

Ann. Naturhist. Mus. Wien	94/95	B	11–34	Wien, 1993
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Redescription of *Philophthalmus lucipetus* (RUDOLPHI, 1819) (Trematoda: Philophthalmidae) with a discussion of its identity and characteristics

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(With 41 Figures)

Manuscript submitted July 6th, 1992

Z u s a m m e n f a s s u n g

Philophthalmus lucipetus wurde in Europa einer Neuuntersuchung in bezug auf typische Fundstätten unterworfen. Nachdem vor nahezu 200 Jahren ihre erste Beschreibung vorliegt, ist diese Art noch heutzutage im Allgemeinen unbekannt. Die in den Augenhöhlen von Vögeln und Säugetieren vorgefundenen erwachsenen Exemplare von *P. lucipetus* sind unter 17 verschiedenen Namen beschrieben. In menschlichen Augenhöhlen sind vorreife Stadien entdeckt und unter 18 verschiedenen Namen beschrieben. Larvenstadien von *P. lucipetus* sind mit 4 weiteren Namen bezeichnet. Einige davon dienen zur Beschreibung von erwachsenen Formen und Larven von 6 verschiedenen Arten und Gattungen. Ferner erwies sich die derzeitige Information über die Charaktermerkmale von *P. lucipetus* als grundlegend ungenau, da unter dem Namen *P. lucipetus* Beschreibungen und Abbildungen von erwachsenen und larvalen Formen von 7 verschiedenen Arten vorliegen, während erwachsene und larvale Formen von *P. lucipetus* als 39 verschiedene Arten beschrieben und abgebildet wurden. Gegenstand der vorliegenden Studie ist deswegen die Diskussion und Berichtigung der ungenauen Information über *P. lucipetus*, sowie die Neubeschreibung mit neuen Charaktermerkmalen in bezug auf Identität, Synonyme, Lebenszyklus, Morphologie, Biologie, Ökologie, Wirte und geographische Verteilung.

S u m m a r y

P. lucipetus was reexamined in its type locality in Europe. This species is generally unknown nearly 200 years after its first description. Adults of *P. lucipetus*, found in the eye cavity of wild and domestic birds and mammals, were described with 17 different names. Preadults found in the eye cavity of humans were described with 18 other names. Larval stages of *P. lucipetus* were described

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with 4 other names. Some of these names, especially *M. mutabile* and *P. lucipetus*, have been used for descriptions of adults and larvae of 6 different species and genera. Also, it was found that present information about the characteristics of *P. lucipetus* were fundamentally inaccurate because it combined under the name of *P. lucipetus* descriptions and illustrations from studies of adults and larvae of 7 different species and, conversely, those of *P. lucipetus* are described and illustrated as 39 different species. Here all this inaccurate information is discussed and corrected. *Philophthalmus lucipetus* is redescribed with up dated information on its identity, synonyms, life history, morphology, biology, ecology, hosts and geographical distributions.

Introduction

A large amount of inaccurate information concerning the species *P. lucipetus* (RUDOLPHI, 1819) is distributed in both the old and modern literature. Some of these errors have remained undiscovered for almost 200 years and have caused confusion in interpreting valid philophthalmid species. In this paper *P. lucipetus* is redescribed based on material from its type locality and wherever it occurs in Europe.

Materials and Methods

The life history of *P. lucipetus* was determined from cercarial material obtained from naturally infected snails *Fagotia acicularis audebartii* (PREVOST, 1823), collected in water ditches in Austria near Vienna, Bad Vöslau (Hansi-Bach) and Bad Fischau (Warme Fische). Laboratory bred, uninfected snails of *F. acicularis acicularis* (FERUSSAC, 1823), and *F. acicularis cornea* (PFEIFFER, 1828), chickens (*Gallus gallus* dom.), geese (*Anser anser* dom.), golden hamsters (*Mesocricetus auratus*) and white rats (*Rattus rattus albus*) were used as intermediate and final hosts from which adults and larvae were obtained. Techniques used to study fixed and stained materials were the same as those described in previous papers on Bulgarian and Georgian philophthalmids (VASSILEV & KANEV, 1984 a,b).

The identity of *P. lucipetus* was determined from a comparative analysis of life history materials from the type locality; from adult worms deposited as the holotype, paratype and neotype specimens in Museum and Institute collections in Vienna, Berlin, Kosice, Moscow and Sofia; and on the basis of a critical review of both old and modern descriptions and illustrations of adults and larvae presented as *P. lucipetus*, including the original description and illustrations made by RUDOLPHI (1819) and BREMSER (1824).

Selected morphological features considered so far as taxonomically important were examined on hundreds of laboratory grown parasite specimens.

The main characteristics of *P. lucipetus* were redescribed on the basis of new results about its identity, synonyms, morphology, biology, ecology, life cycle and geographical distribution.

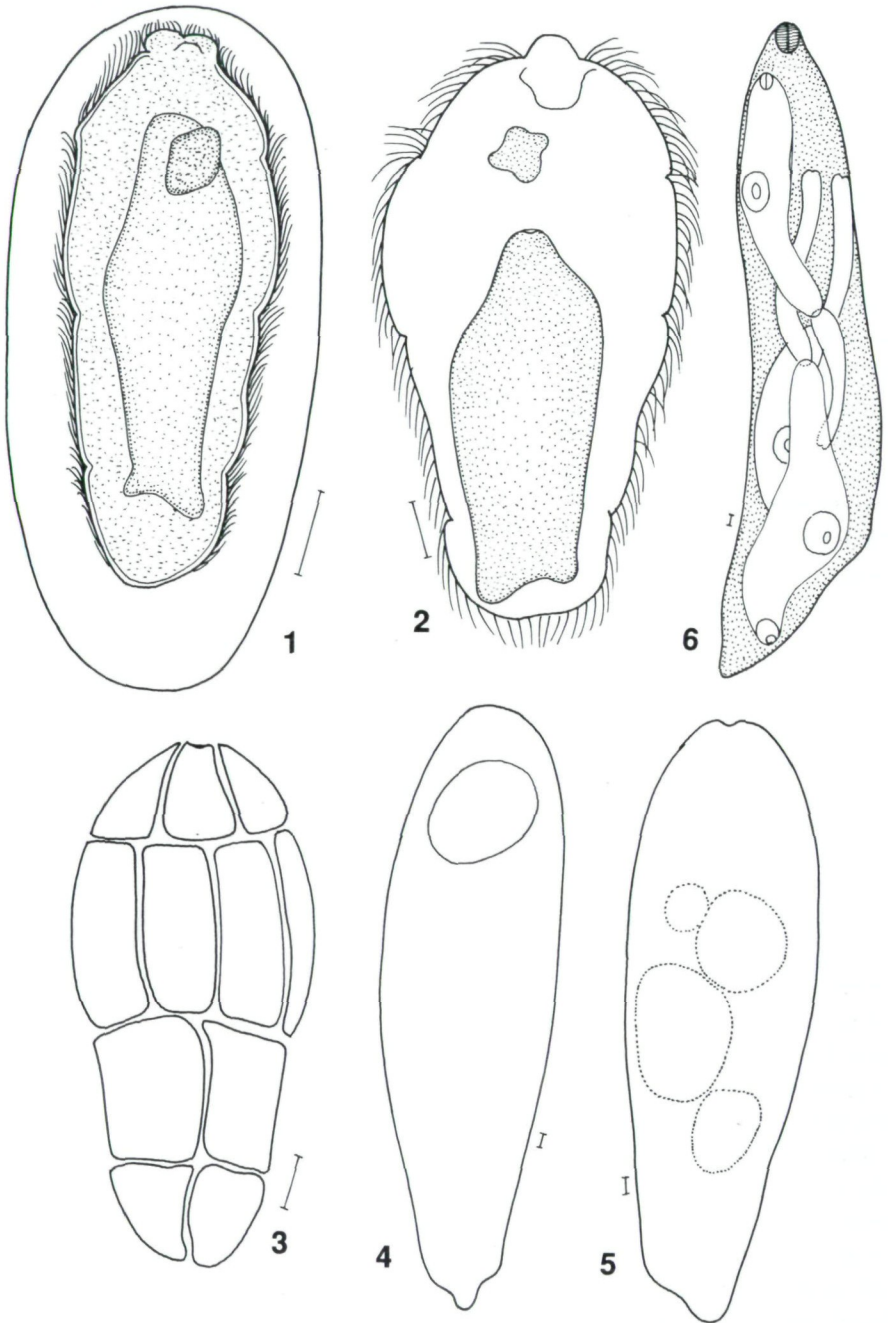
All measurements are in μm unless otherwise stated.

Redescription of *P. lucipetus*

The life history and general morphology.

