Bartolius pierrei n. g., n. sp. (Digenea: Gymnophallidae) from the Península Valdés, Argentina

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Abstract

Bartolius pierrei n. g., n. sp. (Digenea: Gymnophallidae) is described from metacercariae and naturally and cultivated obtained adults from southern Argentina. The second intermediate host is Darina solenoides (King) (Bivalvia: Mactridae) and the definitive host is Larus dominicanus Lichtenstein (Aves: Laridae). The diagnostic characters are as follows: Body small, oval. Oral sucker without lateral projections, twice size of ventral sucker (except in young metacercariae). Caeca short (in adults), without dorsal diverticula. Ventral sucker in posterior third of body. Ventral pit absent. Seminal vesicle bipartite. Ovary post-testicular. Vitelline glands paired, compact, close to ventral sucker. Uterus in fore- and hindbody. Genital atrium tubular. Genital pore inconspicuous, close to anterior margin of ventral sucker. Excretory vesicle Y-shaped with very short stem. Excretory formula: 2[(2+2)+(2+2)] = 16. Bartolius is distinguished from other genera of the Gymnophallidae by the post-testicular position of the ovary.

Introduction

The family Gymnophallidae was erected by Odhner in 1905 and, to date, seven genera have been established (Bartoli, 1974; Hoberg, 1981; Ching, 1995). These genera are included into two subfamilies, the Parvatrematinae Yamaguti, 1958 and the Gymnophallinae Odhner, 1905. This latter is characterised by the presence of a pars prostatica which opens into the genital atrium and includes *Gymnophallus* Odhner, 1900, *Gymnophalloides* Fujita, 1925, *Meiogymnophallus* Ching, 1965, *Paragymnophallus* Ching, 1973 and *Pseudogymnophallus* Hoberg, 1981.

Records of gymnophallid species are scarce in South America. There are only two descriptions of larval stages based on fixed material, *Parvatrema australis* (Szidat, 1962) (see Szidat, 1962, 1965) and *Lacunovermis* sp. (see Martorelli & Morriconi, 1998).

The aim of this paper is to describe a new genus and species of gymnophalline metacercaria parasitic in *Darina solenoides* (King) (Bivalvia: Mactridae) and its corresponding cultured and naturally obtained adults from southern Argentina. Although several authors (Stunkard & Uzmann, 1958; James, 1964; Bar-

toli, 1974) have indicated the need for a taxonomic revision of the genera and species of the Gymnophallidae, the specimens studied in the present work exhibit unique morphological characters which enable it to be readily distinguished from other gymnophallid genera.

Materials and methods

Specimens of *Darina solenoides* (King) (Bivalvia: Mactridae) were collected at Fracasso Beach (42°25′S; 64°07′W), San José Gulf, Argentina. The study area is a sandy beach in the Península Valdés, a Provincial Park and Natural Heritage Site. Clams were maintained in an aquarium and metacercariae were studied alive. Metacercariae were fixed in hot 4% seawater formalin under a coverslip, measured and stored in 70% alcohol. Experimental infection was performed using chicks. Each chick was exposed to 30–60 metacercariae. In the first experiment 2 chicks were infected and examined after 6 days with negative results. Consequently, 6 further chicks were infected, the first was necropsied after 24 hours and parasites were not found. Following this, the remaining 5 chicks were

re-infected and one examined every hour, but worms were not found. Consequently, metacercariae were incubated in vitro at 40 °C in physiological saline with an antibiotic additive and observed for eggs at various times. Additionally, one kelp gull Larus dominicanus Lichtenstein (Aves: Laridae) was collected at the same locality of *D. solenoides* and examined for parasites. Both cultured and ovigerous worms from the kelp gull were killed in same way as the metacercariae, measured, stored in 70% alcohol, stained with Semichons's acetocarmine, cleared in creosote and mounted in Canada balsam. The drawings were made with the aid of a camera lucida. Measurements are given in micrometres with the mean following by the range in parentheses. The sucker-ratios are sucker-length ratios. In order to calculate the prevalence (P) and the mean intensity (Im) of metacercariae, in March 2000, 40 clams (maximum length ranges: 8-12 and 19-30 mm) were fixed and the parasites counted. The nomenclature of the metacercarial habitats follows Bartoli (1974).

