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EXPERIMENTAL INFECTION BY OVINE *MUELLERIUS CAPILLARIS* (NEMATODA, PROTOSTRONGYLIDAE) LARVAE OF FIVE SPECIES OF MOLLUSCS (HYGROMIINAE, HELICODONTINAE AND HELICINAE)*

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SUMMARY. In this study we have tested for the first time the susceptibility of *Ponentina ponentina*, *Euomphalia (M.) brigantina*, *Oestophora (O.) barbula*, as potencial intermediate hosts of *Muellerius capillaris*. At the same time, the development of the above mentioned parasite in *Cepaea nemoralis* and *Helix (C.) aspersa* was followed.

The total number of molluscs used in the infections was 268. The dose of *M. capillaris* L-I used ranged between 65 and 838 larvae per mollusc. Once the snails had been infected, 1 or 2 examples from each species were killed every day between day 6 and 46 post-infection, to study the larval development of the parasite.

In order to define the suitability of the molluscs as intermediate hosts for this parasite, the number of L-I that penetrated the foot of each snail and developed to L-II and L-III has been taken into account, as well as the first day on which the different stages were observed.

The analyses of variance (one way) showed statistically significant differences among the species of molluscs tested, concerning the percentages of penetration, total amount of larvae and L-III. The correlation coefficient showed that there was a relationship between the last two percentages.

According to our results the species: *C. nemoralis*, *P. ponentina*, *Euomphalia (M.) brigantina* and *Helix (C.) aspersa* can be considered as suitable intermediate hosts for *M. capillaris*, whilst *Oestophora (O.) barbula* cannot be considered so.

Key-words: Protostrongylidae. *Muellerius capillaris*. Experimental infection. Molluscs intermediate hosts. Stylommatophora. *Cepaea*. *Euomphalia*. *Helix*. *Oestophora*. *Ponentina*.

Infestation expérimentale par des larves de *Muellerius capillaris* (Nematoda, Protostrongylidae) de cinq espèces de mollusques (Hygromiinae, Helicodontinae et Helicinae).

RÉSUMÉ. Dans ce travail, on recueille les données sur l'infestation expérimentale avec larves I de *Muellerius capillaris* des espèces de mollusques suivantes : *Ponentina ponentina*, *Euomphalia (Mengoana) brigantina*, *Oestophora (Oestophora) barbula*, *Helix (Cryptomphalus) aspersa* et *Cepaea nemoralis*.

Le nombre des mollusques employé pour l'infestation a été 268. Une fois que les mollusques

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sont infestés, on a sacrifié 1 ou 2 exemplaires par jour (de chacune des espèces), dès le 6e jour jusqu'au 46e jour post-infestation, pour suivre le développement larvaire ou parasite.

On a calculé le nombre de larves I qui a pénétré dans chaque mollusque durant son infestation et, d'après ce nombre, les pourcentages de larves totales (I, II, III et de leurs combinations) et de larves III. On a également tenu compte des jours où l'on a observé les différents stades larvaires.

Les analyses de variance à un critère de classification ont montré des différences statistiquement significatives entre les espèces de mollusques testés pour les pourcentages de pénétration, total de larves et de L-III. Avec le coefficient de corrélation, on a observé que les deux derniers pourcentages étaient en relation.

Les espèces de mollusques, *C. nemoralis*, *P. ponentina*, *Euomphalia (M.) brigantina* et *Helix (C.) aspersa* se sont comportés comme des hôtes intermédiaires adéquats pour le développement de *M. capillaris*.

Mots-clés : Protostrongylidae. *Muellerius capillaris*. Infestation expérimentale. Mollusques hôtes intermédiaires. Stylommatophora. *Cepaea*. *Euomphalia*. *Helix*. *Oestophora*. *Ponentina*.

Introduction

Muellerius capillaris (Mueller, 1889) Cameron, 1927, the pulmonary nematode which produces bronchopneumonia in sheep, is the Protostrongylidae species that appears most frequently not only in the province of Leon (Spain) (Morrondo *et al.*, 1978 and Reguera, 1983) but also in other countries (Pavlov, 1937; Gerichter, 1951; Ryšavý, 1969; Cabaret, 1981).

As can be seen from the information compiled by Manga (1983) and Manga *et al.* (1986), many species of molluscs have been named as experimental and/or natural intermediate hosts (I. H.) for this parasite.