Eggs (Fig. 1). Fifty eggs placed in petri dishes with 0.9% NaCl were significantly larger (137×62) than those kept in 70% alcohol or barbital solution (106×44). Seventy-eight (78%) of 100 examined eggs were oval with a symmetrical, smooth surface. Twenty-two (22%) showed asymmetrical, oval shapes which were broad and round at one end but narrow at the other end. The upper side was convex while the lower side was more or less flat. Of 100 eggs 98 (98%) contained fully developed miracidia with sporocysts inside. This stage has been identified by WEST (1961) as a redia for *Philophthalmus megalurus* (CORT 1914), by VASSILEV & KANEV (1984 a) for *Philophthalmus posaviniensis* and by NOLLEN (1990) for both *P. megalurus* and *P. gralli* (MATHIS & LEGER 1910). Externally this stage looks like a redia, but it has no pharynx or gut, and has characteristics of a sporocyst. Thus, we will describe it as a sporocyst stage until further definitive work is done. Two (2%) smaller eggs contained incompletely developed miracidia.

Miracidia (Figs. 2, 3). Miracidia hatch a few minutes after eggs are laid. Killed in hot 2% silver nitrate, 100 specimens were 90–180 (155) long by 56–105 (75) wide. Retractable apical papilla 12 by 6 when protruded, with two pairs of hairs. Body covered with 4 rows of ciliated epidermal plates: 32 (61%) of 50 miracidia showed 20 epidermal plates arranged in 4 rows (6:8:4:2), 12 (24%) showed 21 or 22 plates arranged in 4 rows (6–7:9–10:4:2), and 6 (15%) showed 18–19 plates arranged in 4 rows (5–6:7–8:4:2); first (anterior) row usually with 6 triangular plates, two ventral, two dorsal and two lateral (one on each side) about 25 long and 20 wide at base; second row with 7 to 10 (more often 8) square plates, two dorsal, two ventral, two on the left and two on the right side about 30 long and wide; third row with 4 rectangular plates, one ventral, one dorsal and two lateral about 39 long and 30 wide; fourth row with two triangular plates, one ventral and one dorsal about 35 long and 25 wide at base. Cilia 15 long. Two lateral processes about 5 long each situated posterior to a lateral plate of the first (anterior) row with a short bristle immediately anterior to each process. Eyespots consisting of three pairs of crystalline lenses lodged in two pairs of dark brown pigmented bodies at the level between the first and second rows of epidermal plates. Primitive gut filled with granules and opening at the tip of apical papilla. Penetration glands difficult to observe. Two flame cells, left anterior and dorsal, with duct opening situated on latero-dorsal side of body between third and fourth rows of epidermal plates; right flame cell posterior and ventral with outlet on latero-ventral side of body. Body cavity with one fully developed sporocyst. Miracidia swim rapidly, and attached to the soft tissue of a snail with the anterior end, but they do not penetrate. Only the sporocyst is inoculated into the snail by powerful movements of both the miracidium and the sporocyst itself. Penetration of the sporocyst in *Fagotia (Microcolpia) acicularis*, *F. (M.) a. cornea* and *F. (M.) a. audebartii* is completed within an hour.

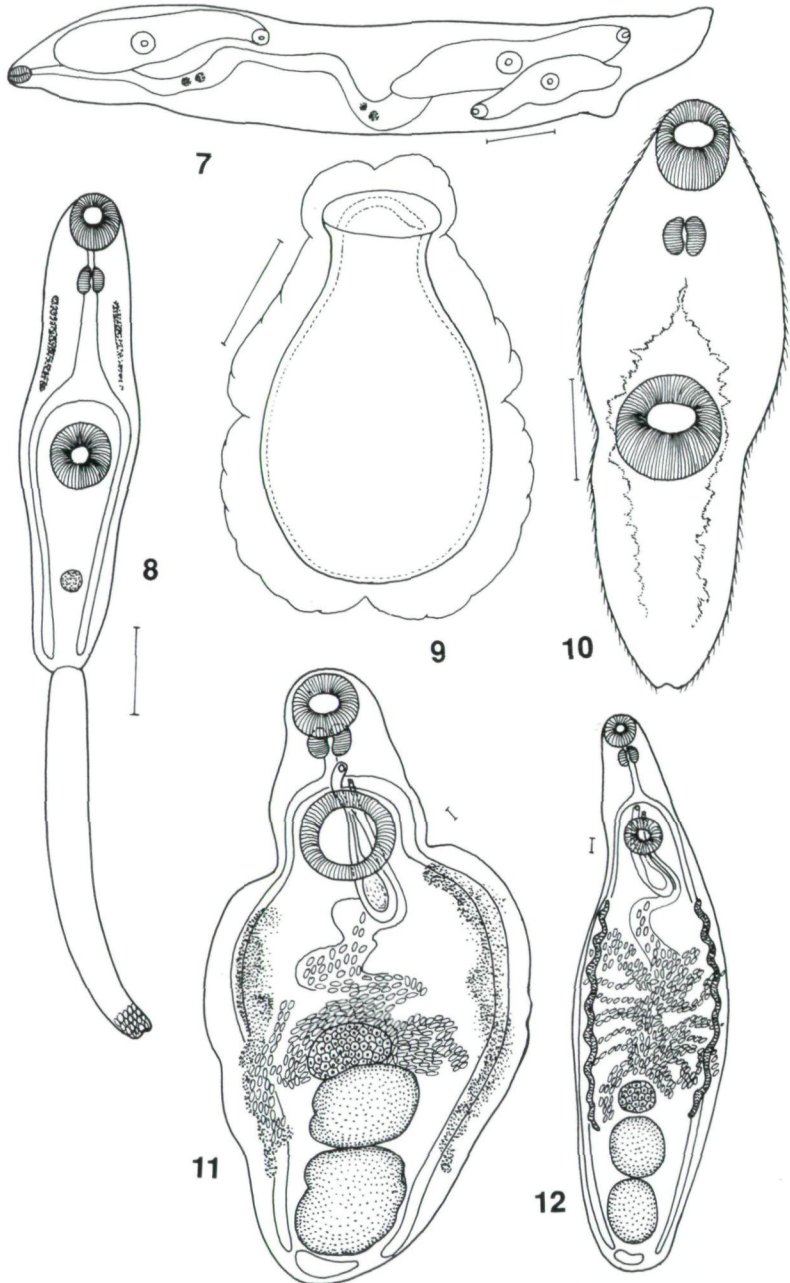


Figs. 1–6. *Philophthalmus lucipetus*: 1. Egg with fully developed miracidium containing sporocyst. 2. Miracidium showing apical papilla, eyespot, sporocyst and cilia. 3. Miracidium fixed in silver nitrate solution, lateral view, showing epidermal plates. 4. Sporocyst in dorsoventral view with one large germ ball. 5. Sporocyst, lateral view, showing locomotor processes and several germ balls. 6. Redia with three cercariae. Camera lucida drawings. Projected scales 10 μ m.

Sporocysts (Figs. 4, 5). Sporocysts were found in the heart cavity 12 hours after exposure of snails to miracidia. Sporocysts found in the heart cavity of snails dissected 40 days post infection showed a cylindrical, elongated body with bilaterally symmetrical enlargements on their anterior part, 100 to 950 (420) long and 40–150 (60) wide; with conspicuous asymmetrical processes at the posterior end. Six to eight unicellular glands and short outlets are visible at the anterior end. Several germ balls or rediae are found in the sporocysts.

