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The morphology, life-cycle and geographical distribution of Paramphistomum cervi (Zeder, 1790) (Trematoda: Paramphistomata)

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ABSTRACT. Paramphistomum cervi (Zeder, 1790) is the first rumen fluke to be discovered, parazitising wild and domestic ruminants, a total of 13 species. Morphology of the fluke, histomorphology of its muscular organs, preparasitic and larval stages, intermediate hosts and the prepatent period as well as the numerous distributional data have been reviewed in full length.

The first information published on the rumen fluke, without designating the species was made by DAUBENTON (1754) and later by FALK (1782) whose data probably referred to this species on the basis of the habitat (rumen) and the locality (Europe) of the parasite[+]. In the same year SCHRANK (1790) and ZEDER (1790) reported on the finding of a fluke in the rumen of red deer under the names Fasciola cervi and Festucaria cervi[++].

After several changes of the generic and specific names Fasciola elaphi Gmelin, 1791; Monostoma elaphi (Zeder, 1800); Monostoma conicum Zeder, 1803 RUDOLPHI (1890) transferred it to the genus Amphistoma and its name was amended Amphistoma conicum. NITSCH (1819) established the genus Amphistomum for the group of species which was included in RUDOLPHI's genus Amphistoma, characterized, among others, by the existence of a mouth at the anterior and a sucker at the posterior body ends.

At the end of the 18th and in the 19th century, several authors (ZEDER, 1790; LAURER, 1830; BLUMBERG, 1871; OTTO, 1896) published information on the morphology of this species. These descriptions, however, were not always exact. At times they dealt, erroneously, with certain organs and from time to time they did not refer with full certainty to P. cervi.

Rumen flukes, accumulated in museums and in private collections were examined by FISCHOEDER (1901-1904) on the basis of a meticulous comparative work concerning morphological characters, when he was able to isolate several new species from the test material regarded to be homogenous, up to that time chiefly comprising A. conicum. Instead of Amphistomum he established the genus Paramphistomum and all flukes of such a type were transferred into the family Paramphistomidae also erected by him. The name "amphistoma" has, however, been used until today as a trivial one, and it seems to be equally suitable to designate certain groups or the whole taxon of this type of flukes.

The guiding principles elaborated by FISCHOEDER (1903) have only been utilized to a somewhat limited extent by subsequent authors but after the publication of MAPLESTONE's (1923)

[+] It became evident only much later that more than one species of rumen flukes exists in Europe.

[++] Since the establishment of priority is difficult or impossible the present author shares FISCHOEDER's (1903) opinion in this respect.

paper, P. cervi became an "assembling" species. By overestimating the individual variations he has sunk eight species into its synonyms whereby P. cervi was furnished with many kinds of morphological pecularities along with a broad geographical range. MAPLESTONE's (1923) notion on the nature of specific features has seemingly influenced succeeding authors (FUKUI, 1929; STUNKARD, 1929; BAYLIS, 1929; TRAVASSOS, 1934; DAWES, 1936), and its effects are, sometimes, recognizable even now.

In his monograph NÄSMARK (1937) successfuly realized LOOSS's (1912) conjecture that the most important, if not the single, specific features of the closely releated species of paramphistomids can be found in the structure of the genital opening. The conception worked out by NÄSMARK (1937) is an important contribution to the classification of the amphistomes but in some cases, as is the case with P. cervi, the critical consideration does not seem indispensable.

Since the first description of scientific value (FISCHOEDER, 1903) the scope of the morphological characters of P. cervi has varied depending on the number of the synonyms designated by subsequent authors writing about newly discovered rumen flukes. Accordingly, its geographical distribution has altered along with the change in synonymous terms and hence P. cervi was indicated in some text-books as a species having cosmopolitan distribution.

This paper intends to clear up the confusion in connection with P. cervi and to summarize information accumulated on this species as to the topics involved by the title.

MATERIALS AND METHODS

Samples of the test material available, suspected to have been involved P. cervi derived from the areas below; countries in brackets are included from which samples were expressly labelled as P. cervi: from Europe almost every country (SEY, 1980b); from Asia: Afganistan, (India), Indonesia, Iraq, (Iran), Malaysia, (Mongolia), China, Syria, Turkey, Vietnam; from Africa: Algeria, (Angola), Cameroon, Central African Republic, Republic of Chad, Congo, Egypt, (Ethiopia), (Ghana), (Guinea), Kenya, Morocco, Niger, Rhodesia, Togoland, Tanzania, Uganda and (Malagassy); from Americas: Argentina, Brazil, Canada, Chile, Columbia, Costa Rica, (Cuba), Guyana, Venezuela, (USA) and New Zealand.

Samples of the said countries were made available for examination, in part, by the USNM Helminthological Collection, Beltsville, USA; the Muséum D'Histoire Naturelle, Geneva, Switzerland; Zoologisches Museum, Berlin, GDR; Muséum D'Histoire Naturelle, Paris, France; Naturhistorisches Museum, Vienna, Austria; Naturhistoriska Riksmuseet, Stockholm, Sweden and several colleagues with whom rumen fluke examinations were carried out in collaboration. More than two hundreds of median sagittal sections were prepared by the usual method.