In order to gain the widest possible knowledge of which species can act as intermediate hosts of *M. capillaris* in our region, we have for several years studied both experimental and natural infection of the Helicidae species, which according to Manga (1983) live in the province of León. This paper farms only one part of these investigations.

The experimental susceptibility of *Ponentina ponentina* (Morelet, 1845), *Euomphalia (Mengoana) brigantina* (Da Silva Mengo, 1867) Ortiz de Zarate, 1949, *Oestophora (Oestophora) barbula* (Rossmässler, 1838), *Cepaea nemoralis* (Linnaeus, 1758) and *Helix (Cryptomphalus) aspersa* Müller, 1774, to *M. capillaris* larvae was studied. These species of snails belonging to three subfamilies of Helicidae: Hygromiinae (the first two), Helicodontinae (the third one) and Helicinae (the two latter).

The first three of the above mentioned species of molluscs were infected with this parasite for the first time. However, *C. nemoralis* had been tested with *M. capillaris* on several occasions by various authors (Zdzitowiecki, 1976; Sauerländer, 1979; Lettner, 1982), although only very specific aspects of its behaviour had been studied. In a like manner, *Helix (C.) aspersa* has been tested by Cabaret (1981)

with a mixture of *M. capillaris* and *N. linearis*. In nature, both species were found by Cabaret (1984) to harbour larvae of *M. capillaris*. Likewise, in studies carried out by us (unpublished) on natural infection of snails by Protostrongylidae, larvae of the above mentioned parasite were observed in both the latter mentioned species.

Materials and methods

The *M. capillaris* larvae-I (L-I) used to infect the molluscs were obtained (Baermann-Wetzel method) from the faeces of a sheep naturally and purely infected by this nematode and which was kept under control in the Parasitology Laboratory animal enclosure. The determination of L-I were done according to Gerichter (1951), Rose (1957) and Ryšavý (1969).

The molluscs used were collected in one of the sampling areas mentioned for each species by Manga (1983). The specimens of *P. ponentina (Fig. 1)* and *Oestophora (O.) barbula (Fig. 2)* were collected from limestone in the Sil basin (in the west of the province) in the environs of the Peñarrubia Reservoir (U. T. M. coordinate: 29TPH8004) at 380 m above sea level. *Euomphalia (M.) brigantina (Fig. 3)* was collected in Acebedo (30TUN2767) at 1,181 m above sea level. The *C. nemoralis* specimens were gathered in Cremenes (30TUN2552) at 997 m above sea level, and those of *Helix (C.) aspersa* were collected in Sabero (30TUN2445) at 1,023 m above sea level. The last three sampling locations are situated in the Esla basin. Only photographs of the less known species of molluscs are included.

Places not grazed by small ruminants were chosen to collect the snails. Moreover, in order to confirm the absence of the natural infection by Protostrongylidae, 10 % of the molluscs of each species were checked.

The number and the age of the molluscs tested in the experiments, together with the dose of L-I used in their infection are summarized in *Table I*.

Although the information does not appear in this *Table I*, one lot of *P. ponentina* was first infected with 200 larvae/mollusc but, due to the early death of the snails (none survived the third day post-infection), a much lower dose (65 larvae/mollusc) was used.

Helix (C.) aspersa and *C. nemoralis* are very commun species and found widely in our province (Manga, 1983), and because of this, in the experiments we used approximately twice as many specimens from each of these as we used from the other species of molluscs tested.

The infection was carried out according to the Kassai (1957) method and the molluscs remained in contact with the infecting liquid for three and half hours.

The calculation of the number of larvae which penetrated each snail's foot was based on the defference between the number of them placed on the Petri dish at the start of infection and that retrieved on completion.