Bartolius n. g.

Diagnosis

Gymnophallidae. Gymnophallinae. Body small, oval. Oral sucker without lateral projections, twice as large as ventral sucker (except in young metacercaria). Caeca short (in adults), without dorsal diverticula. Ventral sucker in posterior third of body. Ventral pit absent. Seminal vesicle bipartite. Ovary post-testicular. Vitelline glands paired, compact, close to ventral sucker. Uterus in fore- and hindbody. Genital atrium tubular. Genital pore inconspicuous, close to anterior margin of ventral sucker. Excretory vesicle Y-shaped, with very short stem. Excretory formula: 2[(2+2)+(2+2)]=16.

Type and only species: Bartolius pierrei n. sp.

Bartolius pierrei n. sp

Type-host: Larus dominicanus Lichtenstein (Aves: Laridae).

Site of infection: Intestine.

Intensity of infection: 592 individuals.

Type-locality: Fracasso Beach (42°25′S; 64°07′W), the Península Valdés, Province of Chubut, Argentina. *Intermediate host: Darina solenoides* (King) (Bivalvia: Mactridae).

Site of infection: Metacercariae are located in the extrapallial cavity of D. solenoides. Large, old metacercariae are dark in appearance and are always individually enveloped by a jelly-like substance. These spheres are generally grouped in vesicles situated in the subarticular space, above the pericardial cavity and also along the rest of the dorsal region in high numbers. Small, young metacercariae, translucent in appearance, are generally free in the general extrapallial space. These young metacercariae are frequently found in the periphery of the vesicles containing older worms. In the sites where old metacercariae were located, there are often numerous calcareous concretions either free or attached to the inner surface of the valve. Prevalence and mean intensity of metacercaria: P = 40% and Im = 2; all metacercariae are in the general extrapallial space (8-12 mm clam size range); P = 70% and Im = 4 in the general extrapallial space and P = 35% and Im = 38 in the subarticular extrapallial space (19-30 mm clam size range).

Etymology: Generic and specific names are for Prof. Pierre Bartoli (Centre d'Océanologie de Marseille, Université de la Méditerranée, France) for his great contributions to the study of gymnophallids.

Specimens deposited: Holotype No. 4791, paratypes No. 4792 (stained whole-mounts of natural adults), voucher specimens No. 4793 (stained whole-mounts of old metacercariae) in the Helminthological Collection of Museo de La Plata (CHMLP), Museo de La Plata, La Plata, Argentina. Paratype No. 2000.11.13.1 and voucher specimen No. 2000.11.13.2 (stained whole-mounts of natural adult and metacercaria, respectively) in The Natural History Museum, London, United Kingdom.

Description (Figures 1–8)

Young metacercariae (20 specimens measured) (Figure 1). Body oval 234 (190–320) \times 147 (120–200) at acetabular level. Spines along body length and on both dorsal and ventral surfaces, transversally arranged. Oral sucker 49 (40–60) \times 50 (42–60), without lateral projections. Pharynx ovoid, 33 (23–40) \times 21 (18–26). Oesophagus 24 (10–40) in length. Caeca 77 (50–110) \times 50 (36–70) at maximum width, usually reaching middle of ventral sucker or surpassing it. Forebody 118 (85–170) in length. Ventral sucker 46 (32–57) \times 49 (40–60), with outer circle of 6 papillae and inner circle of 6 papillae. Sucker-ratio 1:0.93. No genital primordia. Excretory formula: 2[(2+2)+(2+2)]= 16. First pair of flame-cells located at sides of oral

