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Notes on a gymnophallid trematode, assumed to be *Parvatrema affinis* (Jameson & Nicoll, 1913) from *Macoma balthica* (L.) (Bivalvia)

Marketta Pekkarinen

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Confusion concerning certain trematodes which occur in sporocysts in tissues of the clam *Macoma balthica* and which are currently identified as *Parvatrema affinis* is pointed out here. There may be two different species, or else the diagnostic features of the genus *Parvatrema* should be amended.

Metacercariae up to now referred to as *P. affinis* were found in a few individuals of *M. balthica* collected in the northern parts of the Baltic Sea. The prevalence was less than 1 %. These metacercariae had a small, but conspicuous, genital pore slightly anterior to the ventral sucker, whereas members of *Parvatrema* should have a large genital pore. Specimens originating from the Dutch Wadden Sea were similar. The metacercariae resemble those of *Meiogymnophallus multigemmulus* Ching, except that the genital pore in the latter is inconspicuous and close to the ventral sucker. The arrangement of papillae on the suckers and the site of the "genital papillae" at the genital pore of *P. affinis* are compared with those in *Lacunovermis macomae* (Lebour). The tegumental spines are similar, i.e. multi-pointed, in both these species.

Marketta Pekkarinen, Division of Physiology, Department of Zoology. University of Helsinki, Arkadiankatu 7, SF-00100 Helsinki, Finland.

1. Introduction

Larval stages of three gymnophallid trematode species have been reported as occurring in *Macoma balthica* (L.) (Loos-Frank 1971a). These are *Gymnophallus gibberosus* Loos-Frank, 1971, *Lacunovermis macomae* (Lebour, 1908) and a third species which has been identified as *Parvatrema affinis* (Jameson & Nicoll, 1913). In *M. balthica* from the Finnish coast three species were also found (Pekkarinen 1984a, 1987 and this study), but there was some discrepancy in the identification of the third one.

According to Cable (1953), the genital pore in *Parvatrema* (*P. borinquenae*) is large, pit-like and distinctly anterior to the ventral sucker. James (1964) transferred among others the trematode *Gymnophallus affinis* found by Jameson & Nicoll (1913) in *Melanitta nigra* to this genus. Selikman (1953) found metacercariae with a large genital pore in *M. balthica* from the White Sea and showed that they belonged to *G. affinis*. Later, Loos-Frank (1971a) and Swennen & Ching (1974) found similar metacercariae in *M. balthica* from the German and Dutch coasts of the North Sea. These authors also took *Metacercaria morula* described by Markowski (1936) from the southern Baltic *M. balthica*, as representing *Parvatrema affinis*. According to Markowski there was, however, a sucker-like structure at the genital pore of this trematode, leading Cable (1953) to suppose that this metacercaria may represent a genus other than *Parvatrema*.

In this paper the northern Baltic metacercaria is described and compared (along with the adult raised subcutaneously in laboratory mice) with specimens originating from the Dutch Wadden Sea. The genital pore of both specimens was found to be small. The confusion concerning the systematic position of the trematode(s) currently assumed to be *Parvatrema affinis* is discussed. Some comparison with *Lacunovermis macomae* described by Loos-Frank (1970) and Pekkarinen (1984a, 1986 and original figures of the present study) and *Meiogymnophallus multigemmulus* described by Ching (1965) is given. The occurrence of the trematode known as *Parvatrema affinis* in *Macoma balthica* in a few localities in the northern parts of the Baltic Sea (western and southwestern Finnish coasts) is assessed.

2. Material and methods

Metacercariae were obtained from a few individuals of *Macoma balthica* near Tvärminne Zoological Station (59°50'N, 23°15'E) and also off the coast near the town of Pori (61°30'N, 21°45'E). The water depth at Tvärminne was 35–40 m and the salinity 6–7 ‰, those off Pori 4 m and 6 ‰. The prevalence of the metacercariae in *M. balthica* was assessed in samples collected from sites I–III (depths 7–40 m) around Tvärminne Zoological Station during 1983–1984 (see the map in Pekkarinen 1984b). From the Dutch Wadden Sea *M. balthica* were collected at a sandy tidal flat in an area called Balgzand near the town of Den Helder (52°56'N, 4°47'E). The depth was about 25 cm below the mean tide level (tidal range about 1.5 m). The salinity is usually between 20 and 25 ‰, but may sometimes be lower, 10–20 ‰.