In the life-cycle study the eggs had been collected from mature flukes after having been removed from rumina of red deer shot in the State Forestry and Game Reserve, Gemenc, Hungary. Laboratory reared Planorbis planorbis were used as intermediate hosts and susceptibility of young specimens of Bulinus truncatus of Sardinia were also tested. As a final host roe deer was used. In the course of the life-cycle study the applied method was as described earlier (SEY, 1979a).

RESULTS AND DISCUSSION

FISCHOEDER's (1903) description of P. cervi was based on morphological features and it was supplemented by NÄSMARK (1937), attributing an important role to the histological structure of the muscular organs. According to him the pharynx was designated as a Liorchis-, the genital opening as a Gracile- and the acetabulum as a Paramphistomum-type. He remarked that the papillae in the pharynx were inconspicuous and the genital opening was entirely without radial musculature.

Divergent opinions can already be found in the old literature on the presence or the absence of the papillae situated in the pharynx. OTTO (1896) did not find them in specimens which had died in water before fixation while BLUMBERG (1871) and FISCHOEDER (1903) found this structure in every examined specimen. Recent examinations (KATKOV et al., 1971; KAMBUROV, 1977; ZDZITOWIECKI et al., 1977; GRAUBMANN et al., 1978; ODENING & GRÄFNER, 1979) and personal observations, based on sections of specimens both treated and non-treated in water before fixation showed that in the latter ones the papillae were constant elements (about 30 µm in length) of the pharynx and their absence was the consequence of the watery pretreatment, as observed by OTTO (1896).

In the single section of P. cervi found in NÄSMARK's collection, these papillae were also recognizable when they were in the state of the moment of detachment (Fig. 1).

The types of pharynxes, "modified liorchis" and "pseudo liorchis" described by WILLMOTT (1950) and VELICHKO (1966) respectively come within the scope outlined by NÄSMARK (1937) under the name, Liorchis-type (SEY, 1977, 1980b).

The Gracile-type of genital opening in P. cervi, was described in connection with the species, Paramphistomum gracile. It was characterized by NÄSMARK (1937) by the entire absence of the radial musculature. The presence of such a musculature in the genital opening of P.cervi was already pointed out by FISCHOEDER (1903); in NÄSMARK's (1937) paper there is a controversy between the description and the figure accompanying the text (p. 447, Fig. 90). In the drawing the radial musculature is easily recognizable, moreover these muscle elements were also found in the single section of NÄSMARK's collection (Fig. 2). In examining NÄSMARK's section it was ascertained that it was prepared from a specimen kept in water before fixation (pharynx protruded, parenchymal cells enlarged and empty etc.). Thus, the structure attributed by NÄSMARK (1937) to this type of genital opening is rather an artificial picture and it is a consequence of a pre-fixative treatment (SEY, 1980b).

Our observations, based on well-fixed test material of the species belonging to the genus with this type of genital opening (P. cervi, P. gotoi, P. gracile) showed, however, that the radial musculature occurred as more or less developed muscular fibres (Figs. 3, 4, 5). The amended Gracile-type in the sense of the present paper shows similarity to the Epiclitum which was relegated as a synonym of the Gracile-type by KAMBUROV (1976). The Epiclitum-type was reserved by NÄSMARK (1937) for P. leydeni and P. epiclitum of this genus. The writer is of the opinion that the type of genital opening of P. leydeni should be included in the presently amended Gracile-type but accepts the validity of the Epiclitum-type owing to the different structures in the Gracile-type (Fig. 6).

Among the species, now regarded to by synonyms of P. cervi two types of acetabula (Paramphistomum, Liorchis) have been described. The structure of the Liorchis, created by VELICHKO (1966) for P. hiberniae (= Liorchis hiberniae) and P. scotiae (= L. scotiae) did not prove to be constant in the light of the examination carried out later by SEY (1974), KAMBUROV (1976, 1977), ODENING & GRÄFNER (1979). These authors were of the opinion that the Liorchis-type belongs to the Paramphistomum one, as outlined by NÄSMARK (1937). Recently PACENOVSKY & KRUPICER (1979), however, have found that the acetabulum of L. scotiae (= P. cervi in the sense of this paper) is of the Liorchis-type, as specified by VELICHKO (1966). More recently SEY (1980b) came to the conclusion, on the basis of the examination of VELICHKO's specimens that this type of acetabulum comes within the NÄSMARK's Paramphistomum-type.

Diagnosis:

Body dimensions: length 6-14 mm, breadth 2-4 mm, dorso-ventral measurements 2.5-4.5 mm. Pharynx 0.8-1.2 mm in length, Liorchis-type with papillae (23-38 µm in length) along its anterior thirds, median circular layer well observable in its full length. Caeca in lateral region, forming 4-5 convolutions, end parts tend to dorsal side at anterior margin of acetabulum. Oesophagus without muscular thickening.

Genital opening: Gracile-type with weakly developed radial muscle fibres; diameter 0.30-0.93 mm; pars musculosa short, with a single convolution, prostatic cells in several rows. Testes: tandem or one somewhat obliquely behind th other, coarsely lobed with 3-5 lobuli; measurements: anterior, 1.8-2.2 by 2.3-2.9, dorso-ventral dimension: 1.3-1.8; posterior, 1.1-1.7 by 2.7-3.6, dorso-ventral dimension: 1.4-1.9 mm. Size of eggs: 116-189 by 52-116 µm. Acetabulum: 1.0-2.6 mm in diameter; DE1 9-23, DE2 15-48, DI 34-63, VE 12-28, VI 33-64, Paramphistomum-type.