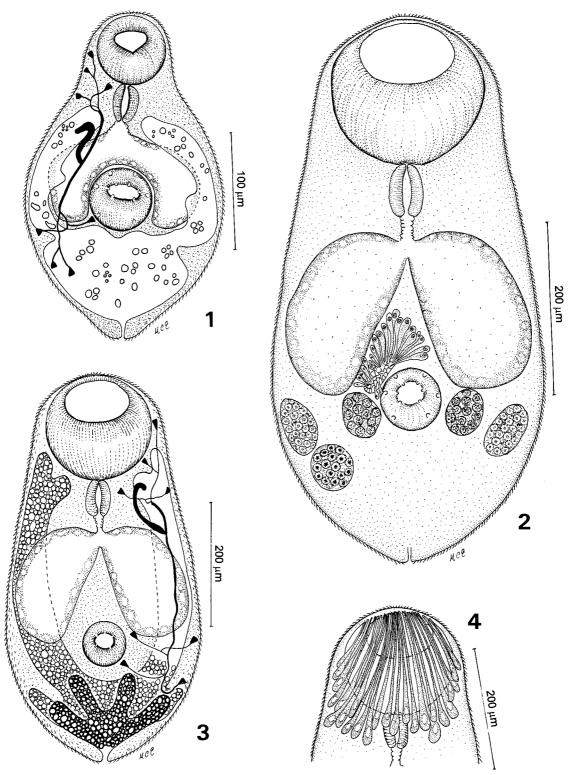


Figure 1–4. Bartolius pierrei n. g., n. sp. 1. Young metacercaria, dorsal view, flame-cells on right side omitted. 2. Old metacercaria, ventral view, cephalic glands, excretory system and part of the terminal genitalia omitted. 3. Excretory system of old metacercaria, ventral view, flame-cells of right side omitted. 4. Anterior end of old metacercaria showing cephalic glands, dorsal view.

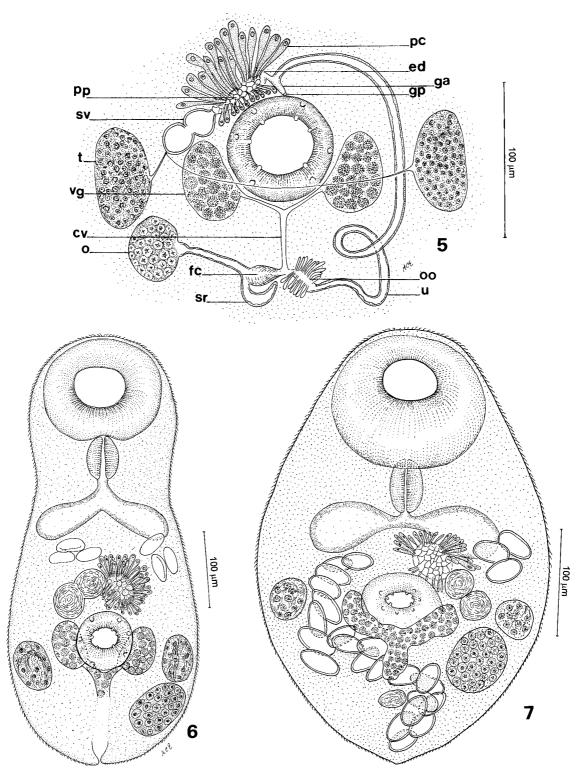


Figure 5–7. Bartolius pierrei n. g., n. sp. 5. Genital system of old metacercaria, dorsal view. 6. Cultured adult, ventral view. 7. Naturally obtained adult, dorsal view. Abbreviations: pc, prostatic cells; ed, ejaculatory duct; ga, genital atrium; gp, genital pore; pp, pars prostatica; sv, seminal vesicle; t. testis; vg, vitelline gland; cv, common vitelloduct; o, ovary; fc, fertilisation chamber; sr, seminal receptacle; oo, oötype; u, uterus.

