome larvae found in both lymnaeid and planorbid snails from Czechoslovakia. Those in planorbid snails cannot be identical with *E. revolutum*, which develops in lymnaeid but not in planorbid snails.

E. revolutum of Tenora (1963) from mammals in Czechoslovakia is not identical with *E. revolutum*, which does not develop in mammals.

E. revolutum complex of Odening (1964, 1970) is a mixture of *E. revolutum*, *E. echinatum*, *E. trivolvis*, *E. jurini* and *E. caproni*. Odening (1964, 1970) has united all 37 collar-spined echinostomes in a common complex divided into planorbid and lymnaeid groups, according to their first intermediate snail host.

E. revolutum of Kosupko (1968, 1969, 1970, 1971, 1972) from the USSR is identical with the *E. revolutum (sensu stricto)* from Europe but not with *E. revolutum* of Beaver (1937) from the USA, as Kosupko (1972) suggested. (Confirmed in a personal communication.)

E. revolutum of Donges (1969, 1971, 1972) from Central Europe is identical with *E. revolutum* from Europe, but not *E. revolutum* of Beaver (1937). (Confirmed in personal communications.)

E. revolutum of McDonald (1969, 1981) is a mixture of adults and larvae of *E. revolutum*, *E. echinatum*, *E. jurini*, *E. trivolvis*, *E. caproni*, *Moliniella anceps*, *Echinoparyphium* sp. of Johnson (1920) and other species described as *E. revolutum* by Dietz (1909a,b), Johnson (1920), Lutz (1924), Beaver (1937), Bisseru (1967), Supperer (1959), Odening (1964, 1970) and others mentioned above.

E. revolutum of Nezvalova (1970) is based on 37-spined cercariae found in different lymnaeid and planorbid snails in Czechoslovakia. Those in planorbid snails cannot be identical to *E. revolutum*, which develops in lymnaeid but not planorbid snails. They are probably *E. echinatum*.

E. revolutum of Kamburov & Vassilev (1972) and Vassilev & Kamburov (1972) is a composite reported from Bulgaria of adults and larvae of *E. echinatum* and *E. revolutum*. This was subsequently demonstrated in experimental studies using the same echinostomes from Bulgaria (Vassilev & Kanev 1979, 1981; Kanev, 1985).

E. revolutum of Balusek & Vojtek (1973) is based on 37-spined cercariae found in lymnaeid and planorbid snails from Czechoslovakia. As for Nezvalova (1970), cercariae found in planorbid snails cannot be *E. revolutum* because in Europe planorbid snails are intermediate hosts of *E. echinatum* but not of *E. revolutum*.

E. revolutum of Prokopic & Genov (1974) from mammals in Czechoslovakia and Bulgaria could belong to *E. echinatum* or *E. jurini*, which develop in mammals in both Bulgaria and Czechoslovakia (Vassilev *et al.*, 1982b; Kanev, 1985). *E. revolutum* does not develop in mammals.

E. revolutum of Rysavy *et al.* (1974, 1975) and Moravec *et al.* (1974) is identical with *E. liei* described by Jeyarasasingham *et al.* (1972) based on material collected in Egypt. According to Rysavy *et al.* (1974) and Moravec *et al.* (1974), *E. liei* is identical with *E. revolutum* described by Beaver (1937). However, they did not discuss the reasons for that identity, stating only that they "appear to be identical". Lie *et al.* (1974) rejected this identity and presented considerable evidence against it. After comparative studies with both *E. liei* from Africa and *E. revolutum* described by Beaver (1937) in America, Kanev (1985) confirmed that these two species are different from one another and different from *E. revolutum* in Europe. Recently, Donovick & Fried (1988) added new data in support of this, and *E. liei* has been found (Kanev, 1985) to be identical with *E. caproni* Richard, 1964, described in detail by Richard & Brygoo (1978). This identity was confirmed by Voltz (1987), Voltz *et al.* (1987), Christensen *et al.* (1990) and Huffman & Fried (1990).

E. revolutum of Christensen and his co-workers used between Christensen (1980) and Christensen *et al.* (1988) is identical with *E. caproni*, as confirmed by Christensen *et al.* (1990) and Huffman & Fried (1990).

E. revolutum of Kolarova (1986) is a mixture of adults and larvae of *E. revolutum* and *E. echinatum* based on material obtained from lymnaeid and planorbid snails in Czechoslovakia. However, those from planorbids could not be *E. revolutum* which does not develop in this group of snails.

E. revolutum of Iskova (1985) is a mixture of adults and larvae of *E. revolutum*, *E. echinatum*, *E. jurini*, *E. trivolvis* and *E. caproni* described by Beaver (1937), Bisseru (1953), Odening (1964), Skrjabin (1956) and Yamaguti (1971, 1975), and was presented by Iskova (1986) in her monograph on the family Echinostomatidae. Based on Beaver (1937) and Sharpilo (1973), she presented the first intermediate hosts of *E. revolutum* in Europe as being prosobranch snails of the genus *Viviparus* and various planorbid snails. These snails are the first intermediate host of *E. echinatum* and *E. jurini*, but not of *E. revolutum*.