Synonyms:

Festucaria cervi, Zeder, 1790; Fasciola cervi Schrank, 1790; Fasciola elaphi Gmelin, 1791; Monostoma elaphi (Zeder, 1800); Monostoma conicum Zeder, 1803; Amphistoma conicum (Rudolphi, 1809); Amphistoma cervi Stiles & Hassal, 1900; Paramphistomum cervi (Zeder, 1790) of Maplestone, 1923, in part; of Travassos, 1934, in part; P. cervi (Schrank, 1790) of Dawes, 1936, in part; P. (Paramphistomum) cervi (Scrank, 1790) of Fukui, 1929, in part; P. leydeni Näsmark, 1937; P. hiberniae Willmott, 1950 (= Liorchis hiberniae Velichko, 1966); P. scotiae Willmott, 1950 (= L. scotiae Velichko, 1966).

Definitive hosts

Alces alces, Bison bonasus, Bos taurus, Bos grunniens, Bubalus bubalis, Capra hircus, Capreolus capreolus, Cervus elaphus, Cervus nippon, Dama dama, Ovis aries, Ovis musimon and Rangifer tarandus.

LIFE-CYCLE EXAMINATIONS

Under the name of P. cervi and in the sense of the scope of P. cervi presented in this paper, information on the whole process or certain stages of its life-cycle was published by LOOSS (1896), NÖLLER & SCHMIDT (1924), TAKAHASHI (1927), KRULL (1933), SZIDAT (1936), WILLMOTT (1952), DADURYAN (1953), WILLMOTT & PESTER (1955), KRYUKOVA (1957), GRETILLAT (1958), ABDEL-GHANI (1961), POGORELYI & MEREMINSKIĬ (1963), BORTNOVSKIĬ (1964), NIKITIN (1967, 1968), GLUZMAN (1969), KRANEBURG (1977), KRANEBURG & BOCH (1978), ODENING et al. (1978) and ODENING et al. (1979).

On the basis of personal examinations and literary data, the life-cycle of P. cervi is summarized as follows.

Preparasitic stages

Eggs and embryonic development

Eggs of P. cervi are greenish yellow, covered by colourless shell. Their shape may be piriform, oval or elliptical. The antiopercular pole bears a minute spine. Measurement of eggs are 116-189 by 52-116 µm. Variations of egg size could be observed not only among the eggs laid by a worm population but also among those of separate specimens. No direct correlation appears to exist between the body dimension of the fluke and that of the eggs.

Newly laid eggs contain zygote situated near to the opercular end of the egg and during the subsequent divisions it moves towards the centre of it and becomes surrounded by vitelline cells.

During incubation at 27°C no significant change can be observed in the first 4-5 days except for the growth of the embryo. On the 5-6th days, the terebratorium, the single apical as well as the four penetrating glands appear. On the 7th day the flame cells, found by the joining of the second-third epidermal cell rows, begin their activity. The formation of the germinal tissue also takes place during this period.

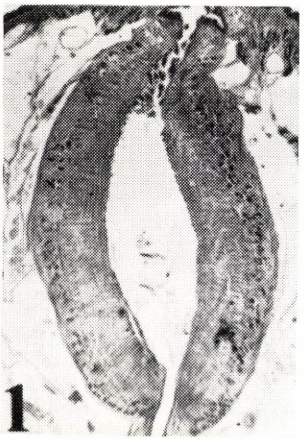
With the growth of the embryo, the vitelline cells gradually decrease and their place is occupied by two large vacuoles. Mucoid plug is not observable (Fig. 7). On the 8th and 10th days, the embryo reaches a size of 110-145 µm and the embryo (miracidium) is ready for hatching. Under controlled temperature (27°C) hatching of miracidia usually begins on the 8th day, and it continues on the following two-four days. After the optimal period of hatchability (10th day) the life span of the embryos is much shorter than that of P. daubneyi (SEY, 1979a).

The eggs maintain vitality, under low temperature (4-6°C) for 5-6 months, suggesting the possibility of hibernation in the temperate belt.

Figs. 1-6. Median sagittal sections of pharynx (1: Paramphistonum cervi, Näsmark's material) and genital openings (2: P. cervi, Näsmark's material; 3: P. cervi, own material; 4: P. gotoi Iraqi material; 5-6: P. garcile and P. epiclitum, Indian material; Figs. 2-6 were taken with the same magnification)

Figs. 7-13. Stages of development of P. cervi - 7: egg with fully developed miracidium; 8: living miracidium; 9: epidermal cells of miracidium; 10: four-day-old sporocyst; 11: mature redia with young cercariae, one of them bears eye spots; 12: mature cercaria; 13: encysted metacercariae on aquatic plant