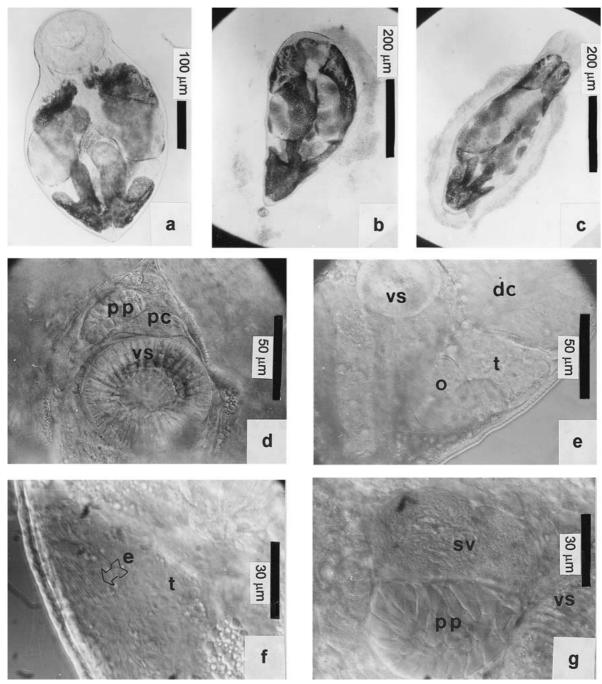


Figure 8. Microphotograph of live Bartolius pierrei n. g., n. sp. a. Old metacercaria, ventral view; b. Old metacercaria, contracted specimen, dorsal view; c. Old metacercaria, elongate specimen showing jelly-like covering, ventral view; d. Mature metacercaria showing ventral sucker and pars prostatica surrounded by numerous prostatic cells; e. Old metacercaria showing ventral sucker, digestive caeca, testis and ovary, ventral view; f. Pre-adult (after 15–20 hours of culture) showing testis with active spermatozoa (arrow); g. Pre-adult (after 15–20 hours of culture) showing well-developed pars prostatica and seminal vesicle distended with spermatozoa. Abbreviations: pp, pars prostatica; pc, prostatic cells; vs, ventral sucker; dc, digestive caeca; t, testis; o, ovary; e, spermatozoa; sv, seminal vesicle.

sucker; second pair at pharyngeal level. Second group of flame-cells with first and second pairs at acetabular and post-acetabular zone, respectively. Excretory vesicle with very short stem and 2 branches that extend to level of oral sucker. Vesicle filled with spherical and elongate excretory granules.

Old metacercariae (20 specimens measured, unless otherwise indicated) (Figures 2-5, 8a-e). Body oval, $612 (462-840) \times 355 (237-412)$ at level of ventral sucker. Spines along body length and on both surfaces, transversally arranged. Oral sucker 147 (117–174) \times 153 (117-180), without lateral projections. Cephalic glands numerous. Pharynx ovoid, 50 (31–62) \times 48 (30–62). Oesophagus 65 (30–170) in length. Caeca $238 (80-328) \times 139 (50-185)$ at maximum width, reaching middle of ventral sucker or surpassing it, filled with brownish material; sometimes triangular or elongate crystals present. Forebody 365 (232–478) in length. Ventral sucker 71 (60–84) \times 72 (60–85), with outer circle of 6 papillae and inner circle of 6 papillae. Sucker-ratio 1:0.48. Testes ovoid, located at level of ventral sucker or slightly posterior to it in lateral fields; one testis sometimes anterior to ovary and slightly diagonal to other testis; left testis 66 $(38-100) \times 54 (27-90)$ (n = 19); right testis 69 (45- $120) \times 52 (27-82) (n = 18)$. Sperm-ducts originate from mid-length of testes and unite at base of seminal vesicle. Seminal vesicle bipartite, 40 (30–49) \times 22 (18–33) (n = 6). Pars prostatica 46 (23–62) \times 18 (13-30) (n = 18), surrounded by numerous prostatic cells, which fill much of intercaecal space. Ejaculatory duct short. Ovary rounded, $52 (30-90) \times 54 (32-91)$ (n = 18), located posterior to right testis in 50% of individuals and posterior to left testis in remainder (n = 50), sometimes displaced slightly towards interior of body. Vitelline glands paired, compact, close to ventral sucker. Oviduct long. Ciliated fertilisation chamber located in wider part of oviduct, with elongate seminal receptacle of canalicular type which opens into its proximal end; common vitelline duct also opens at its distal end, just prior to Mehlis' gland complex. Uterus initially coils at level of ovary and then ascends to genital atrium. Genital atrium tubular, short. Genital pore inconspicuous, located close to anterior edge of ventral sucker in mid-ventral line. Excretory formula and flame-cell location as in young metacercariae. Excretory vesicle with very short stem, forming 2 short and 2 long branches dorsally, which extend to level of oral sucker, and 4 short branches ventrally. Excretory vesicle distended and filled with

spherical and elongate excretory granules.