After being infected the molluscs of each species were kept in wooden boxes, together with the control specimens. The post-infection handling of the snails

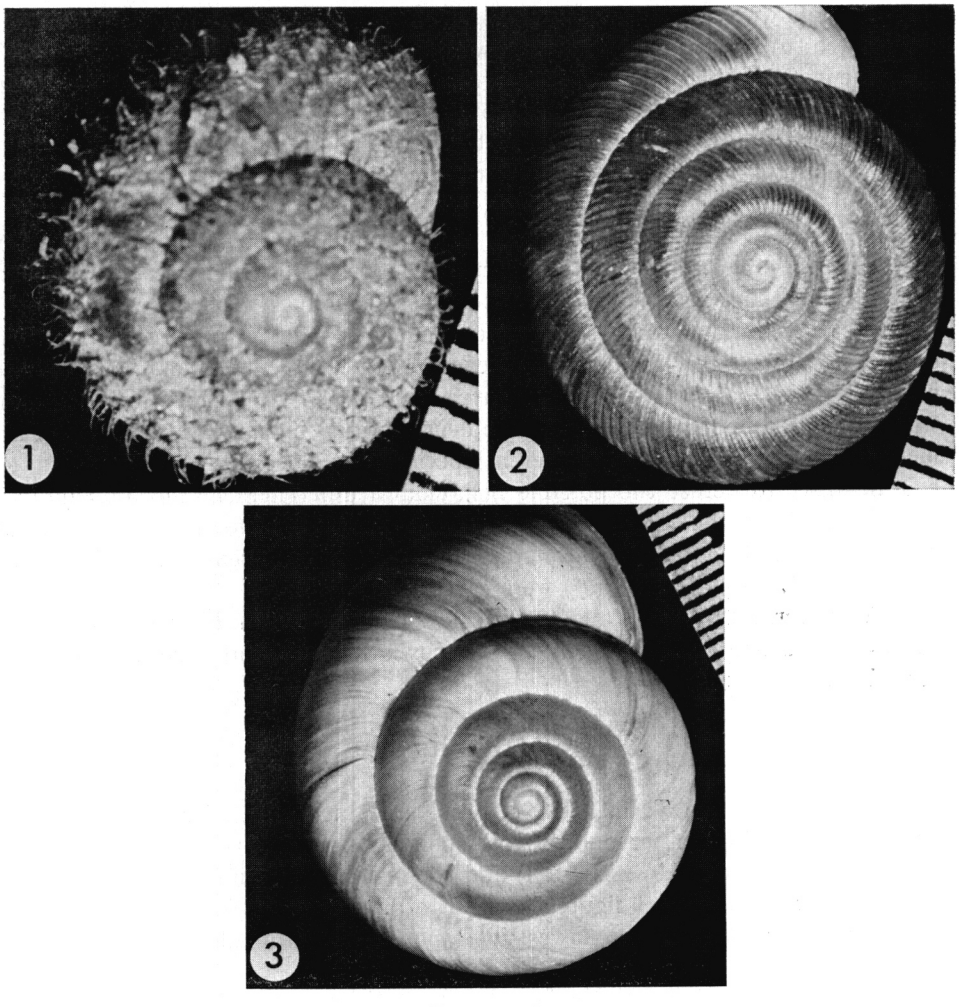

PLANCHE I

FIG. 1. — *Ponentina ponentina* (Morelet, 1845). Scale: 1/2 mm.
FIG. 2. — *Oestophora (Oestophora)barbula* (Rossmässler, 1838). Scale: 1/2 mm.
FIG. 3. — *Euomphalia (Mengoana) brigantina* (Da Silva Mengo, 1867). Scale: 1/2 mm.

was carried out according to Morrondo *et al.* (1980). The average temperature (Avg. t.) at which the molluscs were infected and maintained in the laboratory is shown in *Table II*.

In order to follow the development of the larvae, 1 or 2 molluscs of each species were killed every day from the 6th day post-infection (p. i.) until the end of the experiments.

The methods used for extraction and later identification of the larvae were the same as those used by Morrondo *et al.* (1980) and Manga and Morrondo (1988).

The following parameters were considered in the case of each mollusc and each batch: *a*) percentage of larvae I which penetrated the foot; *b*) total number of larvae found in their different stages (I, II, III); *c*) number of L-III; *d*) percentage of the total larvae and *e*) percentage of the L-III. The last two parameters were calculated on the total number of L-I that had penetrated the foot. The days on which the first L-II and L-III were observed and that on which all of them reached the third larval stage were also taken into account.

The corresponding percentages of larvae found in each mollusc (instead of the absolute values) were used to calculate the statistical analyses, because the dose was not the same for the different species of molluscs tested.

One way variance analyses were carried out to detect possible interspecific differences among the molluscs with regard to the percentages of: L-I that had penetrated the foot, total number of larvae and L-III. The correlation coefficient were calculated in order to discover the degree of dependence between each of the mentioned percentages in the different species of molluscs.