For measurements sporocysts and metacercariae were fixed in 4 % formaldehyde in brackish water. Infected clam bodies were fixed in Bouin's fluid for histological studies. Paraffin sections (7 µm in thickness) of the clams were stained with haematoxylin-chromotrope-fast green (Gray 1954:339). Metacercariae from Pori were cultivated into adults subcutaneously in laboratory mice for 1–2 days in accordance with Pekkarinen (1984a).

For scanning electron microscopy metacercariae and adults were fixed on membrane filters in 3 % glutaraldehyde in 0.1 M phosphate buffer (pH 7.2), dehydrated with ethyl alcohol, critical-point dried and coated with gold. Similarly treated specimens of *Lacunovermis macomae* from Tvärminne were used for comparison.

3. Results

The sporocysts were oval or round, white in the Dutch clams and pink in the Finnish clams. The most severe infestation was in the gonad region of the clams. The digestive gland was occupied to a lesser extent. Occasionally sporocysts were also seen in the mantle, kidney, pericardial gland and gills. 26 fixed sporocysts from one Dutch clam measured 204–516 by 168–360 µm (mean 319 × 256). The mean number of metacercariae per sporocyst was 22 (range 3–52). In another clam sporocysts up to 830 µm in length were found. In one Finnish clam (from Pori) 25 sporocysts measured 210–768 by 203–480 µm (mean 485 × 327). The mean number of metacercariae in these sporocysts was 24 (4–54).

Measurements of metacercariae and of adults are given in Table 1. The metacercariae in the Dutch clams were smaller than those from Pori. Their size (length × breadth × 10^{-3}) was 9–15 in two Dutch clams. The Dutch metacercariae shown in Table 1 are from the clam which harboured the largest individuals. The metacercariae from Pori, as well as one-day-old and two-day-old adults, developed from these metacercariae, were quite similar in their mea-

Table 1. Some measurements (mean and/or range, µm) from the literature, and from the present study for the trematode currently identified as *Parvatrema affinis*. The figures in the parentheses were calculated from the original figures given by Markowski. Abbreviations: Mark. = Markowski (1936), Selikman (1953), S & C = Swennen & Ching (1974), Jameson & Nicoll (1913), *M. b* = *M. balthica*, Metac. = metacercaria, laborat. = laboratory, formald. = formaldehyde, sublim. = sublimate. BL = body length, BB = body breadth, OSL = oral sucker length, OSB = oral sucker breadth, PL = pharynx length, PB = pharynx breadth, VSL = ventral sucker length, VSB = ventral sucker breadth, VSD = ventral sucker (centre) distance from anterior end.

Reference	Present study						Mark.	Selikman	S&C	Jameson & Nicoll	
Locality	Dutch Wadden Sea		Gulf of Bothnia Finland				Baltic, Poland	White Sea	Wadden Sea		
Life stage	Metacercaria		Metacercaria		Adult (2 days)		Metac.	Metac.	Metac.	Adult	
Host	*M. balthica*		*M. balthica*		Laborat. mouse		*M.b.*	*M. b.*	*M. b.*	*Melanitta nigra*	
Preparation	4 % formald.		4 % formald.		4 % formald.		sublim.		fixed		
Number	13		12		11				10		
BL	154	133–174	180	164–208	166	146–195	150	168–244	91–120	200–250	130–190
BB	97	84–108	101	93–108	110	105–115	90	96–144	71–91	110–130	
OSL	55	50–62	66	59–74	60	53–65	54				
OSB	58	53–74	71	62–78	68	62–81	60	56–72	45–55	65–85	
PL	19	18–23	19	16–23	21	19–24	16		12–19	15–18	
PB	17	15–18	19	18–21	18	17–19	16		12–16	12–17	
VSL	31	25–34	33	28–37	34	31–37	35				
VSB	35	31–40	37	34–40	38	37–40	35	20–40	19–32	30–45	
VSD	107	90–118	119	108–136	111	96–124				160–180	
BL×BB×10^{-3}	15	13–17	18	16–21	18	15–21	(14)				
BL/BB	1.61	1.34–2.07	1.79	1.55–2.10	1.52	1.32–1.81	(1.67)				
BL/OSL	2.81	2.42–3.28	2.70	2.51–2.93	2.77	2.45–3.15	(2.78)				
OSL/VSL	1.82	1.47–2.12	2.04	1.74–2.54	1.79	1.68–2.00	(1.54)				
OSB/VSB	1.65	1.43–2.00	1.90	1.68–2.11	1.79	1.55–2.19	(1.71)		2.00	2.00	
VSD/BL	0.69	0.66–0.72	0.66	0.62–0.70	0.67	0.64–0.71					