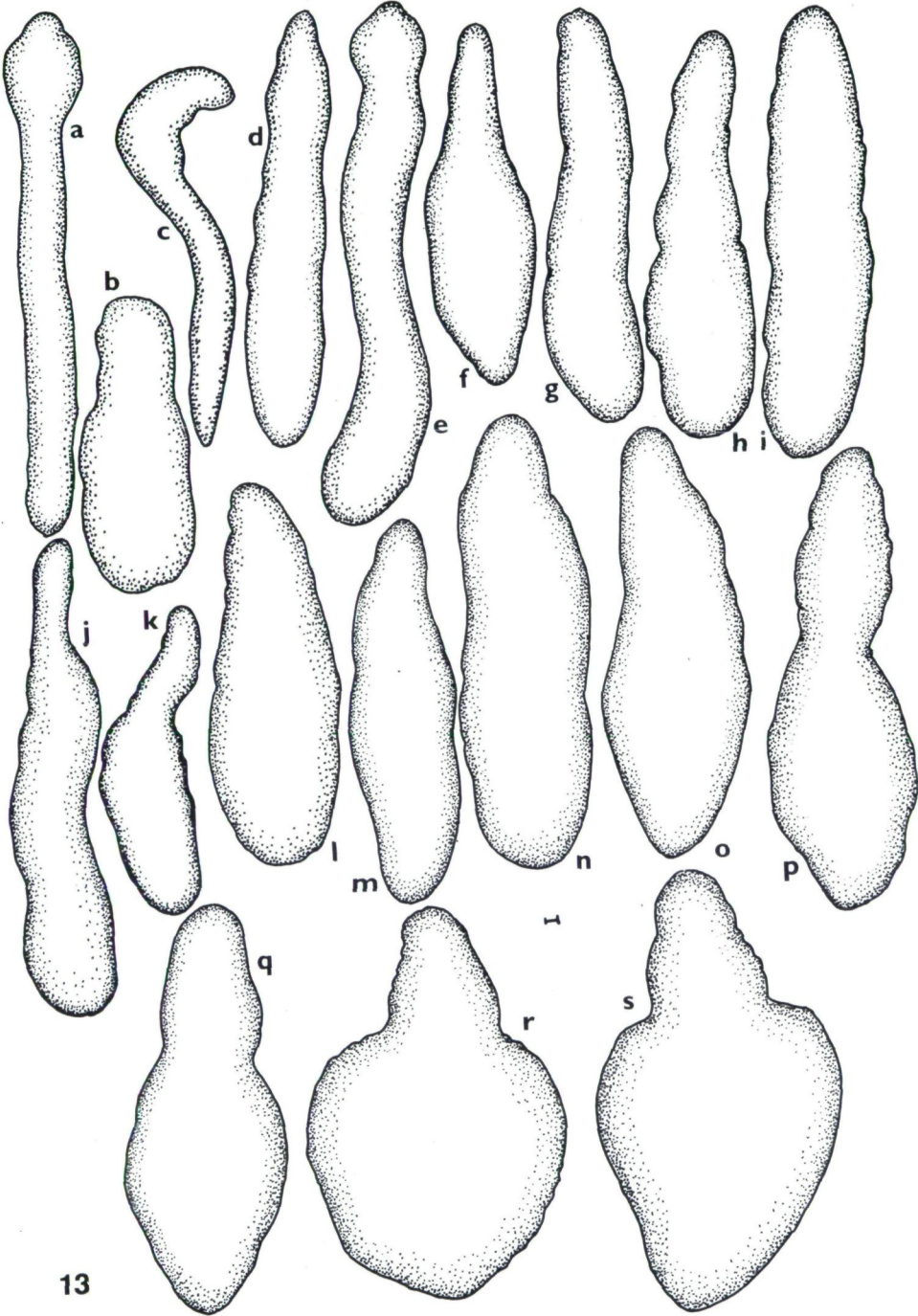
Rediae (Figs. 6, 7). The first generation (mother) rediae released from the sporocysts are found in the heart cavity between 45 to 50 days postinfection of snails. They are cylindrical, 200 to 1200 (580) long and 50 to 250 (88) wide, with two conspicuous processes at the posterior end of the body. They differ from sporocysts by the presence of a well developed, conspicuous pharynx and cylindrical gut reaching almost to the end of body. Body cavity with several germ balls or 1 to 6 rediae of the next generation. Daughter rediae (rediae of the second generation) are cylindrical 270 to 1700 (800) long and 80–350 (150) wide. Pharynx well developed; gut, long, conspicuous. Birth pore in the forebody between the first and second quarter of body length. The lateral processes well developed in the posterior body. Body cavity with numerous germ cells, cercarial embryos or fully developed cercariae.

Cercariae (Fig. 8). The first cercariae are released 96 days after the invasion of snails by sporocysts. Fifty cercariae fixed in hot water showed an asymmetrical, bilateral constriction behind the level of the acetabulum as shown in Fig. 8. Body 450 to 650 (540) long by 100 to 160 (140) wide; oral sucker subterminal 45 to 85 (70) long, 45 to 90 (75) wide; prepharynx short about 7 long; pharynx 22 to 27 (25) long, 12 to 20 (18) wide; oesophagus about 150 long, bifurcating anterior to ventral sucker; caeca, symmetrical, ending blindly at the posterior end of the body. Ventral sucker postequatorial, 60 to 90 (75) long, 55 to 92 (77) wide. Body surface covered with minute spines arranged in longitudinal and transverse rows. Genital primordium consists of two cell masses, one at the anterior margin of acetabulum and one between acetabulum and excretory bladder, connected by a chain of cells dorsal to the acetabulum. Numerous cystogenous unicellular glands 15 to 30 in diameter, filled with ovoid two by one rod-like inclusions, extending from the pharynx to the posterior tip of the body. The excretory system with well developed bladder median at the posterior end of the body, main collecting ducts extending from the anterior level of the pharynx to the anterior end of the bladder. Flame cells difficult to see because of cystogenous cells, perhaps $2(3+3+3) + 2(2+2+2) = 30$. The caudal branch of the excretory system short, ends in the anterior sixth of tail then bifurcates and terminates at a pair of primary pores about 100 from the body-tail junction. Tail cylindrical 330 to 450 (420) long by 35 to 65 (45) wide, tail body is packed with large parenchymal cells which are refractive to vital stains. A group of gland cells are located on the tail tip. Cercariae swim with convulsive movements and are often found attached at the water surface with the tail tip. Within an hour, cercariae encyst on hard surfaces such as plants, snail shells and glass.



Figs. 7–12. *Philophthalmus lucipetus*: 7. Redia with long gut, locomotor processes and three cercariae. 8. Cercaria showing oral and ventral suckers, prepharynx, pharynx, band of cells in the tail tip and tapering hindbody. 9. Metacercarial cyst in pyriform shape. 10. Excysted metacercaria with visible oral and ventral suckers, pharynx, oesophagus, caeca and body spines. 11. Adult worm with body constriction at the level of the ventral sucker, long cirrus pouch and long tubular vitellaria. 12. Adult with fusiform body, long cirrus pouch and long, tubular vitellaria. Camera lucida drawings.

Projected scales 50 µm.

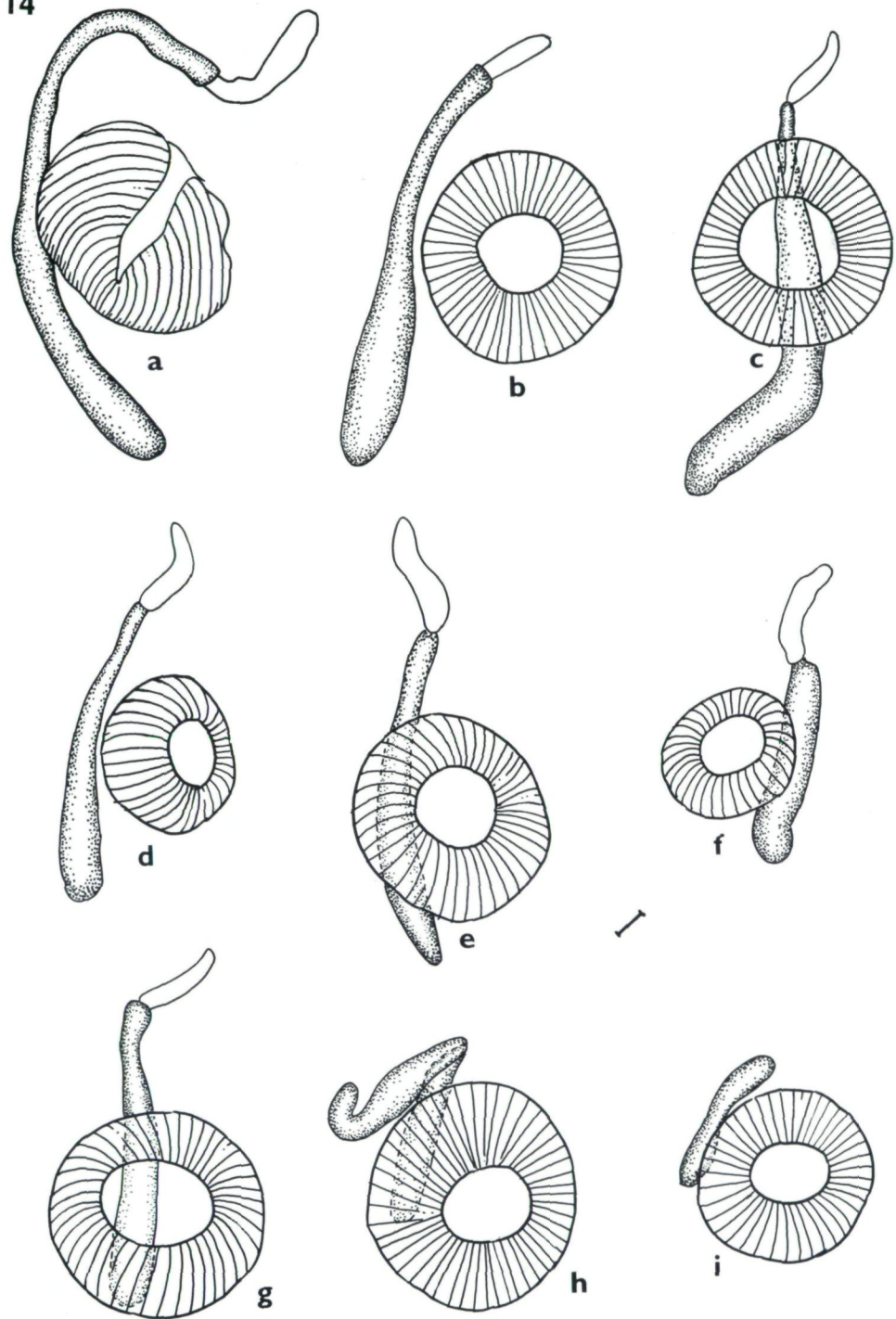


Figs. 13 a–s. *Philophthalmus lucipetus*. Body shape of adults. Camera lucida drawings. Projected scale 100 μ m.

