Parasitol Res (2009) 105:1–15
DOI 10.1007/s00436-009-1444-7

REVIEW

Biology of *Alaria* spp. and human exposition risk to *Alaria mesocercariae*—a review

Katharina Möhl · Knut Große · Ahmad Hamedy · Tanja Wüste · Petra Kabelitz · Ernst Lücker

Received: 8 April 2009 / Accepted: 16 April 2009 / Published online: 9 May 2009

Abstract Recent incidental background findings of *Alaria alata* mesocercariae ["*Distomum muscularis sui*s," Duncker, 1896] in meat of wild boars during official *Trichinella* inspection initiated a re-assessment of the potential human health risk as posed by this parasite. The present review of the literature on *Alaria* biology shows that the human exposition risk should no longer be accepted to be negligible, as it demonstrates a general lack of knowledge in relevant areas of *Alaria* biology confounding any risk analysis. Sound risk assessment needs future studies which should concentrate on the most pressing questions of (1) the optimization and/or development of methods for reliable *Alaria* mesocercariae detection, (2) the distribution of the mesocercariae within their paratenic hosts, i.e., identification of potential predilection sites, particularly in wild boars, and (3) their prevalence in sylvatic populations of animals with respect to their introduction into the human food chain. Further, the degree and possibly also the species specificity of *Alaria* mesocercariae tenacity within the paratenic hosts and respective meat as pertaining to food technological treatments need to be elucidated. While these questions remain unanswered, it is an incontrovertible fact that *Alaria* mesocercariae have a potentially high human pathogenicity by both occupational and alimentary exposition.

K. Möhl (✉) · A. Hamedy · E. Lücker (✉)
Institute of Food Hygiene, Faculty of Veterinary Medicine,
University of Leipzig,
Leipzig, Germany
e-mail: moehl@vetmed.uni-leipzig.de
e-mail: luecker@vetmed.uni-leipzig.de

K. Große · T. Wüste
Stadt Brandenburg an der Havel Gesundheits-,
Veterinär- und Lebensmittelüberwachungsamt,
Klosterstraße 14, 14770 Brandenburg an,
der Havel, Germany

P. Kabelitz
Landkreis Uckermark, Gesundheits- und Veterinäramt,
Karl-Marx-Straße 1,
17291 Prenzlau, Germany

Introduction

Distomum musculorum suis (DMS), Duncker, 1896 (syn. *Agamodistomum suis*, Stiles, 1898) is the mesocercarial stage of the trematode *Alaria alata*, an intestinal parasite of some carnivores. The adult and metacercarial stages of these trematodes have little relevance as pathogens, whereas its mesocercarial stage is known to cause lesions in its paratenic hosts, in particular, in wild boars (Hiepe 1985, Odening 1963). Ljubaschenko and Petrov (1962) report about serious damages in fox, dogs, and arctic fox caused by DMS. The authors distinguish between two different disease patterns: the metacercarial alariosis manifests itself in the lungs, pleura, and the lymphatic vessels of the bronchia, while the adult parasites can cause inflammation of the bowel and a general intoxication (Ljubaschenko and Petrov 1962). Danijarow (1968) mentions high economic losses in fur farms caused by *A. alata*. Several human infections have been reported since Odening (1961a) recovered *A. alata* mesocercariae from an experimentally infected primate. Nevertheless, the risk for humans was generally ignored or at least postulated to be negligible until after about four decades this issue reemerged in Europe: Jakšić et al. (2002) and Große and Wüste (2004, 2006) published results on repeated incidental findings of DMS in meat of wild boars during routine *Trichinella* inspection in certain areas of Croatia and Germany, respectively. In view of their findings, deficiencies in methodology, lack of data on prevalence, and the human DMS cases which were reported, they were the first to point out that the human DMS exposition risk is not negligible and would merit increased scientific attention. The Federal Office for the Environment (FOEN, Switzerland) categorized *A. alata* as a stage 2 risk (Z) for parasites with zoonotic potential (Anonymous 2003) as pertaining to occupational health risks. The Federal Institute of Risk Assessment (BfR 2007) finally concluded in its risk assessment that meat which contains *A. alata* mesocercariae should be regarded as unfit for human consumption. A final statement concerning the health risks for consumers could not be given due to the lack of information about both the prevalence of DMS and the suitability of *Trichinella* inspection methods to detect this parasite in wild boar meat (BfR 2007).

In the present paper, a review of the relevant knowledge on *Alaria* biology is given in order to further our understanding of potential consumer health risks which might be associated with this parasite.

History and taxonomy

The original description of the adult stage of *A. alata* in its definitive host was given by Goeze in 1782. Gestaldi (1854) first described the larval stage of the trematode ("*Distoma tetracystis*") in frogs, and upon trichinellosis control in Saxony, sexually immature trematodes were found in swine muscles, which were studied and described by Duncker in a number of communications (Duncker 1881a, b, 1884, 1896, 1897). It took nearly 50 years to show that there is a link between the appearance of the mesocercarial stage of the parasite in frogs and in pigs (Bugge 1942a). Stefansky and Tarczynski (1953) finally demonstrated the relation between *Alaria alata* and *Distomum musculorum suis*, Duncker, 1896.