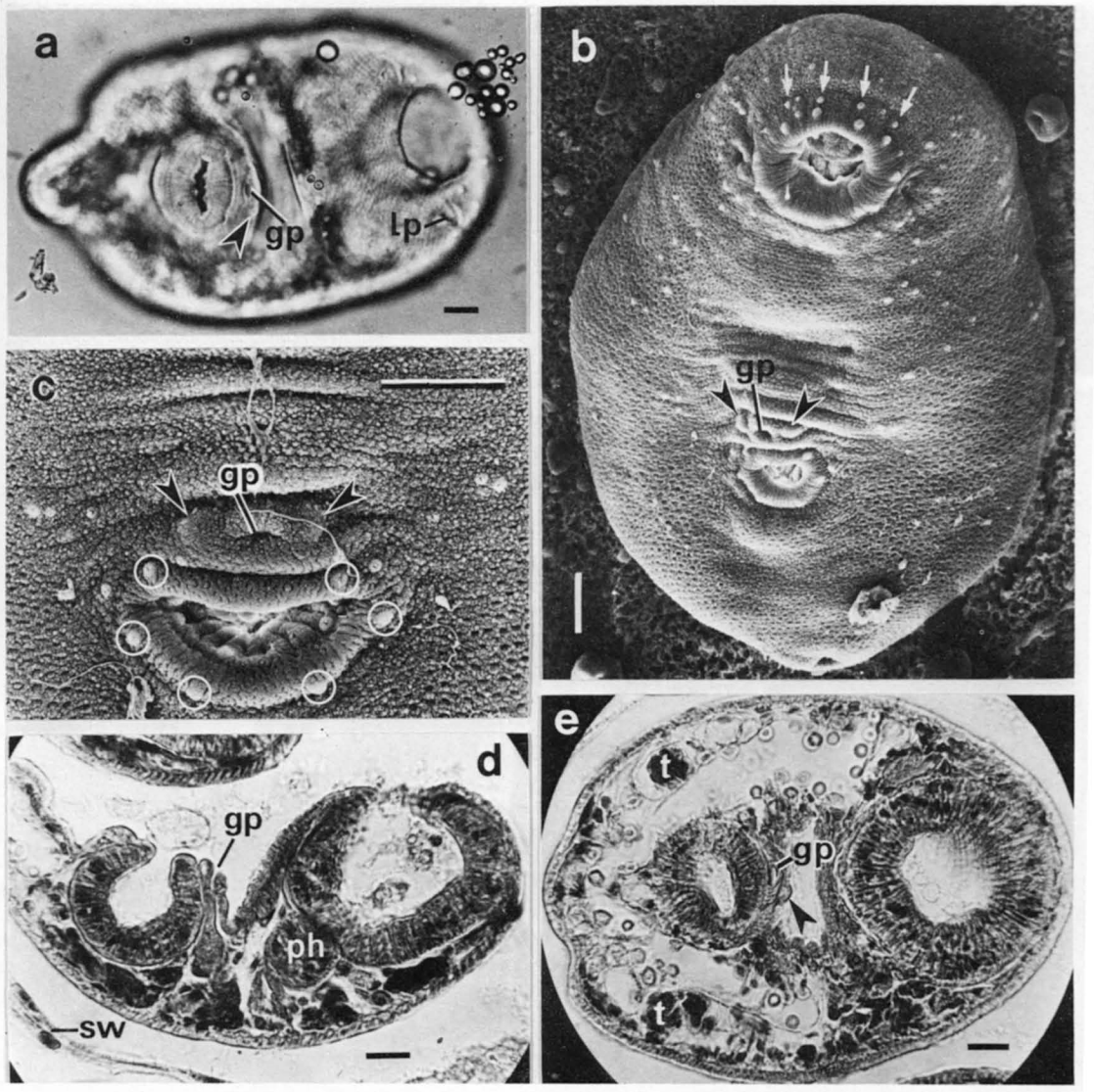

Fig. 1. The metacercaria of the trematode assumed to be *Parvatrema affinis* — a. A living specimen from *Macoma balthica* from the Dutch Wadden Sea. — b. Ventral surface view of a metacercaria from Pori, Finland. The white arrows point to the four papillae typically arranged adjacent to the four papillae of the dorsal lip of the oral sucker. — c. The genital pore and ventral sucker of a metacercaria from Pori (anterior side uppermost). The six papillae of the outer ring on the ventral sucker are circled. — d and e. Median and horizontal sections of metacercariae from Tvärminne, Finland, stained with haematoxylin-chromotrope-fast green. gp = genital pore, lp = lateral papilla of the oral sucker, ph = pharynx, sw = sporocyst wall, t = testis. The arrowheads point to the "genital papillae". Scale bars 10 µm in all pictures.

surements. The adults were contracted (the ratio length/breadth was smaller than in the metacercariae), but the size (length × breadth) was similar.