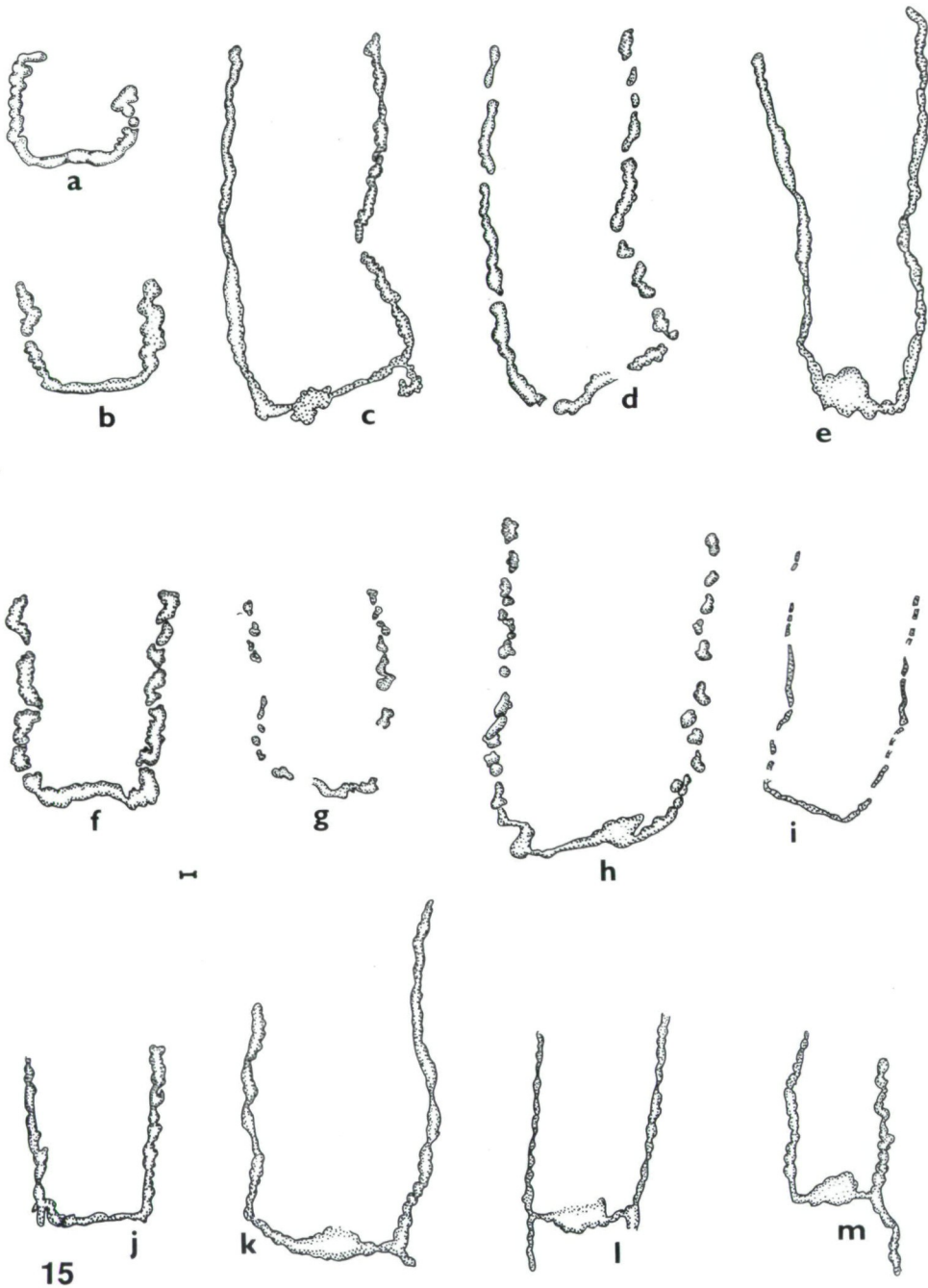
Metacercariae (Figs. 9, 10). Cyst pyriform 310 to 460 (360) long 140 to 175 (160) wide, based on 50 metacercariae encysted on cover glasses. The metacercaria is rolled ventrally into a ball and lies in the posterior, broader part of the cyst. The tail could be found nearby or cast away from the excysted body. The cyst wall is silver white and composed of several layers of materials laid down concentrically. Placed in water at 37–39°C metacercariae excyst and escaped from cyst within a few seconds. The metacercariae are infective immediately after encystment.

Adults (Figs. 11–18). Most adults (160 from 256–62%) showed a body length from 3.5 to 4.5 mm. The smallest worms containing fully developed eggs were two mm long. The largest one 7.4 long. The juvenile worms at age 18–30 days are smaller than those found in the same host at 40–50 days. Worms living in the eye cavity of geese, chickens and turkeys are considerably larger than those of the same age living in ducks. Single worms found in the eye cavity are bigger than those of the same age found in multiple infections of 20–30 specimens per eye. Over half of the adults examined (147 of 248 – 59%) showed a body shape similar to those illustrated in Figs. 12, 13 f, h, i, l, o. Fifteen (6%) specimens were found constricted at the level of the acetabulum as is shown in Figs. 11, 13 p, q, r, s. Eighty-six (35%) specimens were found with a shape like that in Figs. 13 a, b, c, d, g, j, k, m, n. All excysted metacercariae and pre-adult worms (196) up to 7 days old showed body spination. Adults of 60 to 180 days old showed spination only in 50 of 136 (38%) specimens. Complete loss of spines was found in all 32 worms obtained from the eye cavity of birds that were dead for 24 hours and more. The same complete loss of spines was observed in all 42 worms that were kept in Petri dishes with tap water for 12 or more hours. Oral sucker subterminal 190 to 490 (350) long and 200 to 430 (320) wide; prepharynx 0 to 50 long, pharynx 121 to 380 (250) long and 120 to 340 (280) wide; oesophagus 310 to 1000 long, bifurcating anterior to acetabulum; caeca conspicuous, ending blindly in the posterior part of the body at the level of the excretory bladder; ventral sucker rounded 430 to 780 (550) long by 410 to 888 (540) wide, located in anterior half of body. Anterior testis 180 to 650 (450) long by 200 to 780 (510) wide, posterior testis 200 to 750 (450) long by 250 to 790 (540) wide. Over half of the adults (112 of 211 – 53%) were found with smooth, oval testes arranged in tandem at the posterior of body as illustrated in Figs. 11, 12, 16 a, b. Fifty-two specimens (25%) showed more or less lobed testes as shown in Figs. 16 c, d, e, f. Forty-five or 21% were found to be “abnormal” smaller or larger or transversely arranged as illustrated in Figs. 16 g, h, i, j. Two specimens (1%) were found with only one testis as shown in Figs. 16 k, l. Cirrus pouch is shown in Figs. 14 a–i. Ninety-five percent of the specimens (195 of 206) showed a long cirrus pouch that extended beyond the posterior end of ventral sucker as illustrated in Figs. 11, 12, 14 a, b, c, d, e, f. Eleven (5%) adults were found with short cirrus pouches which did not extend beyond the ventral sucker as shown in Figs. 14 g, h, i. In one specimen neither ventral sucker nor cirrus pouch was visible. Ovary round to ovoid, median, immediately pretesticular 140 to 360 (280) in diameter. Vitellaria are shown in Figs. 15 a–m. Sixty-three