Cultured adult (10 specimens measured unless indicated otherwise) (Figure 6). Body oval to elongate, $520 (445-765) \times 210 (170-252)$, at level of ventral sucker. Oral sucker $127 (110-140) \times 145 (130-162)$, without lateral projections. Pharynx ovoid, $55 (50-67) \times 51 (47-62)$. Caeca short and narrow. Forebody 328 (275-417) in length. Ventral sucker $73 (60-83) \times 75 (60-86)$. Sucker-ratio 1:0.57. Testes ovoid; left testis $60 (48-80) \times 48 (29-58) (n=8)$; right testis $60 (52-62) \times 47 (43-50) (n=9)$. Seminal vesicle bipartite, $66 (50-81) \times 41 (32-52)$. Pars prostatica $55 (46-61) \times 38 (32-42) (n=4)$. Ovary ovoid, $71 (48-81) \times 60 (49-70) (n=9)$. Uterus in fore- and hindbody. Eggs $39 (36-43) \times 17 (15-20)$. Excretory vesicle reduced in size, with few excretory granules.

Naturally obtained adult (10 specimens measured unless indicated otherwise) (Figure 7). Body oval, 384 $(290-525) \times 254 (164-347)$ at level of ventral sucker; colour yellowish in specimens with numerous eggs. Oral sucker 132 (91–178) \times 148 (118–169), without lateral projections. Pharynx ovoid, 54 (42-61) × 39 (32-59). Caeca short, narrow. Forebody 229 (205-280) in length. Ventral sucker 68 $(58-89) \times 75$ (64–90), with outer circle of 6 papillae and inner circle of 6 papillae. Sucker-ratio 1:0.52. Testes ovoid; left testis 42 (32–60) \times 34 (21–40) (n = 8); right testis $41 (32-55) \times 34 (28-40)$ (n = 7). Seminal vesicle bipartite, 60 (48–69) \times 36 (31–42). Pars prostatica 43 $(35-61) \times 30 (24-34)$. Ovary ovoid, 63 (40-97) \times 47 (31–74). Seminal receptacle 27 (21–33) \times 15 (12-16) (n = 3). Vitelline glands appear dispersed in specimens with large numbers of eggs. Uterus in fore and hindbody. Eggs 36 (33–41) \times 22 (19–23); 12 (1– 39) in number. Excretory vesicle reduced in size, with few excretory granules.

Ontogenetic development

Observations of pre-adult specimens obtained after 15–20 hours of culturing metacercariae *in vitro* indicated active spermatozoa in their testes and the seminal vesicle distended and full of spermatozoa (Figure 8f,g). The ovary, which is round and smaller than testes in the metacercaria, had become large and oval. The common vitelline duct was also distended and full of vitelline cells. The digestive caeca showed a great reduction in size at this time. After 35–40 hours a great number of specimens died and those alive re-

mained quiescent. Of 179 individuals, 14 contained eggs, generally only one, two or three, but in one case six, were counted. The eggs appeared mainly in the terminal part of the uterus, in the ascending branch, which was located more anteriorly than in the metacercaria (Figure 6). In some specimens abnormal eggs appeared, and clumps of vitelline material were sometimes present in the uterus. The testes did not vary in size but the ovary, the seminal vesicle and the pars prostatica became larger. Both cultured and naturally obtained ovigerous specimens were generally smaller than the metacercariae, possibly due to the great reduction in the size of the intestinal caeca. However, they were similar in other general measurements, such as for the suckers and pharynx. In adults recovered from the intestine of the kelp gull, it was possible to observe some specimens with few eggs very similar to those obtained in vitro; the remainder were in a later developmental stage, with numerous eggs. These latter individuals were yellowish in colour, possibly due to the dispersal of vitelline material; in addition, the vitelline glands had a more follicular appearance and were less conspicuous, and the testes were smaller and the seminal receptacle full of spermatozoa (Figure 7).