The mean ovarian size was 26 by 23 µm in the Dutch metacercariae and the mean testis size 28 by 19 µm. In the Finnish metacercariae and two-day-old adults the mean ovarian size was 28 by 21 µm and 31 by 23 µm, respectively, and the mean testis size 28 by 20 µm in both the metacercariae and the adults. The contour of the vitellaria was smooth or irregular. Their mean size was 21—23 by 17—19 µm in all the groups. The common vitelline reservoir was

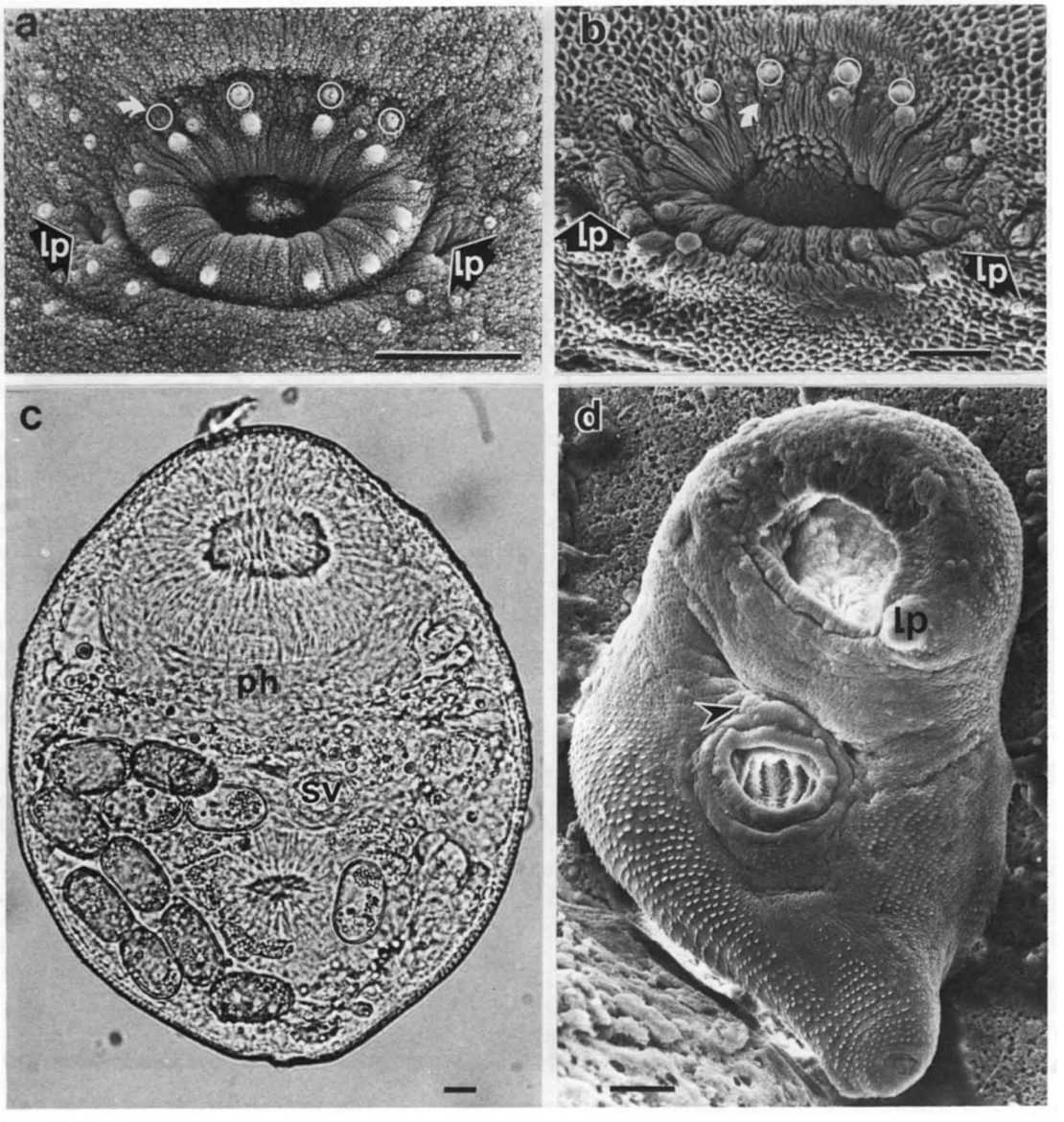

Fig. 2. — a and b. The oral sucker of a metacercaria of *Parvatrema affinis* and *Lacunovermis macomae*, respectively. On both suckers there are ten larger papillae in a ring and four adjacent papillae (circled) on the dorsal lip. The white arrows point to the sites of the papillae which are lacking in these preparations. The lateral papillae (lp) are retracted in these preparations. — c and d Adults of *Parvatrema affinis* (the specimen in c unfixed but slightly pressed). One lateral papilla (lp) and one genital papilla (arrowed) are visible in the individual in d. ph = pharynx, sv = seminal vesicle. Scale bars 10 μm.

distended in the adults. The ovarium was located at about the level of the anterior border of the ventral sucker. In 31 individuals the ovarium was located on the right side of the body and in 17 individuals on the left side. One-day-old adults had produced 1–4 eggs and adults incubated for two days carried 2—11 eggs (Fig. 2c). In 1-day adults the mean size of 14 eggs was 26.2 by 17.1 μm (range 23.8–28.0 by 14.7–18.2), and in 2-day adults 21 eggs measured 25.2 by 16.5 μm (range 21.7–29.4 by 13.3–17.5).

There are about ten gland cells around the oral sucker of the metacercaria. The digestive caeca are thin-walled, about 26–32 μm in length. The arms of the excretory vesicle are bilobed at their distal ends