E. revolutum of Nasincova (1986) is identical with *E. echinatum*. Nasincova (1986) made her description on the same 37 collar-spined echinostomes obtained from the same snail host, *Planorbarius corneus*, collected in the same biotopes in Czechoslovakia as our material of *E. lindoense* (=*E. echinatum*) (see Vassilev *et al.*, 1982a,b; Kanev, 1985). Also, the *E. revolutum* described by Nasincova (1986) has the same morphological features and the same biological characteristics reported for *Cercaria spinifera* (=*E. lindoense*; = *E. echinatum*) (see Vassilev & Kanev, 1979, 1981, 1985; Kanev & Odening, 1983; Lie & Kanev, 1983; Kanev, 1985; Kanev & Vassilev, 1980, 1981).

E. revolutum described by Zdarska & Nasincova (1985) and Zdarska *et al.* (1987) are based on the same echinostomes from Czechoslovakia which Nasincova (1986) described as *E. revolutum* and which are now (in this paper) placed in synonymy with *E. echinatum*.

Remarks

Of the 31 descriptions of *E. revolutum* presented above, 29 (94%) are found to represent adults and larvae of different species and genera, such as *Echinostoma echinatum*, *E. trivolvis*, *E. jurini*, *E. caproni*, *Echinoparyphium recurvatum*, *E. aconiatum*, *Echinoparyphium* sp. of Johnson (1920), *Hypoderaeum conoideum*, *Isthmiophora melis*, *Moliniella anceps*, *Neoacanthoparyphium echinatoides*, *Echinochasmus beleocephalus*, *Cathaemasia hians*, *Paryphostomum radiatum*, *Cercaria echinata*, *C. spinifera* and *C. trivolvis*. Only 2 (6%) of the descriptions relate to the name *E. revolutum* (*sensu stricto*) for both adults and larvae, and even these authors (Donges, 1972; Kosupko, 1972) believed that *E. revolutum* from Europe was identical with *E. revolutum* described in North America by Beaver (1937). For nearly a century, a growing body of literature has included morphological, biological, life-cycle and host information that was incorrectly attributed to *E. revolutum*. From time to time, these data were compiled into new diagnoses of *E. revolutum*. Conversely, but less often, some authors actually working with *E. revolutum* (*sensu stricto*) ascribed their results to different species.

Characteristics of *Echinostoma revolutum*

Synonymy. The synonyms of *Echinostoma revolutum* are: *Fasciola revoluta* Froelich, 1802; *E. audyi* Lie & Umathevy, 1965; *E. ivaniosi* Mohandas, 1973; and *E. paraulum* Dietz, 1909. *E. revolutum* possesses, therefore, only four synonyms, not the 65 listed in the past (see Kanev, 1985). The main synonym of *E. revolutum* is *E. audyi* and not *E. echinatum* as previously believed. The previous information was fundamentally inaccurate because of the numerous erroneous diagnoses discussed above.

Morphology. See redescriptions and illustrations (this paper).

Life-history. The complete life-cycle of *E. revolu-*

tum has been elucidated experimentally many times, but the data obtained have been described mainly under the names of *E. audyi* and *E. ivaniosi*. These studies were carried out by Lie & Umathevy (1965) and Lie *et al.* (1973) in Malaysia and Thailand; Mohandas (1973) in India; Kanev (1980, 1982b, 1985) and Kanev *et al.* (1983) in Bulgaria, Austria, Germany, England and Vietnam; Vassilev *et al.* (1982a,b) in Poland and Czechoslovakia; and Kosupko (1972) in Russia. The life-cycle of *E. revolutum*, as described by Johnson (1920), Lutz (1924), Beaver (1937), Bisseru (1953, 1967), Supperer (1959), Odening (1964), Moravec *et al.* (1974), Rysavy *et al.* (1974), Nasincova (1986), Iskova (1985), Mendheim (1940, 1943), Skrjabin (1947, 1956), Yamaguti (1971, 1975) and McDonald (1969, 1981) cannot be accepted because of the problems of identification outlined above.

First intermediate host. *E. revolutum* uses only snails of the family Lymnaeidae: *Lymnaea auricularis*, *L. auricularis* var. *rufescens*, *L. luteola typica*, *L. luteola gracilor*, *L. ovata*, *L. palustris*, *L. peregra*, *L. rubiginosa*, *L. stagnalis*, *L. swinhoei*, *L. truncatula* and *L. viridis*. *E. revolutum* does not develop in some 100 other prosobranch and pulmonate snails, notably planorbid, physid and viviparid snails (see names listed in Kanev, 1985). Under experimental conditions, miracidia of *E. revolutum* invaded *Lymnaea truncatula* most easily and at the highest rate. Field studies show that spontaneous invasion of *L. stagnalis* by *E. revolutum* is the most common and most widely spread.