Discussion

The genus *Bartolius* differs from all other gymnophallid genera in having the ovary post-testicular. By contrast, the other known genera have the ovary in a pre-testicular position, with the exception of the monotypic genus *Pseudogymnophallus* Hoberg, 1981 in which it is located between the testes (Fujita, 1925; Cable, 1953; Stunkard & Uzmann, 1958; James, 1964; Ching, 1965, 1973a; Bartoli, 1974; Hoberg, 1981). The new genus is included in the Gymnophallinae Odhner, 1905 because of the possession of a pars prostatica which opens into genital atrium. Thus, it differs from *Parvatrema* Cable, 1953 and *Lacunovermis* Ching, 1965, which belong to the Parvatrematinae Yamaguti, 1958, in possessing a pars prostatica.

Bartolius is most similar to Gymnophallus Odhner, 1900 and Meiogymnophallus Ching, 1965 due to the absence of a ventral pit and the presence of an inconspicuous genital pore located close to the anterior margin of the ventral sucker. These two genera share most characteristics but exhibit different morphological combinations of the seminal vesicle and vitellarium. Thus, Gymnophallus choledochus Odhner, 1900, Meiogymnophallus nereicola (Rebecq & Prévot,

1962), M. fossarum (Bartoli, 1965), G. gibberosus Loos-Frank, 1971 and M. rebecqui (Bartoli, 1983) have a bipartite seminal vesicle and follicular vitellarium (Rebecq & Prévot, 1962; Bartoli, 1965, 1972, 1983a; Loos-Frank, 1971; Bowers et al., 1996). On the other hand, G. rostratus Bartoli, 1982 has an undivided seminal vesicle and a unique compact vitellarium (Bartoli, 1982), and G. somateriae (Levinsen, 1881) has a bipartite seminal vesicle and a vitellarium composed of irregular-shaped masses (Ching, 1973b). In other species of Meiogymnophallus, the seminal vesicle is undivided and the vitelline glands compact [e.g. M. multigemmulus Ching, 1965 and M. strigatus (Lebour, 1908)] (Ching, 1965; Bartoli, 1983b). M. minutus (Cobbold, 1859) is the only species to share with Bartolius pierrei n. sp. the possession of a bipartite seminal vesicle and compact vitelline glands (Bowers & James, 1967; Bowers et al., 1990). This latter species differs from B. pierrei in having a small pars prostatica that opens directly into the genital atrium. The new genus and species can be further distinguished from Gymnophalloides Fujita, 1925 by the absence of a ventral pit (Fujita, 1925; Ching, 1972; Soon-Hyung et al., 1993). It can be differentiated from Paragymnophallus Ching, 1973 by its possession of an inconspicuous genital pore and compact vitelline glands (Ching, 1973a), and from Pseudogymnophallus Hoberg, 1981 in the location of the ventral sucker and the morphology of the vitellarium and intestinal caeca (Hoberg, 1981).

The ontogenetic development observed in this study is similar to that reported by Bartoli (1963, 1965, 1983a) and Pekkarinen (1984). Pekkarinen (1984) obtained the adult form of *Lacunovermis macomae* (Lebour, 1908) in vitro, and her adults were smaller than the metacercariae and either in a quiescent stage or dead. The speed of spermatogenesis and egg production and the fact that they only needed a rise in temperature to develop suggest that the lifespan of this gymnophallid in its final host is very short. A similar observation was first noted by Bartoli (1965), who obtained the adult of *Meiogymnophallus fossarum* (Bartoli, 1965) from *Larus cachinnans michaellis* Naumann in which its longevity was only three or four days.