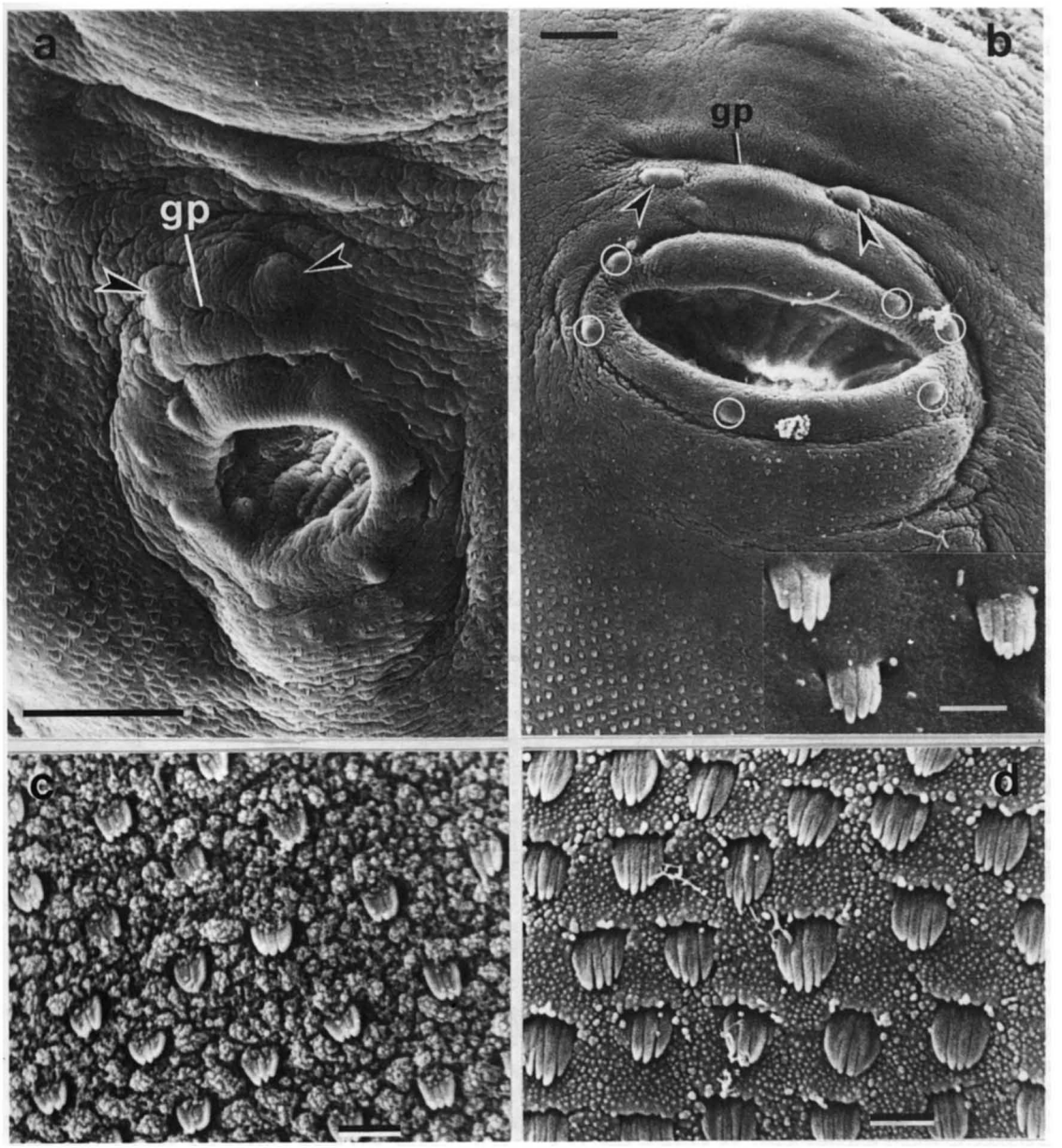

Fig. 3. — a and b. The genital pore (gp) with genital papillae (arrowed) and ventral sucker of adult *Parvatrema affinis* (a) and *Lacunovermis macomae* (b). The three uppermost papillae in picture b indicate the site of the ventral pit, which has bulged out in this preparation. The six outer papillae of the ventral sucker are circled. Insert: Tegumental spines of *L. macomae*. — c and d. Tegument of *Parvatrema affinis*: metacercaria (c) and adult (d). Bars 10 μm in a and b, and 1 μm in the insert in b and in c and d.

(Fig. 1a). Excretory concretions were present in the vesicle, and also freely in the sprocysts in Dutch specimens. The genital pore of the trematode is located slightly anterior to the ventral sucker. It is usually conspicuous but not very wide (Fig.1a–c, e, Fig. 3a). Its mean transverse width was 4.8 μm (range 3.7–6.2) in fixed Dutch specimens, and 4.7 μm in the Finnish specimens. In the adults the dimension was 4.2 μm. Two round papillae are present at the genital pore (Fig. 1b, c, 3a). The distance of the papillae from each other (lateral sides) was about 9–22 μm in fixed metacercariae. Larger

metacercariae are usually curved towards the ventral side, as in Fig. 1d. The ventral surface is usually depressed in front of the genital pore (Fig. 1a, b, d, e), but the walls of the depression are less muscular than those in the ventral pit of *Lacunovermis macomae*.

The number of flame cells in the metacercariae is at least 2 × 10. When the Dutch metacercariae were incubated in Tyrode's solution at 37–40°C for less than one day the flame cell number was found to be 2 × 12. The flame cells either became more clearly discernible or their number in fact increased from 2 × 10 to 2 × 12. At 4°C in Tyrode's solution (without glucose), which was changed to fresh solution daily, the metacercariae lived for one week.