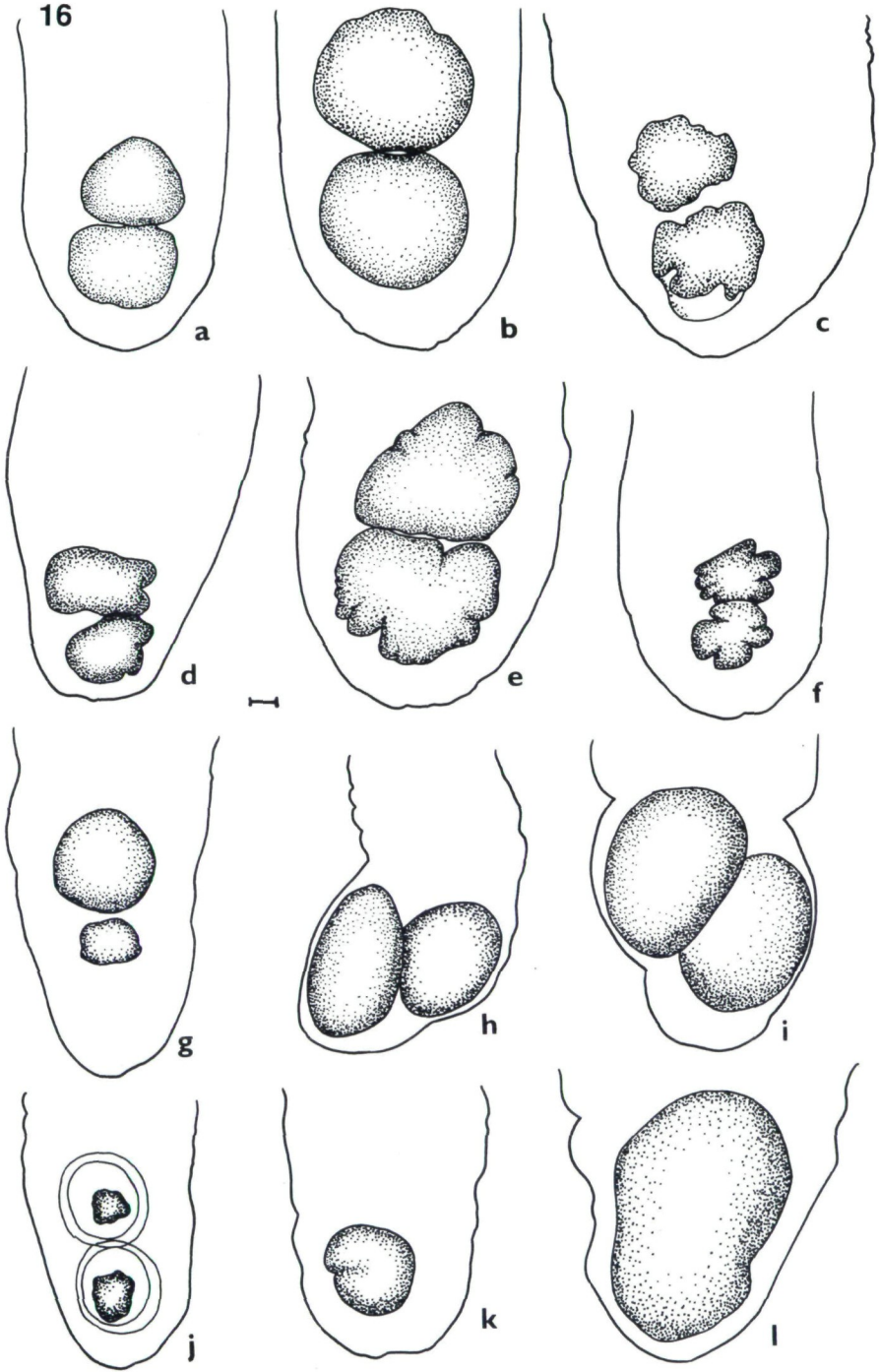
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Figs. 14 a–i. *Philophthalmus lucipetus*. Ventral sucker and cirrus pouch. Camera lucida drawings. Projected scale 100 μ m.



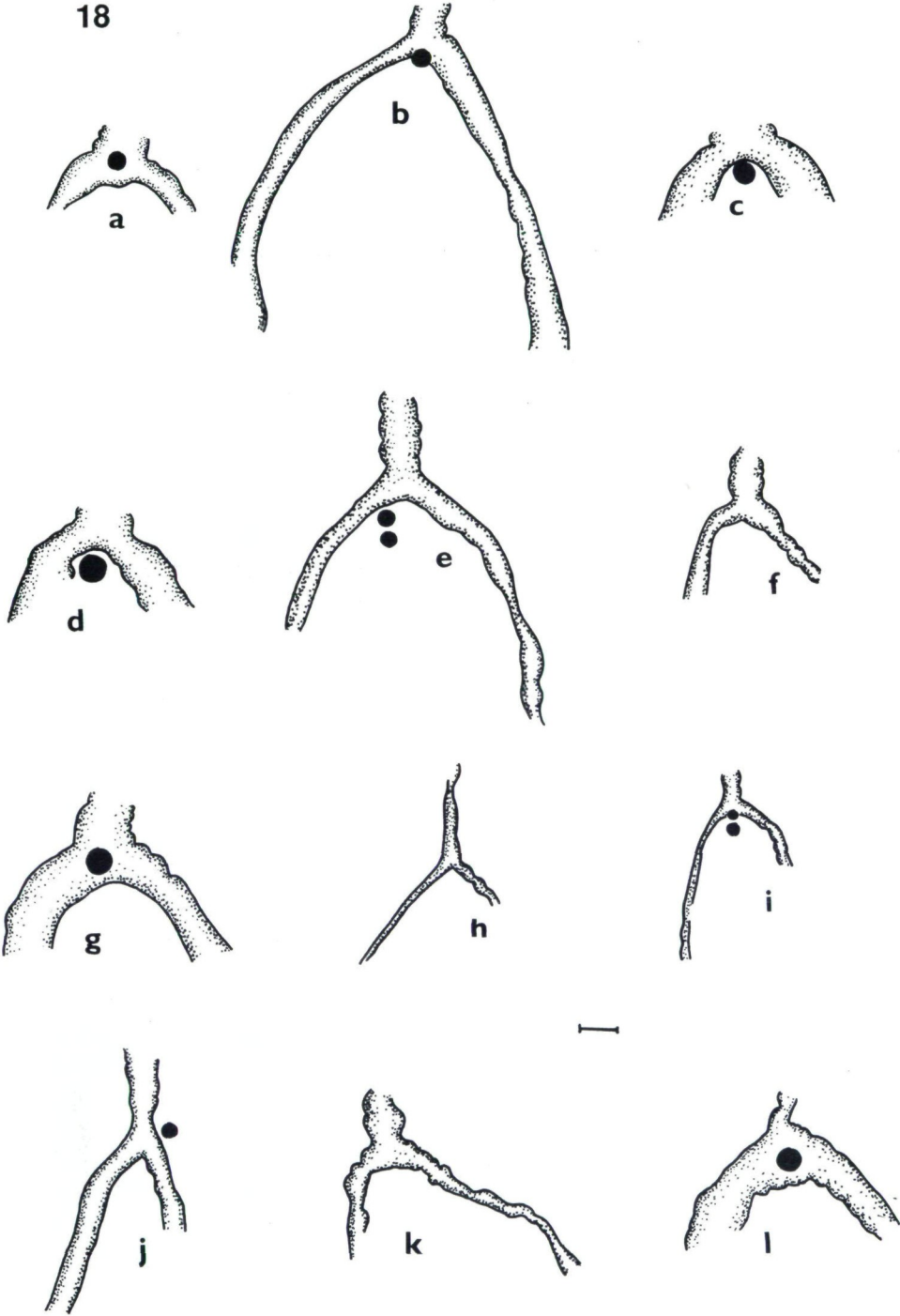
Figs. 15 a–m. *Philophthalmus lucipetus*. Vitellaria. Camera lucida drawings. Projected scale 100 μ m.



Figs. 16 a–l. *Philophthalmus lucipetus*. Testes. Camera lucida drawings. Projected scale 100 μ m.



Figs. 17 a–m. *Philophthalmus lucipetus*. Uterus. Camera lucida drawings. Projected scale 100 μ m.



Figs. 18 a–l. *Philophthalmus lucipetus*. Genital pore. Camera lucida drawings. Projected scale 100 μ m.

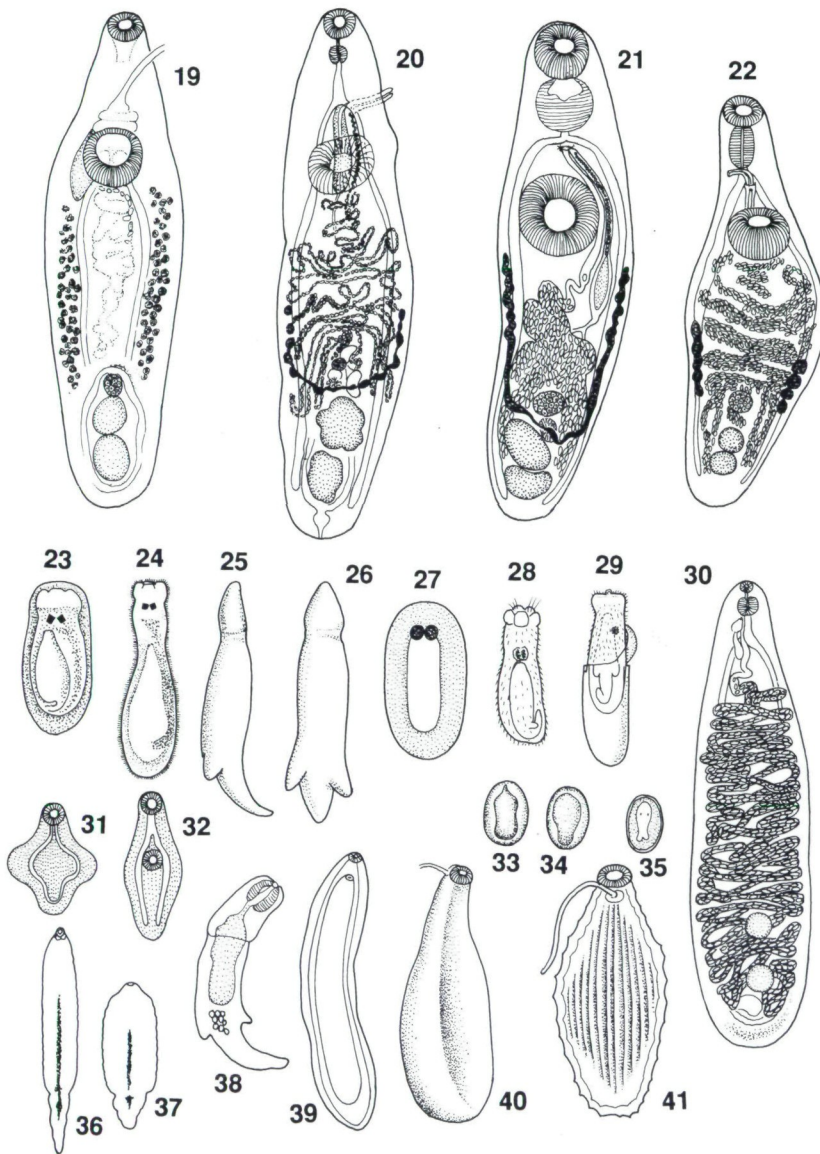
percent of the adults (122 of 193) showed long, bilaterally symmetrical, non-interrupted vitellaria of the tubular type (Figs. 11, 12, 15 c, e). Forty-two adults (28%) were found with an asymmetrically arranged tubular type vitellaria as shown in Figs. 15 a, j, k, l, m, and 29 (15%) showed more or less interrupted vitellaria of the follicular type as shown in Figs 15 d, f, g, h, i. Uterus long, coiled confined to the space between the ventral sucker and testes containing numerous embryonated eggs. Over half of the worms (124 of 217 – 57%) were found with a well developed, bilaterally symmetrical uterus as shown in Figs. 17 e, f, g, h, i, j, k, m. Sixty-two or 29% of the specimens showed asymmetrically long and branched loops on the left or right side of uterus as shown in Figs. 17 d, l. Thirty-one worms (14%) exhibited poorly developed uteri as shown in Figs. 17 a, b, c. Uterine seminal receptacle between ovary and anterior testis containing numerous spermatozoa. Genital pore is shown in Figs. 18 a–l. Nearly three-fourths of the specimens (111 of 152 – 73%) showed genital pores located between the bifurcation of the caeca and the anterior margin of the acetabulum as shown in Figs. 18 b, c, d, e, i. In 36 (24%) specimens the genital pores were not visible as documented in Figs. 18 f, h, k. In 5 (3%) adults these pores were observed at the level of bifurcation as shown in Figs. 18 a, g, l. Usually these worms were twisted or with marked constrictions in the anterior part of body. Excretory bladder Y shaped, with arms extending anteriorly to level of pharynx. Adult worms develop in the cavity under *m e m b r a n a n i c t i t a n t e* (*m e m b r a n a t e r c i a*) in chickens (*Gallus gallus* dom.), geese (*Anser anser* dom.), golden hamsters (*Mesocricetus auratus*) and white rats (*Rattus rattus albus*). Birds could be infected both by feeding the metacercariae or placing them directly into the conjunctival sack. Mammals could be infected only by direct inoculation of excysted metacercariae into the eye cavity.