In order to detect the possible behavioural differences in the *M. capillaris* infection between the adult and young specimens of *Euomphalia (M.) brigantina*, and between both lots of *C. nemoralis* infected with different doses of L-I, the appropriate Chi-square tests (χ^2) were carried out.

To perform the above mentioned statistical studies a Hewlett-Packard-97 calculator was used, and the book of the renown Snedecor and Cochran (1971) was consulted.

Results

As can be seen in *Table I*, the highest percentage values for the total larvae (in all stages) and L-III per mollusc, corresponded to one of the experiments carried out with *C. nemoralis* (dose 150 L-I) and the lowest to the infection of *Oestophora (O.) barbula*. The highest figures for the total larvae and L-III were obtained in *Helix (C.) aspersa* and the lowest in *P. ponentina*, although it should be taken into account that the doses used were different.

On considering the infection results for both lots of *C. nemoralis (Table I)* the highest percentage values of L-I, total larvae and L-III, in each mollusc, were obtained with a dose of 150 L-I. However, the total number of larvae and L-III per mollusc was higher in the molluscs infected with 270 L-I. Using χ^2 test, statistically significant differences (for $p \leqslant 0.001$ and $df = 1$) were recorded between these batches of *C. nemoralis* as far as penetration of L-I ($\chi^2 = 185.8$) and the total number of larvae per mollusc ($\chi^2 = 120.4$) are concerned.

The percentage of L-I that had penetrated the foot and the absolute values of the total number of larvae and L-III per mollusc were slightly higher in the adult specimens of *Euomphalia (M.) brigantina* than in the young ones *(Table I)*. However, the percentage of L-III was a little higher in young snails. On applying chi-square test we were able to detect statistically significant differences (for $p \leqslant 0.01$ and $df = 1$), as regards the percentages of L-I ($\chi^2 = 2.42$), between adult

TABLE I. — Larva development of *Muellerius capillaris* in the five species of molluscs tested.

Dose	Molluscs														
L-I per mollusc	Species	Age	No. tested	No. infected with L-I	% ($\bar{x}$) of L-I per mollusc	No. with larvae*	No. larvae* per mollusc			% ($\bar{x}$) of larvae* per mollusc	No. with L-III	No. L-III per mollusc			% ($\bar{x}$) of L-III per mollusc
							min.	max.	$\bar{x}$			min.	max.	$\bar{x}$	
65	*Ponentina ponentina*	A	38	38	57.3	38	1	13	3.1	8.6	17	2	13	4.7	10.8
200	*Euomphalia (Mengoana) brigantina*	A	27	27	70.5	27	2	31	11.1	7.8	19	1	31	13.1	6.5
		Y	8	8	64.1	8	1	27	10.1	7.8	7	1	27	9.8	7.7
200	*Oestophora (O.) barbula*	A	35	35	73.6	34	1	15	2.5	1.7	17	1	15	2.8	1.9
150	*Cepaea nemoralis*	A	40	40	93.2	40	1	57	15.0	11.1	29	2	57	19.0	15.2
270	*Cepaea nemoralis*	A	40	40	86.2	40	1	58	21.5	9.7	26	1	82	26.8	6.9
838	*Helix (Cryptomphalus) aspersa*	A	80	80	72.6	76	1	160	42.1	5.5	48	1	160	39.7	6.9

* Larvae I, II, III and their combinations found in the molluscs after 6th day p. i.
A = Adult; Y = Young.

and young specimens, but not as regards the percentage of the total amount of larvae ($\chi^2 = 0.043$) found in them. Nevertheless, as the number of snails used was small, studies with a larger number of molluscs must be done in order to confirm these preliminary results.

Using variance analyses (one way), it was proved that statistically significant differences exist (for $p \leqslant 0.001$ and $df = 5$) between the species of molluscs tested, when taking into consideration the percentages of L-I penetration ($F = 43.97$), total number of larvae ($F = 8.85$) and L-III ($F = 6.09$). On calculating the correlation coefficient between the previous percentages, it seems that there is neither a relationship between the first two ($r = 0.346$), nor between the first and the third ($r = 0.316$), though, there is one between the total number of larvae and L-III ($r = 0.989$, for $p \leqslant 0.001$ and $df = 5$).