The arrangement of sensory papillae at the oral and ventral suckers is shown in Figs. 1b, c, 2a and 3a. There are typically ten larger papillae in a circle on the oral sucker. Between these larger papillae there are a few smaller ones. Outside the four larger papillae on the dorsal lip there are four adjacent papillae (arrowed in Fig. 1b; one of them is lacking in Fig. 2a). There are 2 × 6 papillae on the ventral sucker. The "lateral papillae" of the oral sucker are proportionally large (one is visible in Fig. 2d). The tegumental spines are multi-pointed — in the adults they are broad like scales (Figs. 2d, 3c, 3d).

The infection prevalence of this trematode in *M. balthica* at Tvärminne, Finland, was very small. At collecting site I (depth 7–8 m) no infected individuals were found among 1402 clams of shell lengths about 6–22 mm. At sites II and III at depths of 20–40 m two individuals among 1003 clams of shell lengths 13–24 mm were infected (0.2 %). The shell lengths of these infected clams were 17.3 and 20.8 mm. Histological sections revealed that the metacercariae in the first clam were smaller and less developed than those in the latter clam. Cercariae and germinal balls were also detected. Among 117 clams of shell lengths 9–19 mm from Pori (4 m) one infected clam (shell length 15.5 mm) was found. Four infected individuals (shell lengths 13.1, 15.5, 16.5 and 18.4 mm) were found among 113 *M. balthica* individuals (shell lengths 10–22 mm) obtained from the Dutch Wadden Sea.

4. Discussion

Metacercaria morula described by Markowski (1936), *Gymnophallus affinis* described by Jameson & Nicoll (1913) and Selikman (1953) and similar trematodes found later in *Macoma balthica* or in water birds (Loos-Frank 1971a, Swennen & Ching 1974, Sulgostowska & Grytner-Zięcina 1974, Grytner-Zięcina & Sulgostowska 1978 and Lauckner 1983) have been grouped into one species known as *Parvatrema affinis*. James (1964) placed *Gymnophallus affinis* within *Parvatrema*. On the basis of their own material Sulgostowska & Grytner-Zięcina (1974) doubted the correctness of this assignment, but nevertheless adopted the name *Parvatrema affinis*.