Figs. 14-18. Median sagittal sections of pharynxes (14: P. gotoi, Iraqi material; 15: P. liorchis, Näsmark's material; 16: P. cervi, own material) and genital openings (17-18: P. liorchis, Natterer's material from Vienna Museum) (Photo by O. SEY)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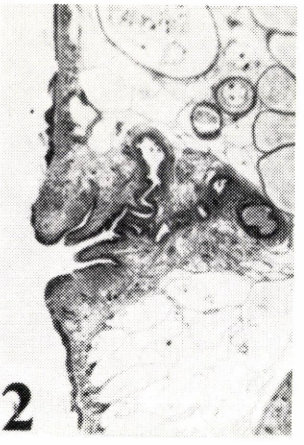
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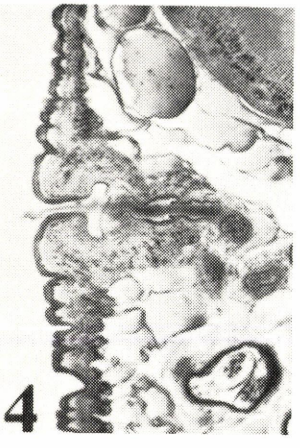
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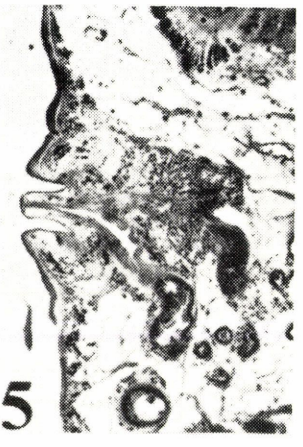
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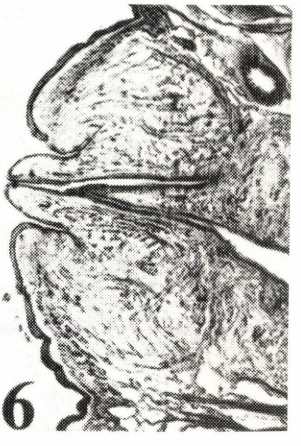
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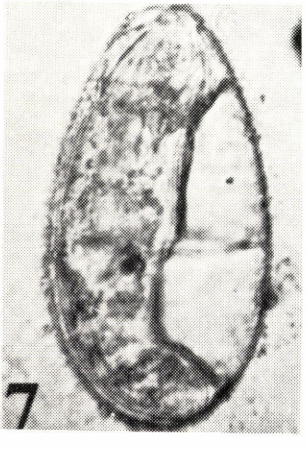
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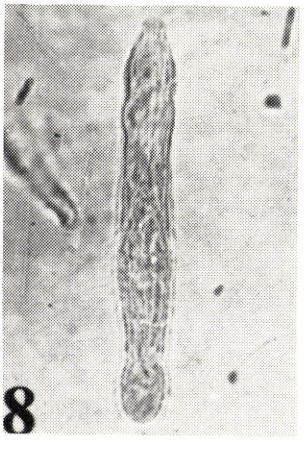
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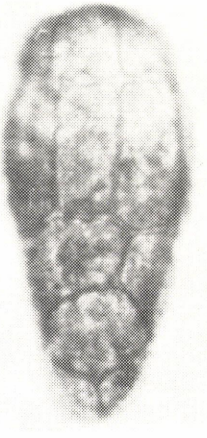
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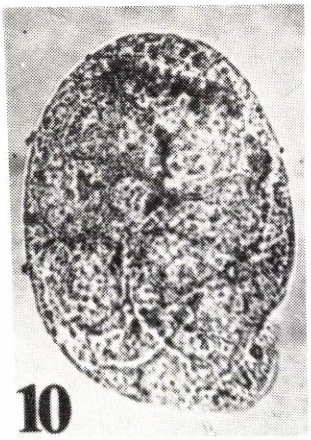
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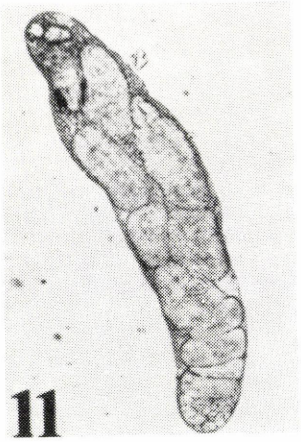
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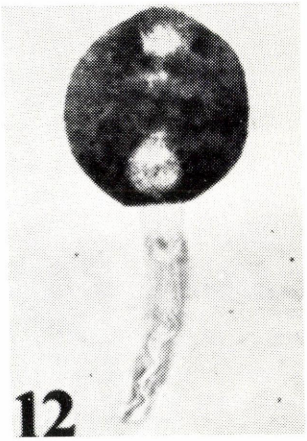
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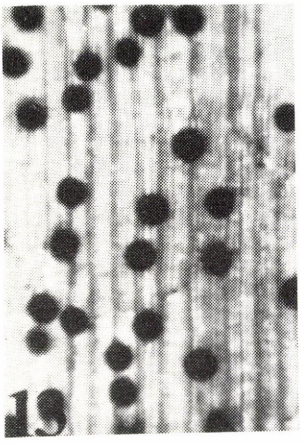
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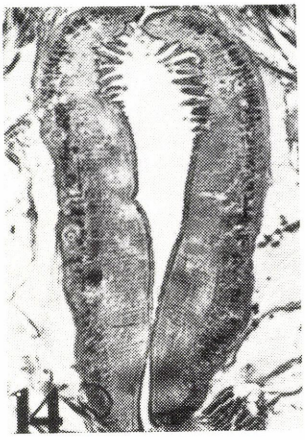
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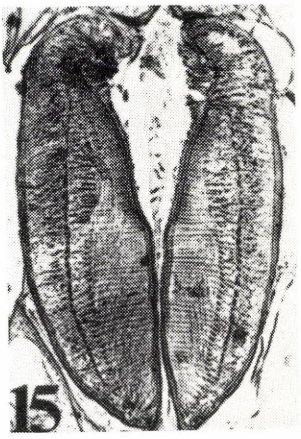
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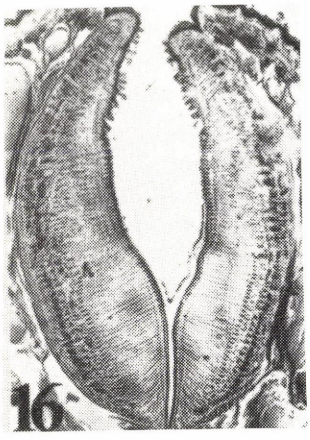
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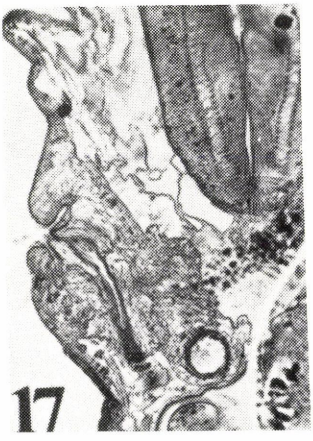
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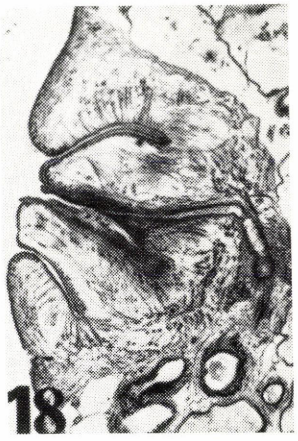
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Miracidium