The first L-II of *M. capillaris (Table II)* were observed on day 10 p. i., except in *Helix (C.) aspersa* and young specimens of *Euomphalia (M.) brigantina*. The periods of time taken for the first L-III to appear and for all the larvae to reach the 3rd stage were shorter in *Euomphalia (M.) brigantina* than in the other species of molluscs, while it was longer in *Oestophora (O.) barbula*.

The different larval stages of *M. capillaris* were observed *(Table II)* sooner in the specimens of *C. nemoralis* which had been infected and maintained at 25° C than in those maintained at 19° C. Larval development was also a little faster in the young specimens of *Euomphalia (M.) brigantina* than in the adults.

As has been seen, the number of larvae I that penetrated each mollusc was

TABLE II. — Days in which the first L-II and L-III were observed, and days in which all the larvae reached the third stage.

Dose L-I per mollusc	Avg. t. °C	Molluscs				Post-infection days		
		Species	Age	No. tested	No. infected with L-I	1st L-II	1st L-III	All L-III
65	22	*Ponentina ponentina*	A	38	38	10	28	42
200	20	*Euomphalia (Mengoana) brigantina*	A	27	27	10	15	20
			Y	8	8	8	14	20
200	22	*Oestophora (O.) barbula*	A	35	35	10	29	46
150	19	*Cepaea nemoralis*	A	40	40	10	21	36
270	25	*Cepaea nemoralis*	A	40	40	10	18	32
838	22	*Helix (Cryptomphalus) aspersa*	A	80	80	11	26	43

high in all the species tested. However, in some of the species the number of larvae to reach the later stages of development was very low. This fact has already been observed by Morrondo *et al.* (1980). Because of this, for stating the suitability of the studied species as intermediate hosts of *M. capillaris*, we took into account firstly the absolute values and percentages of the total number of larvae and the L-III per mollusc, and secondly the days on which the larvae were observed to reach the different stages of development.

On the bases of all this information, it can be said that *C. nemoralis*, *Helix (C.) aspersa*, *Euomphalia (M.) brigantina* and *P. ponentina* are suitable experimentally intermediate hosts for *M. capillaris*, whilst this is not so, in the case of *Oestophora (O.) barbula*.

Discussion

We are going to compare our results *(Tables I, II)* with those observed by other authors *(Tables III, IV)* for different species of molluscs, to the ones used in this study.

The percentages of: L-I that had penetrated the foot, total number of larvae and L-III obtained in this study, were similar to those found by Morrondo *et al.* (1980) in three species of *Cernuella*. However, these last two percentages were lower than those obtained by us (Morrondo and Manga, 1982) when we infected other species of Helicidae with *M. capillaris (Table III)*.

The total number of larvae per mollusc found in this study was similar to that observed by Egorov (1960) and Trushin (1974), whilst this figure and that of L-III were higher than those recorded by Trushin (1971) and Sultanov *et al.* (1975). The number of L-III per molluscs was similar to that indicated by Reguera (1983) and Reguera *et al.* (1983).

In both experiments with *C. nemoralis (Table III)*, the percentage of L-I that had penetrated each mollusc was much higher than that recorded by Lettner (1982), who used doses of L-I similar to ours. In the experiment carried out with the lowest dose, the penetration percentage of L-I which we obtained was the highest, which coincides with that obtained by Lettner (1982) and Sauerländer (1979), although, the latter used a much higher dose. However, in our experiment, the values for number and percentage of L-III per mollusc were lower than those cited by Sauerländer (1979) for both parameters and by Zdzitowiecki (1976) for the former. If the time needed by the *M. capillaris* larvae to reach the third stage in *C. nemoralis* is considered *(Table II)*, it seems that higher temperatures induce faster development, and this agrees with the observations of Rose (1957) and Ryšavý (1969).

As far as *Euomphalia (M.) brigantina* is concerned, the percentage of *M. capillaris* L-I that had penetrated the foot of each mollusc was higher in the adult snails than in the young ones, which is the opposite of what Lettner (1982) and Reguera (1983) observed when they infected other Helicidae species with this

TABLE III. — Data concerning the larval development of *Muellerius capillaris* in adult specimens of: *Cepaea nemoralis* (**) and other species of molluscs (*).