The trematode studied here has many basic characteristics typical of *Parvatrema affinis*. Among them are e.g. the minute body size, large oral sucker, large eggs and a shorter life cycle (i.e. its metacercariae develop directly within the sporocysts without change of host).

According to the key to the genera of Gymnophallidae given by Ching (1973) the members of the genus *Parvatrema* have a wide genital pore some distance anterior to the ventral sucker, as is also the case in *Lacunovermis* and *Paragymnophallus*. The ventral pit, which is present in *Lacunovermis* and *Gymnophalloides*, is lacking in *Parvatrema*. The lateral lips (papillae) of the oral sucker are present in *Parvatrema*, as they are in *Lacunovermis* (Ching 1965, Loos-Frank 1970) and *Meiogymnophallus*. The seminal vesicle is club-shaped, and the excretory vesicle V-shaped, in *Parvatrema*.

The ventral surface anterior to the genital pore of the trematode described here was depressed, but the walls of the depression were less muscular than those of the real ventral pit in *L. macomae* (Loos-Frank 1970, Pekkarinen 1984a), and in *Gymnophalloides tokiensis* Fujita, 1925 (Ching 1972). The exact form of the seminal vesicle could not be established. There is one greater contradiction with *Parvatrema* in the anatomy of the present trematode, i.e. the size of the genital pore. Selikman (1953) described a wide transverse genital pore with two papillae in *Gymnophallus affinis* from the White Sea. According to Swennen & Ching (1974) the genital pore of *P. affinis* from the Dutch coast is a transverse slit, 13 to 23 µm across. The genital pore described in the present study resembles the sucker-like structure described by Markowski (1936) in *Metacercaria morula* from the southern Baltic Sea. The genital papillae of *L. macomae* are slightly more posterior in relation to the opening of the metraterm than they are in relation to the genital atrium in the present trematode (cf. Figs. 3a and 3b and Pekkarinen 1984a: Fig. 5). In *L. macomae* the genital atrium,

and hence the large genital pore, probably develop by depression during later metacercarial development (Pekkarinen 1986).

The distribution of the main sensory papillae on the oral and ventral suckers of the trematode described here resembles that of *L. macomae* (Figs. 2a, b and 3a, b). The tegumental spines of both these species are similar in structure (Figs. 2d and 3 and Pekkarinen 1984a and 1986) and in the size of the visible part of the adult spines (insert in Fig. 3b and Fig. 3d). Due to the smaller body size, in comparison with *L. macomae,* of the trematode assumed to be *Parvatrema affinis*, its spines appear proportionally large. Multi-pointed tegumental spines are widespread within Digenea. In addition to the references in Pekkarinen (1986) there are reports on such spines occurring in the tegument of *Urogonimus macrostomus* (Rudolphi) by Bakke (1978), *Clonorchis sinensis* (Cobbold) by Fujino et al. (1979), *Leucochloridium* (L.) *variae* McIntosh by Bakke (1982), *Hasstilesia ovis* (Orloff, Erschoff et Badanin by Ždárská et al. (1983), *Alaria marcianae* (La Rue) by Shoop & Corkum (1984), *Lepidapedon elongatum* (Lebour) by Køie (1985) (and also in a cestode, *Parachristianella monomegacantha* Kruse by Whittaker et al. 1985).

Meiogymnophallus multigemmulus parasitizes *Macoma inconspicua* (Broderip & Sowerby), a relative of *M. balthica,* in Canada (Ching 1965). It resembles *P. affinis* in its measurements and some other characteristics. Its oral sucker has lateral papillae like that of *P. affinis*. The bilobed arms of the excretory vesicle of *M. multigemmulus* are similar to those reported in the trematode assumed to be *P. affinis* in Swennen & Ching (1974), Lauckner (1983) and the present study. It had 2 × 12 flame cells, as had the maturing metacercaria in the present study. It also has an abbreviated life cycle. Its sporocysts were pink as were the northern Baltic sporocysts and those found by Reimer (1971) in the southern Baltic *M. balthica*. The sporocysts from the Wadden Sea *M. balthica* were, however, white (Swennen & Ching 1974 and present study). The colour may not be a reliable characteristic. Furthermore, the spines of *M. multigemmulus* are flat. The genital pore is, however, inconspicuous and close to the ventral sucker. This trematode inhabiting *Macoma inconspicua* may be a close relative of that parasitizing the related clam *M. balthica*.