Second intermediate host. *Echinostoma revolutum* uses various freshwater pulmonate and prosobranch snails, mussels, frogs and turtles (see names listed in Kanev, 1985). Experimental studies showed that cercariae of *E. revolutum* placed in Petri dishes with lymnaeid, planorbid, physid and viviparid snails preferentially penetrated and infected physid and planorbid snails but not lymnaeid snails, which are their first intermediate host. Turbellarians, leeches, worms, snails, fishes, amphibians and reptiles reported from Africa, North and South America cannot be regarded as genuine second intermediate hosts of *E. revolutum* because the species does not occur there. A long list of these animals (Kanev, 1985) has been presented as second intermediate hosts for *E. revolutum* because of the incorrect determinations discussed above.

Final host. *E. revolutum* does not develop in mammals and humans; such reports were based on inaccurate identifications. Experimental studies with *E. revolutum* showed that its adults infected and developed more easily in pigeons which are rarely infected in nature. Conversely, ducks, which are common final hosts in the field, exhibited a well-expressed age resistance.

Geographical distribution. To date, *E. revolutum* has been reported from 11 countries in Europe and Asia, as follows (Fig. 22): Germany (Froelich, 1802; Donges, 1969; Kanev, 1985), Austria (Kanev, 1982b), Poland (Vassilev *et al.*, 1982b), Czechoslovakia (Vassilev *et al.*, 1982b), Bulgaria (Kanev, 1980), England (Kanev, 1985), the USSR (Kosupko, 1972), Malaysia (Lie & Umathevy, 1965), Thailand (Lie *et al.*, 1973), India (Mohandas, 1973) and Vietnam (Kanev *et al.*, 1983). It is likely that *E. revolutum* occurs elsewhere in Europe and Asia. Previous reports of *E. revolutum* as a cosmopolitan species were based on incorrect identifications. Snails with the larval stages of *E. revolutum* have not been found in Africa, Australia or North America.

Other characteristics. Numerous other characteristics of *E. revolutum* have been examined, but they are described and illustrated under different names, mainly as characteristics of *E. audyi*, *E. paraulum* and *E. ivaniosi*. All these features should be considered as genuine information on the species *E. revolutum*, because they are based on examination of larvae and adults belonging to *E. revolutum* (*sensu stricto*). Its histology, histochemistry, protein fractions, antagonism, hyperparasites and other characteristics are described in Kanev (1985).

Voucher specimens. Adults of *E. revolutum* obtained experimentally during these studies are deposited in the Naturhistorisches Museum Vienna, Austria, slide Nos 3285, 3286 and 3287; the Naturhistorisches Museum Berlin, Germany, slide Nos 7215, 7216 and 7217; and the Harold W. Manter Laboratory of Parasitology, (HWML), Lincoln, Nebraska, USA, slide Nos 34801, 34802, 34803.

Conclusions

In summary, no specimens collected from naturally infected hosts in Africa and both North and South America can represent *Echinostoma revolutum* (*sensu stricto*) because this species does not occur in these regions. No specimens collected from mammals can represent *E. revolutum* because this species does not infect these hosts. To date, *E. revolutum* has not been documented from Australia. From western Europe to east Asia, many specimens labelled as *E. revolutum* are available in private and museum collections, but only those obtained from experimental studies beginning with known stocks (and reports of such studies under the synonyms *E. audyi*, *E. ivaniosi* and *E. paraulum*) can be accepted as documented representatives of the species, because the distinguishing characteristics are found only in the larvae and the host/parasite relationship. Unfortunately, it must be concluded that adults of *E. revolutum* cannot be identified using morphological criteria.

It is proposed that worms with 37 collar-spines belonging to genus *Echinostoma* that are found in naturally infected birds in Europe and Asia be referred to an "*E. revolutum* group" unless enough information is available to differentiate them.

With regard to literary sources of information, the descriptions and illustrations of *E. revolutum* published by Dietz (1909a,b, 1910), Johnson (1920), Lutz (1924), Beaver (1937), Mendheim (1940, 1943), Supperer (1959), Skrjabin (1947, 1956), Bisseru (1953, 1967), Yamaguti (1958, 1971, 1975), Odening (1964), Patnaik & Ray (1966), McDonald (1969, 1981), Kosupko (1972), Moravec *et al.* (1974) and Nasincova (1986) are not considered valid, because adults and larvae of other species were described under this name. The present paper should be considered as a valid source of information on *E. revolutum* (*sensu stricto*).

Acknowledgements

This work was supported by research grants from the Bulgarian Academy of Sciences and the Fond National Investigations (grant No. NIB-231). Some studies and travel expenses were sponsored by grants from the Naturhistorisches Museum, Vienna, Austria; CNRS, France; Consejo Superior de Investigationes Cientificas, Spain; DAAD, Germany; British Council, UK; William C. Campbell Endowment Fund, USA; Private Company "VEDIZA", Bulgaria; Holiday Travel Service, USA; National Academic Foundation, Sofia; and Open Society. Dr E. Kritscher, Vienna, and Dr G. Hartwich, Berlin, provided specimens and original descriptions and illustrations, and U. Eisenhud, Erlangen, helped with live material. Mrs I. Petkova, Mrs M. Macheva, Mrs E. Kazandjieva, Dr V. Radev and Mr D. Vlaev are also gratefully acknowledged for their excellent technical assistance. Thanks are given to Prof. M. Pritchard, Prof. C. Arme and Dr A. Jones for their critical reading of the manuscript.

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