Authors	Dose L-I/ mollusc	% Penetration of L-I	Total larvae/ mollusc	% Total larvae	L-III/ mollusc	% L-III
Egorov (1960) (*)	2,000	—	1-131	—	—	—
Trushin (1971) (*)	—	—	43-55	—	23-24	—
Trushin (1974) (*)	250	—	1-152	—	—	—
Sultanov *et al.* (1975) (*)	—	—	—	—	1-27	—
Zdzitowiecki (1976) (**)	4,000?	—	21-430	—	—	—
Sauerländer (1979) (**)	1,000	72.5	—	—	4-770	0.8-43.0
Morrondo *et al.* (1980) (*)	169- 280	60.8-81.1	—	1.9-20.0	—	1.1-16.2
Lettner (1982) (**)	100- 250	17.3- 8.6	—	—	—	—
Morrondo, Manga (1982) (*)	169- 300	38.0-81.1	—	1.9-52.4	—	2.9-49.8
Reguera (1983) (*) Reguera *et al.* (1983) (*)	50-1,000	—	—	—	3-160	—
Cabaret (1987) (*)	80- 600		$\bar{x}$ 2.0-9.6			

nematode. The average number of larvae (I, II, III and their combinations) per snail obtained by us, was also higher in the adult molluscs than in the young ones which coincides with that obtained by Cabaret (1987) when he tested medium-size species of molluscs *(Theba pisana)* with *M. capillaris.*

The time needed *(Table IV)* to detect the first L-II (10-11 days p. i.) was similar to that indicated by Rehnova (1955), Soltys (1964), Morrondo *et al.* (1980), Morrondo and Manga (1982) and Reguera (1983). However, this period was shorter than that observed by Gerichter (1951) in his study and longer than that quoted by Pavlov (1937), Williams (1942) and Rose (1957).

The first L-III were seen between day 15 and day 29 p. i., which coincides in general, with the periods recorded by Rehnova (1955), Egorov (1960), Soltys (1964), Trushin (1974), Sultanov *et al.* (1975), Sauerländer (1979), Morrondo *et al.* (1980), Morrondo and Manga (1982) and Reguera (1983). The periods of time observed

TABLE IV. — Days when the different larval stages of *Muellerius capillaris* were detected in adult specimens of: *Cepaea nemoralis* (**) and other species of molluscs (*).

Authors	Avg. t. °C	Post-infection days		
		1st L-II	1st L-III	All L-III
Pavlov (1937) (*)	Laboratory	7-8	11-12	—
Williams (1942) (*)	Laboratory	8	14	—
Davtian (1945) (*)	17-25	—	14-80	—
Gerichter (1948) (*)	20-30	—	34-35	—
Mapes (1949) (*)	Laboratory	—	27	—
Gerichter (1951) (*)	20-30	28	35	—
Rehnova (1955) (*)	Laboratory	9-15	18-29	—
Rose (1957) (*)	20	8	13	—
Egorov (1960) (*)	16-22	—	15-32	—
Soltys (1964) (*)	22-25	6-12	19-30	—
Ryšavý (1969) (*)	29-30	—	12-15	—
Trushin (1971) (*)	18-20	—	27-47	—
Trushin (1974) (*)	20-24	—	12-30	—
Sultanov *et al.* (1975) (*)	22-30	—	12-26	—
Sauerländer (1979) (**)	20	—	15	—
Morrondo *et al.* (1980) (*)	18-22	8-14	14-29	23-34
Urban (1980) (*)	20-26	—	14-80	—
Morrondo, Manga (1982) (*)	19-22	6-14	10-29	26-34
Reguera (1983) (*)	22-23	6-13	14-21	25-45

by us were longer than those given by Pavlov (1937), Williams (1942), Rose (1957) and shorter than those of Gerichter (1948, 1951), Trushin (1971) and Urban (1980).

The number of days p. i. taken by *M. capillaris* larvae, in each species of molluscs, to reach the third stage was similar to that indicated by Morrondo *et al.* (1980), Morrondo and Manga (1982) and Reguera (1983).

According to Urban (1980), the five species of molluscs tested by us could

be considered as potential I. H. of *M. capillaris*, because the third larval stage was reached in all of them between day 19 and 45 p. i. However, in our opinion, *Oestophora (O.) barbula* should not be considered as such an intermediate host because the absolute values and percentages of both the total number of larvae and L-III obtained in each mollusc were very low.

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