As to the discrepancy in the size of the genital pore in different descriptions of the European species, this may result from errors, or intraspecific variation, or there may really be two different species. Puckering occurring in front of the genital pore, or the ventral depression, may have been interpreted as a genital pore. A similar error in the case of *Gymnophalloides tokiensis,* was revealed by Ching (1972). The mid-ventral pit present in *G. tokiensis* had been mistaken in the original description for a wide genital pore. Due to a small, but conspicuous, genital pore found in the trematode in the present study, the species ought to be transferred to its own genus, or the diagnostic features of the genus *Parvatrema* should be amended. Meanwhile the trematode described here is referred to as *Parvatrema affinis*.

If there is only one species, differences in the metacercarial size (Table 1) may result from different ages, fixation, host conditions, or possibly also from different salinities in the animals' environment. The Dutch metacercariae measured by Swennen & Ching (1974) were small and they had proportionally small testes (testis 14–19 by 9–16 µm, ovary 16–23 by 13–21 µm), which suggests that they were young specimens. The number of sporocysts is dependent upon the size and age of the host and the number of metacercariae varies according to the sporocyst size (Swennen & Ching 1974). The adult sizes differ markedly in different hosts, as Selikman (1953) showed. The sizes of the adults may also depend on their former, metacercarial sizes. Jameson & Nicoll (1913) found proportionally large adults, 200–250 µm in length, in *Melanitta nigra,* but besides these there was a large number of much smaller specimens, 130–190 µm in length, (c.f. Table 1). These smaller ones probably did represent the same species. Again James (1964) found in *Melanitta nigra* not only larger ones, but also tiny gravid specimens measuring only 140 µm in length. The egg size reported by Jameson & Nicoll was 21–28 by 13–18 µm. The eggs of *P. affinis* reported by Grytner-Zięcina & Sulgostowska (1978) in three duck species were narrower, i.e. 12 µm in breadth.

The number of vitellaria (two and/or one) and presence of lateral papillae on the oral sucker in the diagnosis of *Parvatrema* are not well established (cf. e.g. James 1964 and Schell 1985). Shimazu (1975) included a new species, *Parvatrema rebunense*, in the genus. As is apparent from the English summary, he was forced to amend the generic diagnosis of *Parvatrema* at the point of the site of the genital pore. If this can be accepted, then *Meiogymnophallus multigemmulus* comes even closer to *P. affinis*. According to Stunkard & Uzmann (1958) and James

(1964), the location of the genital pore of *P. borealis* and *P. homoeotecnum* varies widely in different individuals. Bakke (1982) discusses intraspecific variation and conspecificity within and between Palaearctic and Nearctic leucochloriids. Different forms of *Gymnophallus macroporus* Jameson & Nicoll, 1913 (= *Lacunovermis macomae*) were described by Ryzhikov et al. (1966) in *Somateria* species.

The prevalence of *P. affinis* in *Macoma balthica* was low in the northern parts of the Baltic Sea. It was low (0.7 %) also according to Markowski (1936) in the southern Baltic off Poland. The figures 1.4–3.7 % given by Wenne & Klusek (1985) from the same region (Gdańsk Bay, Poland) may include sporocysts of other species; close species determination was not made (Wenne, personal communication). However, Wenne believes that the prevalence has increased, a phenomenon correlated indirectly with increased contamination of the Gdańsk Bay. The infection rate on the Swedish coast of the northern Baltic Sea (Askö-Landsort area, 58°49′N, 17°38′E) seems to be much higher than 0.7 % (Ankar & Elmgren 1978). On the German coast of the Baltic Sea the prevalence was also higher, i.e. 6.2 % (Reimer 1971). This is similar to the prevalence in the White Sea (6.6 %, Selikman 1953) and in the North Sea, Germany (7.5 %, Loos-Frank 1971a). The infection prevalence correlates positively with the shell length of *M. balthica* (Hulscher 1973, Swennen & Ching 1974). In one place in the Wadden Sea up to 44 % of *M. balthica* of over 19 mm shell length were infected (Hulscher 1973).

The parasites occupying the place of the gonad suppress the fecundity of the infected clam. The infection by *P. affinis* has been reported as causing crawling tracks of the clams on the sediment (Swennen & Ching 1974) and increased mortality of the clams (Hulscher 1973). The surfacing clams are easily preyed on by the definitive hosts of the trematode. The oystercatcher (*Haematopus ostralegus*), however, often rejects parasitized clams (Hulscher 1982).

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