R e m a r k s : In its type locality *P. lucipetus* was found to possess a long cirrus pouch and long tubular vitellaria as described and illustrated originally by RUDOLPHI (1819) and BREMSER (1824) (see Fig. 19). Also, our studies found that *P. lucipetus* develops with the same life cycle pattern, using the same snail and bird species as intermediate and final hosts, and having the same morphological and biological features as those of the following previously described species: *P. posaviniensis*, *P. cupensis*, *P. hovorkai*, *P. rhionica* and *Philophthalmus* sp. (see BUSA, 1956, VASSILEV, 1962, 1973, VASSILEV & DENEV, 1965, VASSILEV & KANEV, 1984 a, TICHOMIROV, 1976).

Identification notice

The original descriptions and illustrations of *P. lucipetus*.

P. lucipetus was originally described from 6 specimens found in the eye cavity (under *m e m b r a n a n i c t i t a n t e*) of naturally infected gulls, *Larus glaucus* and *L. fuscus*. Three adults were found in three of 4 birds examined in Vienna on April 26, 1815 and three additional specimens were found in 3 of 11 birds examined in Vienna on May 12, 1815.



Figs. 19–41. Adults and larvae found identical or different from *Philophthalmus lucipetus*. 19. *Distoma lucipetum* after BREMSER (1824); 20. *Philophthalmus lucipetus* after BRAUN (1902); 21. *Philophthalmus palpebrarum* after LOOSS (1899); 22. *Philophthalmus lacrymosus* after BRAUN (1902); 23–26. *Monostomum mutabile* after SIEBOLD (1835); 23. Egg with miracidia containing sporocyst; 24. Miracidium with sporocyst; 25–26. Rediae in lateral and dorso-ventral view; 27. *Monostomum nigropunctatum* (egg with miracidium) after LINSTOW (1886); 28–30. *Monostomum mutabile* after van BENEDEN (1858). 28. Miracidium with sporocyst; 29. Miracidium sporocyst hatching from an egg; 30. Adult worm; 31–32. *Monostomum lentis* after AMON (1833); 33–35. *Distomum cygnoides* (eggs with miracidia) after DUJARDIN (1837); 36–37. *Monostomum constrictum* after DIESING (1856); 38. *Monostomum mutabile* ("nursing animal") after STEENSTRUP (1842); 39. *Monostomum microstomum* after CREPLIN (1829 a); 40. *Monostomum mutabilae* after ZEDER (1800); 41. *Monostomum plicatum* after CREPLIN (1839).

J. G. BREMSER, curator of the Naturhistorisches Museum in Vienna, examined these parasites and made detailed drawings, but he failed to give them an appropriate name because they were discovered in the eye cavity where no previous parasites had been found. For this reason he sent 3 of his specimens to RUDOLPHI in Berlin for further identification. RUDOLPHI (1819) described these worms as *Distomum lucipetum* (lucipetum = toward the light). In addition, BREMSER (1824) published his original drawings of *D. lucipetum* (Fig. 19). Both authors described *D. lucipetum* with a long cirrus pouch which extended posterior to the ventral sucker. Vitellaria were illustrated as long, uninterrupted tubules today called "tubular vitellaria". These original characteristics were used as a basis for further identification of adult worms described as identical or different from *P. lucipetus*.

After RUDOLPHI's (1819) original description, *P. lucipetus* went through descriptions and illustrations published by DUJARDIN (1845), DIESING (1850, 1858) and BRAUN (1897, 1902). These authors have described as *P. lucipetus* adults labeled as *D. lucipetum* in the Naturhistorisches Museum in Vienna and Berlin. According to these descriptions, *P. lucipetus* possesses a short cirrus pouch which does not extend posterior to the ventral sucker (Fig. 20). Vitellaria are described as short, interrupted (in 5–6 places) bodies called "follicular vitellaria", but such worms have never been found in Vienna and along the river Danube. For this reason, SKRJABIN (1947) specified that *P. lucipetus* was a very rare species, which had never been found again in its type locality in Austria. The present day knowledge of *P. lucipetus* is based mainly on BRAUN's (1902) descriptions and his illustrations copied by SKRJABIN (1947) and YAMAGUTI (1958, 1971). In this paper we present new evidence about the identity of *P. lucipetus*.

Related species in Europe

All of the data given below indicate that *P. lucipetus* is the only species of the genus *Philophthalmus* along the river Danube. After 20 years of extensive comparative studies, no infections in snails with other related species were found. This information then synonymized all previously described species of eyeflukes from several rivers emptying into the Black Sea, including the rivers Danube, Dniepar, Dniester and the Rhionica, with *P. lucipetus* (see below).

Species considered identical to *P. lucipetus*.

Synonymy list of adults, preadults and larval stages considered identical to *P. lucipetus*:

Adults found in the eye cavity of birds

1819 RUDOLPHI, *Distomum lucipetum*, Entoz. Synops., Berolini, 811 pp.

1824 BREMSER, *Distomum lucipetum*, Icon. Helm. Viennae, 1–12.

1939 MARCOVIC & GARZICIC, *Philophthalmus lacrymosus*, Zool. Anz., (Zagreb), 127: 267–270.

1938 TROFIMOV, *Philophthalmus gnedini*, In Tretyakova (1948), Sb. gel'mintol. rabot., (Moscow), 232–236.

- 1948 TRETYAKOVA, *Philophthalmus muraschkinsevi*, Sb. gel'mintol. rabot., (Moscow), 232–236.
- 1952 SAAKOVA, *Philophthalmus palpebrarum*, Dis. Theses. Moscow, 250 pp.
- 1953 BYCHOVSKAYA-PAVLOVSKAYA, *Philophthalmus nocturnus*, Parasitol. Sb. Zool. Inst. AN SSSR, Moscow, 5: 5–117.
- 1953 BYCHOVSKAYA-PAVLOVSKAYA, *Philophthalmus nyrocae*, Parasitol. Sb. Zool. Inst. AN SSSR, Moscow, 5: 5–117.
- 1953 RICHTER et al., *Philophthalmus cupensis*, Vet. Archiv, (Beograd) 23: 193–205.
- 1953 RICHTER et al., *Philophthalmus posaviniensis*, Vet. Archiv, (Beograd) 23: 193–205.
- 1956 BUSA, *Philophthalmus (Tubolecithalmus) hovorkai*, Biologia (Praha), 2: 151–258.
- 1956 SMOGORZEWSKAYA, *Philophthalmus (Tubolecithalmus) gralli*, Parasitol. Sb. Zool. Inst. AN SSSR, 16: 244–263.
- 1957 SHIGIN, *Philophthalmus lacrymosus*, Tr. Darwin. Zapoved., (Moscow), 4: 254–289.
- 1957 SHIGIN, *Philophthalmus oschmarini*, ibid
- 1957 SHIGIN, *Philophthalmus palpebrarum*, ibid
- 1957 SHIGIN, *Philophthalmus problematicus*, ibid
- 1957 SHIGIN, *Philophthalmus rhizalensis*, ibid
- 1962 VASSILEV, *Philophthalmus* sp., Izvestja Tsentral Khelminthol. Lab., (Sofia), 7: 11–17.
- 1964 MACKO, *Philophthalmus nocturnus*, Helminthologia (Kosice) 1: 85–106.
- 1966 SAY, *Philophthalmus nocturnus*, Acta Acad. Paedag. in civit Pecs 10 ser. Biologia, 53–71.
- 1968 SERGIENKO, *Philophthalmus nyrocae*, Dis. Theses, Lvov, 186 pp.
- 1976 DZAVELIDZE, *Philophthalmus* sp. (*nyrocae?*), Soob. Gruz. AN SSR, 84: 721–724.
- 1976 ISKOVA, *Philophthalmus (Tubolecithalmus) stugii*, Donovidii AN URST B., 2: 164–166.
- 1976 TICHOMIROV, *Philophthalmus rhionica*, Vest. Leningr. Univ., 15: 33–47.
- 1984 VASSILEV, *Philophthalmus posaviniensis*, Faunae, taxonomy and ecology of helminths on birds, Pub. House BAS (Sofia) 7–14.
- 1984 VASSILEV & KANEV, *Philophthalmus posaviniensis*, Faunae, taxonomy and ecology of helminths on birds, Pub. House BAS (Sofia) 45–52.

Preadults found in the eye cavity of humans

- 1832 NORDMANN, *Monostomum lentis*, Mikrograph. Beiträge zur Naturgeschichte der wirbellosen Thiere, Berlin, 2: 1–118.
- 1833 AMMON, *Distoma lentis*, Zeitschr. Ophth., Dresden, 3: 70–99.
- 1833 GESCHIEDT, *Distoma oculi-humani*, Ztschr. Ophth., 3: 405–462.
- 1850 DIESING, *Distoma amoni*, Syst. Helm. Wien, 680 pp.
- 1850 DIESING, *Distoma ophthalmobium*, Syst. Helm. Wien, 680 pp.
- 1855 KUCHENMEISTER, *Cysticercus cellulosae*, Wien, Med. Wochenschr., 5: 1–4.
- 1859 WEINLAND, *Distoma oculi-humani*, Arch. Naturg., Berlin, 25: 276–285.
- 1860 MOQUIN-TANDON, *Distoma oculare*, Elements de zoologie medicale, Paris, 16: 1–428.
- 1860 MOQUIN-TANDON, *Festucaria lentis*, Elements de zoologie medicale, Paris, 16: 1–428.
- 1860 MOQUIN-TANDON, *Fasciola oculare*, Elements de zoologie medicale, Paris, 16: 1–428.
- 1864 COBBOLD, *Distoma lanceolatum*, Entozoa, London, 480 pp.
- 1882 BONIS, *Distoma ocular*, Tradicida del italiano... por Carlos Mariam Cortezo Madrid, 311 pp.
- 1892 BRANDES, *Monostomum lentis*, Centrbl. Bakt. Parasitenkd., XII (15):504–511.
- 1892 STOSSICH, *Agamodistom ophthalmobium*, Bull. Soc. Sci. Adviat. Nat. Lavoro monografico, Trieste, 13: 143–169.
- 1893 BRAUN, *Fasciola hepatica*, BRONN's Klass. u. Ordnung Thier-Reichs, Leipzig, 4: 817–925.
- 1895 RAILLIET, *Monostoma du cristalín*, Traite Zool. Med. et Agricole, Paris, 1303 pp.
- 1903 WARD, *Dicrocoelium lanceolatum*, Rev. Handb. Med. Sc., 7: 860–873.
- 1919 CASTELLANI & CHALMERS, *Distoma ophthalmicum*, Manual of tropical medicine. 3 ed., London, 2436 pp.
- 1939 MARCOVIC & GARZICIC, *Philophthalmus lacrymosus*, Zool. Anz., 127: 267–270.

Larvae (miracidia, rediae and cercariae) found free or in the freshwater snails

1842 FRANCIS, *Monostomum mutabile*, Ann. Mag. Nat. Hist., London, **63**: 118–121.

1850 DIESING, *Monostomum mutabile*, Syst. Helm. Wien, 680 pp.

1971 ZDARSKA, *Philophthalmus* sp., Folia Parasit. (Praha), **18**: 119–125.

1975 OLENOV & DOBROVOLSKI, *Philophthalmus* sp., Ecol. and Exper. parasitol., Leningrad, 53–69.

1976 TICHOMIROV, *Cercaria rhionica*, Vest. Leningr. Univ., **15**: 33–47.

We suggest all these names are synonyms of *P. lucipetus*. In support of that suggestion are several important factors. First, in their morphology and biology, including when they are reported as *Monostoma*, they were described and illustrated with morphological structures which are identical to our redescription of *P. lucipetus*. Secondly, *P. lucipetus* is very common and widely spread in these regions in Europe. Freshwater snails of the genus *Fagotia* and rarely of the genus *Amphimelania* serve as the first intermediate host in the field. Thirdly, they were found in the same host and from the same localities along the Danube and other rivers in Europe where *P. lucipetus* and its intermediate snail hosts are found. Extensive comparative studies of adults, preadults and larval stages obtained along the Danube River in Austria, Czechoslovakia, Yugoslavia and Bulgaria and along the Rhionica River in Georgia (VASSILEV, 1984 a, b; VASSILEV & KANEV, 1984 a, b; OSSIKOVSKI et al., 1990; POLYAKOVA et al., 1990, this paper) also showed all these species mentioned above to be identical with *P. lucipetus*. These studies found only one philophthalmid species in Europe, called previously *P. posaviniensis* (see VASSILEV & KANEV, 1984 a, b), but here described as identical to *P. lucipetus*.

Invalid descriptions of *P. lucipetus*

The following reports are considered invalid descriptions of *P. lucipetus*: *Distomum lucipetum* of DUJARDIN (1845) described from a specimen sent to Paris from Naturhistorisches Museum in Vienna; *D. lucipetum* of BRAUN (1897) based on 3 specimens found in the eye cavity of naturally infected *Larus maculipennis* from Brazil and sent to Vienna in 1893 by A. DE MIRANDA-RUBEIRO; *D. lucipetum* of MIRANDA (1903) on specimens from *Larus maculipennis* from Brazil; *Philophthalmus lucipetus* of BRAUN (1902) on specimens from *Larus fuscus* and *Larus glaucus* in the Naturhistorisches Museum of Vienna and Berlin. All these species are described and illustrated (Fig. 19) with a short cirrus pouch which does not extend beyond the posterior end of the ventral sucker and short vitellaria interrupted in 6–7 follicles. The data available suggested that all these specimens belong to one and the same species from Brazil known as *P. lacrymosus* (BRAUN, 1902) (Fig. 22). In support of this suggestion are several important points. It is known that JOHANN NATTERER, a curator at the Naturhistorisches Museum in Vienna, spent about 20 years in Brazil from where he sent to Vienna numerous parasite specimens. In the Museum notebooks 35 eye flukes are registered imported from Brazil between September, 1822 and August, 1831. Some of these worms were found in birds classified in Brazil as *Larus fuscus* and *Larus glaucus*. For this reason and because of their location in the eye cavity and their

morphological similarities to adults found in Europe, these Brazilian worms were recognized as identical with *D. lucipetum* and mixed with the 6 original specimens of *D. lucipetum* found in Europe. This explains how the original specimens of *D. lucipetum* increased from 6 to 40 without any registration of new materials from Europe. Twenty-five of these specimens labeled with Collection No 4473 and 4474 were kept in Vienna until 1966 when they were borrowed by BUSA in Czechoslovakia and lost with his unexpected death. Fourteen specimens are available in Berlin labeled under Col. No 1435 and 1436. As mentioned above, one specimen was sent to Paris. This explains why BRAUN (1902) described both *P. lucipetus* and *P. lacrymosus* with the same morphological structures and why these structures were no longer found in the adults from the type locality of *P. lucipetus* in Austria and along the river Danube in Europe and even in Africa (see Fig. 21). These and other data available in Vienna showed that the eye flukes sent to Vienna in 1822–1831 by NATTERER from his expedition in Brazil were recognized and described as identical with *Distomum lucipetum*=*Philophthalmus lucipetus*. Those sent by de MIRANDA-RUBEIRO in 1893 were first recognized by BRAUN (1897) as *D. lucipetum*, but five years later redescribed (BRAUN, 1902) as members of a new species named as *P. lacrymosus* (Fig. 2).