The hatched and free-swimming miracidium is fusiform without eye spot, covered with cilia (Fig. 8). The measurements of the living miracidia: 175-200 by 40-50 µm, the fiexed ones are 120-125 by 55-58 µm. The body is covered with flat epidermal cells in four transverse rows according to the formula 6:8:4:1 (Fig. 9).

At the anterior end of the miracidium lies the cilium-free terebratorium with argentophilic structures. They are situated along three axes, $T_1 = 5$, $T_2 = 14$, $T_3 = 10$; a further 12 similar structures can be found along the body, 10 of them between the first and the second epidermal cell rows and two between the second and the third ones.

The inner miracidial structure consists of the apical gland, the penetration glands, the nervous system, the excretory ducts and the germinal tissue, similar to that of other miracidia of rumen flukes (LENGY, 1960; SEY, 1979a).

The life-span of miracidia kept in tap water at room temperature was 10-12 hours but their virulence limited to the first four hours only.

Intermediate hosts and infectional experiments

Several sets of infections were performed with young (2-3 weeks old) Planorbis planorbis under room temperature (20-22°C). Two-five miracidia were added to snails kept in water individually in the hollows of a microtiter plastic plate. Infection was successful in 75-90% of the snails thus treated.

Three hundred of young specimens (2-3 weeks old) of Bulinus truncatus were also infected by the same method with miracidia of P. cervi. These snails suffered no infestation indicating that the miracidia of P. cervi are not susceptible to this snails.

According to literary data (SZIDAT, 1936; KRYUKOVA, 1957; WILLMOTT & PESTER, 1955; ZDUN, 1958; NIKITIN, 1968; GLUZMAN, 1969; MEREMINSKIĬ et al., 1971; ASADOV et al., 1972; KATKOV, 1973; KRANEBURG, 1977; KRANEBURG & BOCH, 1978; ODENING et al., 1978; ODENING et al.,1979) the following planorbid snails have been recorded as intermediate hosts: Anisus leucostomus, A. spirorbis, A. septemgiratus, A. vortex, Argimer crista, A. inermis, Bathyomphalus contortus, Choanophalus anophalus, Gyraulus albus, G. gredleri, G. elenbergi, Hippeutis complanatus, Planorbis carinatus, P. planorbis and Segmentina nitida.

Susceptibility of P. cervi to different planorbid snails and the unsuccessful experiments with Bulinus truncatus as well as the resistence to other than planorbids (Lymnaea, Physa, Radix, ODENING et al.,1979) allow us to support that LOOSS (1896), GRETILLAT (1958) and ABDEL-GHANI (1961), who indicated bulinid snails in their life-cycle studies, in fact had worked with other species of flukes, probably with P. microbothrium which is a common rumen fluke of that area (SWART, 1954; PRUD'HON et al., 1968; SEY, 1976, 1977; SEY & ABDEL-RAHMAN, 1975) and of which intermediate hosts are bulinid snails. KRULL's (1933) species has probably been other than P. cervi because the intermediate hosts listed by him are lymnaeid snails.

Intramolluscan larval stages

Sporocyst

After penetration, the invading miracidium continues its development in the snail tissue; undergoing noticable changes: shedding of epidermal plates, losing some internal structures (apical papilla, apical and penetration glands) and breaking down of embryo balls into separate germinal cells (Fig. 10).

The sporocyst shows a marked increase in size; e.g. the four-day-old specimen measures 160-170 by 140-150 µm; it reaches maturity in 10-15 days. NIKITIN (1968) and KRANEBURG (1977) indicated longer periods of maturation while GLUZMAN's (1969) findings agree with our observations.

Mature sporocyts are located in the body cavity of the snail, along the digestive truct; it is covered by a thin, transparent envelope and contains some fully developed rediae and numerous embryo balls. One pair of flame cells was found in the sporocyst; neither the process of liberation of the rediae nor the opening of the sporocyst's surface were observed.