Regarding the life-cycle of the new species, gymnophallid cercariae were found in *Darina solenoides*, the same host as the metacercaria. Because cercariae of different gymnophallid species are almost indistinguishable, experimental infections are necessary in order to test whether they belong to the

same species. *Larus dominicanus* was found parasitised, but other birds probably also act as definitive host for this parasite, because *D. solenoides* is the most important prey for migratory birds in the study area (Pagnoni, 1997). For example, dead adult worms found in the faeces of *Calidris canutus rufa* (Wilson) (Aves: Scolopacidae) in a study of the meiobenthos had no eggs and were too contracted to measure, but they are easily recognisable as *B. pierrei* by their posttesticular ovary and the shape and location of the vitelline masses.

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References

- Bartoli, P. (1963) Note préliminaire sur l'anatomie et la biologie de Parvatrema timondavidi n. sp. (Trematoda, Digenea). Comptes Rendus de l'Académie des Sciences, Paris, 273, 518–520.
- Bartoli, P. (1965) Développement expérimental d'une metacercaire nouvelle de la famille des Gymnophallidae Morozov, 1955 (Trematoda: Digenea), parasite de lamellibranches marins. *Bulletin de la Société Zoologique de France*, **90**, 571–580.
- Bartoli, P. (1972) Les cycles biologiques de Gymnophallus nereicola J. Rebecq et G. Prévot, 1962 et G. fossarum P. Bartoli, 1965, espèces jumelles parasites d'oiseaux de rivages marins (Trematoda, Digenea, Gymnophallidae). Annales de Parasitologie Humaine et Comparée, 47, 193–223.
- Bartoli, P. (1974) Recherches sur les Gymnophallidae F. N. Morozov, 1955 (Digenea) parasites d'oiseaux des côtes de Camargue: systématique, biologie et ecologie. Thèse, Université d'Aix-Marseille, 338 pp.
- Bartoli, P. (1982) Gymnophallus rostratus n. sp. (Trematoda: Gymnophallidae) parasite of marine bivalves from Camargue. Vie-Marine. 4. 51–58.
- Bartoli, P. (1983a) Gymnophallus rebecqui n. sp. (syn. Parvatrema sp. 1, J. Rebecq, 1964) (Digenea: Gymnophallidae) parasite intestinal d'Anatidés de Camargue (France). Annales de Parasitologie Humaine et Comparée, 58, 211–225.
- Bartoli, P. (1983b) Les stades larvaires de *Meiogymnophallus stri-gatus* (M.V. Lebour, 1908) n. comb. (Trematoda: Gymnophal-