The following adults and larvae of *Monostomum mutabile* reported by SIEBOLD (1842 in FRANCIS, 1842), DIESING (1850, 1858) and others are considered different from *P. lucipetus*: *M. mutabile* of SIEBOLD (1835) described from eggs, miracidia and sporocyst of the adult worms found in the cella infraorbitallis of naturally infected *Anser anser* dom. examined in Germany (SIEBOLD, 1835) and France (van BENEDEN, 1858). As seen from (Figs. 23–26 and 29–30) these larvae are very similar in morphology and biology to those of *P. lucipetus*, but the adults (see Fig. 30) belong to genus *Cyclocoelium* and differ from *Philophthalmus* in their general morphology and biology. Also, different from *P. lucipetus* are the adults and larvae described in originally as *Monostomum nigropunctatum* of LINSTOW (1886) (Fig. 27); Nursing animals and Agamozoids of STEENSTRUP (1842 (Fig. 38); *Distoma cygnoides* of DUJARDIN (1837) (Figs. 33–35); and *Monostomum plicatum* and *M. microstomum* of CREPLIN (1829 a, b and 1839) (Figs. 39, 41). All these adults and larvae are considered to be identical with *Monostomum mutabile* ZEDER, 1800 (Fig. 40). They look very similar and perhaps are identical with those known today as *Gorgoderia*, *Notocotylus* and *Cathaemasia*.

DIESING (1856) described from the eye cavity (oculi camera anteriore) of naturally infected fish (*Abramis brama*) in Austria larval stages as *Monostomum constrictum* which are also different from *P. lucipetus* (Figs. 31, 32). In morphology and biology these worms are very similar and perhaps identical with those known today as *Diplostomum* and for this reason they will not be discussed here in detail.

P. lucipetus was not studied in detail in its type locality in Europe and remained there with incompletely and incorrectly known morphology and life cycle, and this is a primary factor in the inaccurate descriptions of eye fluke

species in Europe and wherever they occur. Because of limited space, the following three examples will be given. 1. SKRJABIN (1947) and KARYAKARTE (1967) divided the genus *Philophthalmus* into three subgenera – *Philophthalmus* to describe adults with short vitellaria consisting of 6–7 follicles, *Tubolecithalmus* to describe those with long tubular vitellaria and *Mixophthalmus* for those with intermediate forms. This would not have happened if the data presented above in Figs. 15 a–m had been known. 2. SOBOLEV (1943) established the genus *Ophthalmotrema* to describe adults with a bilateral body constriction at the acetabulum level. NASIR & DIAZ (1972) and BELOPOLSKAYA (1953) described a new species on the basis of this feature. From this SOBOLEV (1943) developed a new concept about the origin, relationship and evolution of the family Philophthalmidae. This would not have happened if the data presented above in Figs. 11, 13 q, p, r, s had been known. 3. DIESING (1850), LEUCKART (1863), KUCHENMEISTER (1855), KUCHENMEISTER & ZURN (1878–81), BRAUN (1893, 1902), STOSSICH (1892), DOLLEY (1894), WARD (1895), RICHTER et al. (1953), BUSA (1956), VASSILEV (1962), TICHOMIROV (1976) and others used over 40 different names to describe adults, preadults and larvae found in naturally infected freshwater snails, birds and humans along the rivers Danube, Dniester, Dnieper, Volga and Rhionica in Europe. If the life history of *P. lucipetus* had been known, none of these species could have been described as a new and an independent.

Main characteristics of *P. lucipetus* known to date

Synonyms: Included about 35 names given to adults, preadults and larvae of *P. lucipetus* presented above in the synonymy list (this paper).

Life cycle: BUSA (1956) in Czechoslovakia, VASSILEV & DENEV (1965, 1971), VASSILEV (1973), VASSILEV & KANEV (1984 a, b) Bulgaria, Yugoslavia and Georgia, TICHOMIROV (1976) Georgia, Austria (this paper).

Snail host: *Fagotia (Microcolpia) acicularis acicularis* FERUSSAC, 1823; *F.(M.) acicularis cornea* PFEIFFER, 1828; *A. (M.) acicularis audebartii* (PREVOST, 1823), *Amphimelania holandri* FERUSSAC, 1823, *Melanopsis praemorsa* LINNAEUS, 1758 (all in this paper).

Final host: (Table I.) At least 30 different bird species, 5 mammal species and humans living in different parts of Europe have been found infected with *P. lucipetus* adults and preadults.

Geographical distribution: Naturally infected snails are found in Austria, Czechoslovakia, Yugoslavia, Bulgaria and Georgia (BUSA, 1956, VASSILEV, 1973, ZDARSKA, 1971, VASSILEV & DENEV, 1965, VASSILEV & KANEV, 1984 b, TICHOMIROV (1976). Adult and preadult worms are found also in Germany, Hungary, Ukraine and Russia (NORDMANN, 1832, SAY, 1966, ISKOVA, 1976). Probably *P. lucipetus* occurs elsewhere in Europe where its snail host is distributed. Also, it is suggested that individual adult worms may have been transferred from Europe to other areas by the migration of birds.

Table I. Final host: Birds and mammals found infected with *P. lucipetus*
(Based on the data from the list of synonymy reported above).

Species	Place
<i>Alectoris graeca cypriotis</i>	Bulgaria
<i>Anas angustirostris</i>	Armenia
<i>Anas platyrhynchos</i>	Czechoslovakia
<i>Anas platyrhynchos dom.</i>	Czechoslovakia
	Bulgaria
	Russia
<i>Anser anser</i>	Ukraine
<i>Anser anser dom.</i>	Yugoslavia
	Czechoslovakia
	Bulgaria
<i>Athene noctua</i>	Bulgaria
<i>Aythya ferina</i>	Russia
<i>Buteo buteo</i>	Bulgaria
<i>Circus aeruginosus</i>	Russia
<i>Circus macrourus</i>	Russia
<i>Columbia liva</i>	Bulgaria
<i>Colymbus (Podiceps) cristatus</i>	Russia
<i>Coturnix coturnix jap.</i>	Bulgaria
<i>Egretta alba</i>	Ukraine
<i>Fulica atra</i>	Ukraine
<i>Gallus gallus dom.</i>	Russia
	Bulgaria
<i>Halleatus albicilla</i>	Hungary
<i>Hydrochelidon (Childonias) nigra</i>	Yugoslavia
<i>Homo sapiens</i>	Austria
	Germany
	Yugoslavia
	Ukraine
<i>Larus argentatus armenicus</i>	Armenia
<i>Larus argentatus michaelis</i>	France
<i>Larus fuscus</i>	Austria
<i>Larus glaucus</i>	Austria
<i>Larus ichthyaetus</i>	Russia
<i>Larus ridibundus</i>	Hungary
	Yugoslavia
	Russia
<i>Lepus europeus</i>	Russia
<i>Meleagris gallopavo</i>	Bulgaria
<i>Mesocricetus auratus</i>	Bulgaria
<i>Numida meleagris</i>	Bulgaria
<i>Nycticorax nycticorax</i>	Ukraine
<i>Rattus rattus</i>	Bulgaria

Parasite collections: Adults of *P. lucipetus* are deposited in Naturhistorisches Museum Vienna, Austria slides Nos. 3305 to 3311; The Naturhistorisches Museum, Berlin, Germany slides Nos. 7237 to 7243; The Harold W. Manter Laboratory of Parasitology, Lincoln, Nebraska, USA, slides Nos. 34842 to 34848.

Literature sources of information: Descriptions and illustrations for *P. lucipetus* published by BRAUN (1902), SKRJABIN (1947) and YAMAGUTI (1958, 1971) are not considered valid because adults and larvae of another species are described under this name. As valid sources of information for *P. lucipetus* should be considered all descriptions and illustrations published under different names listed above as synonyms of *P. lucipetus*.

Remarks: The data presented above showed that *P. lucipetus* was fundamentally unknown in respect of its main characteristics after 173 years of studies. This occurs because its own characteristics were described and illustrated with over 40 different names as characteristics of different species and conversely those of other species have been described and illustrated as characteristics of *P. lucipetus*. This misunderstandings were unknown for many years. Now they are discovered and clarified.

Acknowledgements

These studies have been conducted with financial support of the Bulgarian Academy of Sciences and Fund National Investigations. Some studies and travel expenses were sponsored by grants from Naturhistorisches Museum Vienna, William Campbell Endowment Fund USA, Private Company "VEDIZA" Bulgaria, National Academic Foundation Sofia, Open Society and Western Illinois University. Dr. E. KRITSCHER, Dr. G. HARTWICH, Dr. H. SATTMANN and Mag. M. HAASE provided specimens and original descriptions and illustrations, and also aided in the collection of live material in Austria. Mrs. I. PETKOVA and Mr. D. VLAEV are also gratefully acknowledged for their excellent technical assistance. Thanks to Prof. Mary H. PRITCHARD for the critical reading of the manuscript.

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Annalen des Naturhistorischen Museums in Wien](#)

Jahr/Year: 1993

Band/Volume: [94_95B](#)

Autor(en)/Author(s): Dimitrov Vassil, Radev Valentin, Vassilev Ivan, Nollen Paul, Kanev Ivan

Artikel/Article: [Redescription of *Philophthalmus lucipetus* \(Rudolphi, 1819\) \(Trematoda: Philophtalmidae\) with a discussion of its identity and characteristics. 11-34](#)