Redia

The first free rediae emerged on the 13-15th days after infection. Young rediae measure 150-230 μm in length and 75-180 μm in width. During their further development they grow markedly and appear to reach their maximum when liberation of cercariae begins. The first mature rediae were perceived on the 15th day after liberation and their measurements were 700-1100 by 200-250 μm (Fig. 11).

In the inner structure, a digestive system, a nervous system, an excretory system and a germinal tissue can be distinguished. The digestive system includes a mouth, a pharynx, an oesophagus and an unpaired gut. The mouth is a minute opening followed by the muscular pharynx, measuring 30-50 by 38-50 μm. The oesophagus is short, 15-20 μm in length, sourrounded by the so-called salivery glands and leading to the gut. The latter measures 75-125 μm in length and 50-80 μm in width.

The centre of the nervous system is situated at the level of the oesophagus and it is very similar to that of the miracidium.

The excretory system comprises three pairs of flame cells and their ducts which unite at about the middle of the body and they open to the outside through a small common bladder.

The germinal system is situated in the second half of the young rediae consisting of the germinal epithelium, germinal cells and embryo balls. The latter develop gradually into cercariae.

The birth pore becomes prominent only later, when young cercariae begin to accumulate in the first part of the body. The distance from the anterior body end is 300-320 μm. In about fifty days the signs of aging could be discerned (dirty grey and dark spots are found, body cavity is empty) and these rediae were gradually dying off.

Cercaria

Cercariae at birth are poorly developed; the first free cercariae were recovered on the 30-37th days after infection, measuring 250-375 μm with a tail appendage of 100-125 μm in length and 75-80 μm in width. The eye spots can already be seen when cercariae are within the redia.

The first mature cercariae develop between the 45-55th days after infection. They are dark brown, quikly swimming organisms, with a body measuring 300-340 by 200-325 μm and tail 400-500 by 65-75 μm.

The body is covered with tegument, having cystogenous cells and rods. These rods make the body opaque, the scattered pigment granules lend a brown colour to the body.

A pair of eyes are located on the dorsal surface of the mature cercaria, they are conical in shape. The acetabulum is situated at the posterior end on the ventral body surface, measuring 95-110 by 90-110 μm in living specimens (Fig. 12).

The inner structure of the cercariae consists of the digestive system (pharynx, oesophagus, gut), excretory system (flame cells, ascending and descending excretory ducts, caudal exretory tube and bladder), nervous system and primordia of the reproductive system. The number of the flame cells was not detectable exactly due to the opacity of the body.

Sensory papillae could be observed along the tail, twenty-five pairs were found in the region above the excretory pores and two pairs beyond it.

Larval stages of P. cervi hibernate in the intermediate host (Planorbis planorbis); in an endemic area of Hungary (Gemenc) 11.9% of P. planorbis, born in the previous year, dissected at the end of April, 1975 contained fully developed cercariae.

Metacercaria

Shortly after emergence, the cercariae encyst on the vegetation (Fig. 13). The metacercariae are spherical in appearance, measuring 180-250 μm in diameter. Among environmental factors strong illumination stimulated emergence. Under low temperature (4-8^{o}C) the life-span of metacercariae lasted for two-three months.

Development in definitive hosts

In order to determine the prepatent period of P. cervi, a seven-month-old roe deer was infected with 2000, two-week-old metacercariae. Feacal samples were regularly controlled and the first eggs were found on the 85th day after infection. The percentage take was 42.3%.

The prepatent period was 96-130 days in cattle (NIKITIN, 1968; GLUZMAN, 1969; GLUZMAN & ARTEMENKO, 1969; MEREMINSKIĬ et al., 1971; KLESOV & MEREMINSKIĬ, 1973;

KRANEBURG & BOCH, 1978), 96-107 in sheep (GLUZMAN, 1969; GLUZMAN & ARTEMENKO, 1969; KRANEBURG & BOCH, 1978) and 82-96 in roe deer (KRANEBURG & BOCH, 1978).

The life-span of P. cervi was estimated to be four years in cattle (KLESOV & MEREMINSKIĬ, 1973).

GEOGRAPHICAL DISTRIBUTION

On the analysis of the range of P. cervi it seems to be reliable to examine the specific identity of the other three, closely related species, P. gotoi Fukui, 1922, P. gracile Fischoeder, 1901 and P. liorchis Fischoeder, 1901 because these species are morphologically similar to each other, their distribution coincides with that of P. cervi in certain areas and because P. gracile and P. liorchis were regarded to be synonyms of P. cervi by DAWES (1936).

P. gotoi was described by FUKUI in Japan; later it was discovered in different localities of the Palaearctic region by RAFYI et al., (1968), Iran; STEPANOV (1969), USSR; SEY (1978), Roumania; PACENOVSKY et al., (1975), Mongolia.

P. cervi and P. gotoi can be distinguished by the longer papillae (75-80 µm) found in the pharynx of P. gotoi (Fig. 14) and by the pharynx/body length index (NÄSMARK, 1937, unpublished own ata) but the specific value of the latter is in need of further verification based on properly fixed and more extensive test material. The range of these species overlaps in the Palaearctic region.