- lidae). Annales de Parasitologie Humaine et Comparée, 58, 227-242.
- Bowers, E.A. & James, B.L. (1967) Studies on the morphology, ecology and life-cycle of *Meiogymnophallus minutus* (Cobbold, 1895) comb. nov. (Trematoda: Gymnophallidae). *Parasitology*, 57, 281–300.
- Bowers, E.A., Bartoli, P., Russell-Pinto, F. & James, B.L. (1996)
 The metacercariae of sibling species of *Meiogymnophallus* including *M. rebecqui* comb. nov. (Digenea: Gymnophallidae), and their effects on closely related *Cerastoderma* host species (Mollusca: Bivalvia). *Parasitology Research*, 82, 505–510.
- Bowers, E.A., Bartoli, P. & James, B.L. (1990) A demonstration of allopatric sibling species within the Gymnophallidae (Digenea). Systematic Parasitology, 17, 143–152.
- Cable, R.M. (1953) The life cycle of *Parvatrema borinqueñae* gen. et sp. nov. (Trematoda: Gymnophallidae) and the systematic position of the subfamily Gymnophallinae. *Journal of Parasitology*, 39, 408–421.
- Ching, H.L. (1965) Life cycles of Lacunovermis conspicuus n. gen., n. sp. and Meiogymnophallus multigemmulus n. gen., n. sp. (Gymnophallidae: Trematoda) from Macoma inconspicua and diving ducks from Vancouver, Canada. Proceedings of the Helminthological Society of Washington, 32, 53–63.
- Ching, H.L. (1972) A redescription of Gymnophalloides tokiensis Fujita, 1925 (Trematoda: Gymnophallidae). Canadian Journal of Zoology, 50, 1299–1302.
- Ching, H.L. (1973a) Paragymnophallus odhneri gen. n., sp. n. (Trematoda: Gymnophallidae) for Gymnophallus somateriae sensu Odhner (1900, 1905). Canadian Journal of Zoology, 51, 807–810.
- Ching, H.L. (1973b) Gymnophallus somateriae (Levinsen, 1881) from Macoma inconspicua and diving ducks from Vancouver, Canada. Canadian Journal of Zoology, 51, 801–806.
- Ching, H.L. (1995) Evaluation of characters of the family Gymnophallidae Morozov, 1955. Canadian Journal of Fisheries and Aquatic Sciences, 52 (Suppl. 1), 78–83.
- Fujita, T. (1925) Etude sur les parasites de l'huitre comestible du Japon Ostrea gigas Thunberg. Annales de Parasitologie Humaine et Comparée, 3, 37–59.
- Hoberg, E.P. (1981) Pseudogymnophallus alcae gen. n. et sp. n. (Trematoda: Gymnophallidae) from alcids (Charadriiformes) in Subarctic seas. Proceedings of the Helminthological Society of Washington, 48, 190–194.
- James, L.B. (1964) The life cycle of *Parvatrena homoeotecnum* sp. nov. (Trematoda: Digenea) and a review of the family Gymnophallidae Morozov, 1955. *Parasitology*, 54, 1–41.
- Loos-Frank, B. (1971) Zur Kenntnis der gymnophalliden Trematoden des Nordseeraumes III. Gymnophallus gibberosus n. sp. und seine Metacercarie. Zeitschrift für Parasitenkunde, 35, 270–281.
- Martorelli, S.R. & Morriconi, E. (1998) A new gymnophallid metacercaria (Digenea) in *Nacella (P.) magallanica* and *N. (P.) deaurata* (Mollusca, Patellidae) from the Beagle Channel, Tierra del Fuego, Argentina. *Acta Parasitologica*, 43, 20–25.
- Pagnoni, G.O. (1997) Poblamiento de la infauna de la zona intermareal del golfo San José (Pcia. del Chubut) y su importancia en la alimentación de aves migratorias. Tesis Doctoral, Universidad Nacional La Plata, 282 pp.
- Pekkarinen, M. (1984) Anatomy, histology and maturing of the metacercaria of *Lacunovermis macomae* (Trematoda: Gymnophallidae) from brackish-water *Macoma balthica* (South-western Finland, Baltic Sea). *Annales Zoologici Fennici*, 21, 481–498.

- Rebecq, J. & Prévot, G. (1962) Développement expérimental d'un *Gymnophallus* (Trematoda, Digenea). *Comptes Rendus de l'Académie des Sciences, Paris*, **255**, 3,272–3,274.
- Soon-Hyung, L., Jong-Yil, C. & Sung-Tae, H. (1993) Gymnophalloides seoi n. sp. (Digenea: Gymnophallidae), the first report of human infestation by a gymnophallid. Journal of Parasitology, 79, 677–680.
- Stunkard, H.W. & Uzmann, J.R. (1958) Studies on digenetic trematodes of the genera *Gymnophallus* and *Parvatrema*. *Biological Bulletin*. *Woods Hole Biological Station*, **115**, 276–302.
- Szidat, L. (1962) Über eine ungewöhnliche Form parthenogenetischer Vermehrung bei Metacercarien einer *Gymnophallus*-Art aus *Mytilus platensis*, *Gymnophallus australis* n. sp. des Südatlantik. *Zeitschrift für Parasitenkunde*, **22**, 196–213.
- Szidat, L. (1965) Los parásitos de los mitílidos y los daños por ellos causados II. Los parásitos de Mytilus edulis platensis (mejillón del plata). Comunicaciones del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, 1, 1–16.