P. gracile was found for the first time in the Oriental region and described by FISCHOEDER (1901- 1903). Outside this region it was reported from Mongolia (PACENOVSKY et al. 1975), Iran (SEY, unpublished data). PACENOVSKY et al.'s (1975) findings seem, however, to be questionable. The structure of the pharynx attributed to this species by the those authors (Paramphistomum) has the appearance (seen on the drawing, p. 194, Fig. 2) of the Liorchis-type devoid of papillae which is also characteristic for P. cervi. Otherwise, in the amphistome collection, available to the present writer from domestic ruminants of Mongolia only P. cervi was discovered.

P. cervi and P. gracile are easily distinguishable by the structure of the pharynx, the former has Liorchis-, the latter Paramphistomum-types. The distributional area of these species coincides in the Palaearctic region.

P. liorchis was described by FISCHOEDER (1903) on the basis of the samples collected by NATTERER from different deers in Brazil. As the main specific features, the shape and size of the body as well as the spherical testes were, designated among others. NÄSMARK (1937) examined the histomorphology of the muscular organs of specimens derived from the same collection. The pharynx and the genital opening were depicted as Liorchis-type with special emphasis on the length of papillae of the pharynx (Fig. 15) and the circular musculature in the genital opening.

The writer had the possibility to examine specimens of NATTERER's collection (Vienna Museum), as well as sections of FISCHOEDER's and NÄSMARK's. It can be stated that NATTERER's specimens had been treated in water before fixation. Thus sections prepared from these samples showed different pictures as to the main specific features mentioned by the authors above. The papillae in the pharynx were present in some specimens (50-75 µm in length), so that is longer than that of P. cervi (Fig. 16) while in others the papillae were eliminated, probably due to the watery treatment. The testes were spherical with either smooth boundaries or with some narrow infoldings which do not, however, form such coarse lobuli as known in P. cervi. In the genital opening the circular muscle elements occurred in some specimens (Figs 17, 18) while in others they were not observable. In the latter cases it can be supposed that their absence is the consequence of pre-fixative treatment.

Anyway, it should be remembered that the structure of the muscular organs of P. liorchis has been examined up to now on specimens derived from NATTERER's collection and thus it is difficult to ascertain the scope of the alteration caused by unsuitable fixation. Nevertheless, our knowledge on the consistency of the structure of the muscular organs comes from the examinations of several other amphistomes allowing to suppose that the characteristics of this species designated by NÄSMARK (1937) can be regarded to be stable and specific even if these were not observable in every specimen of the writer's preparations due to reasons mentioned above.

P. cervi and P. liorchis can share the same distributional range in the Nearctic and ? Neotropic regions. The species identity of P. gracile and P. liorchis is unquestionable but the differentiation of the four species in question requires well-prepared median sagittal sections because the relatively small specific features can be detected only in such preparations.

A great number of papers have been published on the occurrence of P. cervi in different parts of the world. These papers can be divided into two groups on the basis of their capacity.

The first comprises papers containing nomination of this species only, without further information or comments. Since P. cervi and the closely related species in question are characterized by minute histo-morphological features, in the case of these papers it is almost impossible to ascertain the proper systematic status of species involved by these papers, unless by any indirect way. The usage of such papers in the outline of the distribution of P.cervi is rather limited. The second group of papers either deal with this species explicitly or include descriptions or drawings from which the species' status can be decided more or less accurately.

FISCHOEDER (1903) and NÄSMARK (1937) were of the opinion that P. cervi has an European distribution only. Information accumulated in the last decades has, on the one hand, increased the range of P. cervi and, on the other made our knowledge on its distribution more precise, supporting well-established evidence that P. cervi occurs in the Palaearctic region and in some other territories, too.

Of the numerous reports referring to its presence in the Palaearctic region and in the European part of the Mediterranean area, the distributional data of P. cervi were summarized in the author's earlier paper (SEY, 1980b), pointing out that it was found in almost every European country.

Many papers are concerned with the distribution of P. cervi in the Siberian and the Manchurian areas and the present paper can be confined to the most important ones. In these areas it was recovered in the USSR (SKRJABIN & SCHULTS, 1937; EVRANOVA, 1954; ASADOV, 1960; KADENATSII, 1963; MITSKEVICH, 1963; OVCHARENKO, 1963; ROMASHOV, 1963; VELICHKO, 1966, 1968; ZHALTHANOVA, 1969; RUZIEV, 1972), in Mongolia (IVASHKIN, 1955; own unpublished data), Korea (HI, 1958; CHU, 1972), in Japan (TAKAHASHI, 1927; FUKUI, 1929[+]), and China (HSU, 1935; WU et al. 1956 and the material, deposited in the USNM, derived from Lanchov, China).

In the Asian part of the Mediterranean area P. cervi was reported from Turkey (MERDIVENCI, 1957; own unpublished data), in Pakistan (RAHMAN, 1958), Iran (RAFYI et al. 1968; own unpublished data) and Iraq (ALTAIF et al. 1978; but taking the intermediate hosts listed in this paper into account, this species does not seem to be P. cervi).

In the Nearctic and the Neotropic regions P. cervi was reported from Canada (THRELFORD, 1967; LANKESTER et al., 1979), from the USA (OLSEN & FENSTERMACHER, 1942; DIKMANS, 1939; PRICE, 1953; BECHLUND, 1964), Mexico (QUIROZ & OCHOA, 1973), in Cuba (KOTRLA & PROKOPIC, 1973), Panama (FOSTER, 1939), Costa Rica (BRENES, 1961; CABALLERO et al. 1957), Venezuela (VOGELSANG, 1935; CABALLERO & DIAZ-UNGRIA, 1958), Argentina (NIEC, 1972) and Brazil (VELÁZQUEZ-MALDONADO, 1976). TRAVASSOS et al. (1969) and DIAZ-UNGRIA (1973) seemingly are of the opinion that P. cervi is not found in Brazil and Venezuela, respectively.

On the basis of the amphistome material derived from Canada as well as the sections deposited in the USNM, examined by the writer, it seems that the occurrence of P. cervi in the in the Nearctic region is rather questionable. The same can be said, in spite of several reports as to the presence of this species in the Neotropic region because it is difficult to ascertain (in the absence of appropriately fixed test material and histo-morphological examinations) whether they really refer to P. cervi or the species indigenous in this region (P. liorchis).

The number of publications on the presence of P. cervi in the Ethiopian region and the African part of the Mediterranean area (North Africa) is more than could be listed in the scope of this paper, consequently, we should be limited to those which bring sufficient proof that the species described under this name is not P. cervi.

LOOSS (1912) stated that what he himself had earlier (1896) believed to be P. cervi (= Amphistomum conicum) from Egypt was P. microbothrium. DINNIK (1951) found P. cervi in East Africa but subsequent examination (DINNIK, 1952; DINNIK & DINNIK, 1954) showed that in fact it was P. microbothrium. Recent investigations in Egypt (SEY, 1976, 1977; SEY & ABDEL-RAHMAN, 1975) revealed that P. cervi of ABDEL-GHANI (1961) and of TADROS (1958) were again identical with P. microbothrium.

SWART (1954), after examination of the amphistome material from cattle in the Republic of South Africa, came to the conclusion that the so-called P. cervi was in fact P. microbothrium. CEIRO (1961) also expressed his doubt concerning the presence of P. cervi in Angola.

[+] YAMAGUTI (1971), however, is of the opinion that TAKAHASHI (1927) had before him P. gotoi and not P. cervi. At the same time, ASIZAWA et al. (1969) again discovered a P. cervi-type fluke in Japan.

After studying the amphistome collection of the Geneva Museum, the writer found that samples from Angola, Ghana, Guinea and Mozambique, labelled as P. cervi proved to be another species of amphistomes of the local fauna (SEY, 1980a).

Papers including drawings on the genital opening of P. cervi (DOLLFUS, 1932, Niger; EZZAT, 1945, Giza Zoo Garden, Egypt) indicate that the authors had worked with species other than P. cervi.

BALOZET & CALLOT (1938) examined bulinid snails in Tunisia and found them to be infected with cercariae of P. cervi. GRETILLAT (1958) studied the life-cycle of P. cervi in Madagascar, the intermediate hosts were listed as Bulinus mariei and B. liratus. Both BALOZET & CALLOT's (1938) as well as GRETILLAT's (1958) findings indirectly indicate that their material was not P. cervi because this species, according to our observations, is resistant to Bulinus truncatus and probably to other bulinids, too.

It appears that P. cervi is not to be found as an endemic species in Africa. Whereas we may not preclude the possibility of its introduction by the importation of livestock, presently there is no correct data on the occurrence of P. cervi in Africa

In the Oriental region there are several papers reporting on the presence of P. cervi in India (BHALERAO, 1935; THAPAR, 1956; MUKHERJEE & CHAUHAN, 1965), Malaysia (DAWES, 1936; LANKESTER, 1957); Vietnam and Cambodia (DROZDZ & MALCZEWSKI, 1967; SEGAL et al., 1968; LE, 1978), Philippines (TUBANGUI, 1925) and Celebes (YAMAGUTI, 1954).

TUBANGUI (1933) himself made a correction as to his earlier determinations and EDUARDO & MANUEL (1975) regarded the presence of P. cervi in Philippines to be questionable. MUKHERJEE & CHAUHAN (1972) were of the opinion that P. cervi is not so common, if at all found, as other authors described it. The present writer having examined several samples from different parts of India as well as of Indian institutes, labelled as P. cervi, found (SEY, 1979b) that they proved to be either P. epiclitum or P. gracile but none of P. cervi. It is difficult to decide on or check the proper identifications of the other papers, nevertheless it is most likely that P. cervi is not found in the Oriental region.

In the Australian region ROBERTS (1934), ROSS & GORDON (1936), EDGAR (1938), SEDDON (1947), DURIE (1949) reported on the occurrence of P. cervi in Australia but later DURIE (1951) revealed that in fact Ceylonocotyle streptocoelium and Calicophoron calicophorum had been studied under this name. In New Zealand, however, P. cervi was discovered in the amphistome collection from cattle (SEY et al. in press) which fact can be explained by the intensive introduction of different domestic and wild ruminants to this country (WODZICKI, 1950).

To sum it up, it can be said that P. cervi is a parasite indigenous to the Palaearctic region (except the Ethiopian region and the African part of the Mediterranean area). It is supported by reliable and up-to-date examinations on sections as well as by the fact that the final hosts along its distribution are both wild and domestic ruminants. The many other reports of the other regions, especially those which were not based on histological sections need further examination and justification by the terms of the present standard of amphistome diagnosis. Anthropochore dispersal by importation of exotic stock can operate as it had in the past and the wide spectra of intermediate hosts might to enlarge the range of P. cervi.

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