A. alata (*Diplosomatidea, Strigeata*) is a parasitic trematode of carnivores in Europe and the former Soviet republics (Schnieder 2006). Further *Alaria* species can be found in North and South America: *A. mustelae* (Bosma 1931), *A. intermedia* (Olivier and Odlaug 1938), *A. marcianae* (La Rue 1917), *Alaria arisaemoides* (Augustine and Uribe 1927), *Alaria canis* (La Rue and Falis 1934) (Paerson 1956), *Alaria taxideae* (Swanson and Erickson 1946). According to Sudarikov (1960) *A. mustelae* was also found in Europe; however, only in imported cases from America.

Morphology

The adult and mesocercarial stages of *Alaria* spp. are depicted in Fig. 1. The adult stage of *A. alata* measures approximately 3–6 × 1–2 mm (Schnieder 2006, Hiepe 1985, Wojcik et al., 2002). The body is clearly divided into two sections. The anterior end has a wing-like shape (*alata*, "winged") and contains four clavate cells, with granular cytoplasm and spherical nuclei, within the oral sucker. They are glandular in appearance, but ducts were not observed (Pearson 1956). The posterior end is short and cylindric with a typical short intestine. The tribocystic organ shows a tongue-like shape (Hiepe 1985). The muscular ventral sucker, or acetabulum, measures approximately 0.04–0.1 × 0.04–0.09 mm and is therefore slightly smaller than the oral sucker (0.06–0.07 × 0.06–0.08 mm) (Andreas 2006). In order to receive nutrients, the ventral sucker is used for digestion and absorption of mucus and tissue from the wall of the host intestine (Roberts and Janovy, 2000).The lobed testicles of the male individuals are located one after the other in the rear body section. Anterior to them, the germarium is situated in the transient area of both body sections. The gonads of the female parasites lie in pairs in the anterior body region. *Alaria* species from North and South America differ morphologically in some aspects (Marshall 1972; Roberts and Janovy, 2000).

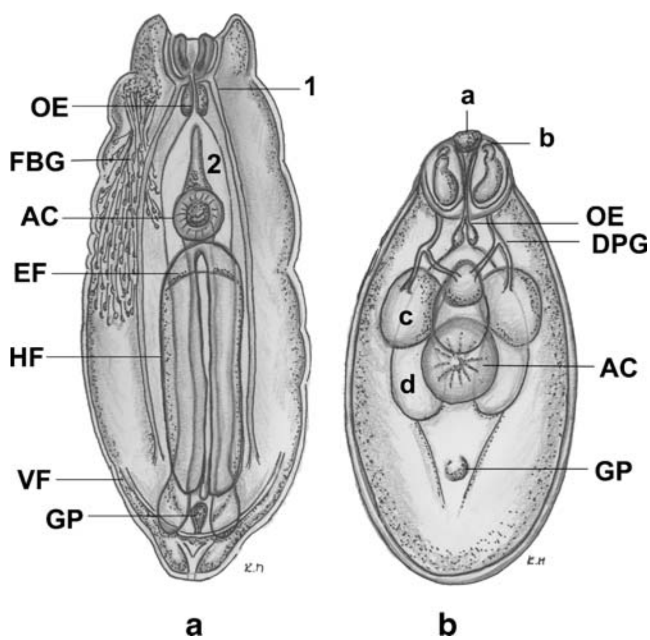

Fig. 1 Fully developed adult (**a**) and mesocercarial (**b**) stage of *Alaria* spp. *1* remnant of penetration gland duct, *2* caecum (elonged), *OE* oesophagus, *FBG* forebody glands and their ducts, *AC* acetabulum, *EF* edge of fold over anterior and of holdfast organ, *HF* holdfast organ, *VF* ventral lip of spathiform forebody, *GP* genital primordium, *a* oral opening and oral sucker, *b* gland cells, *c* penetration glands, *d* caecum, *DPG* duct of penetration gland

The eggs measure 110–140×70–80 µm (Hiepe 1985, Lucius et al., 1988). Development from egg to full-grown individual takes 92–114 days (Lucius et al., 1988).

The mesocercariae of *A. alata* are morphologically similar to the mesocercariae of american *Alaria* species (Odening 1961a). In the front body, anterior to the ventral sucker, lie two pairs of characteristic finely granular penetration glands which measure 300–500 µm and show a typical leaf-shaped appearance (Wirkerhauser 1980). According to Odening (1961a) the excretory bladder is V-shaped with dilatations at the posterior ends. Its branches lead in twisted attachments. These attachments are connected with the primary excretion system. The junction starts at the area approximately between the ventral sucker and the intestine, and the vessels bend laterally and to the rear, meandering until they reach the main excretory vessels. The reserve bladder system is developed within the larvae only in the form of a small anteromedial arranged tap (Odening 1961a). A ciliar trimming of the attachments, as shown in the respective larvae of *A. intermedia*, is missing (Olivier and Odlaug, 1938). In the rhesus monkey (scarpula region) the mesocercarial stage of *A. alata* is fully developed and enclosed by host tissue within 38 days (Odening 1963). The mesocercarial stage is characterized intra vitam by a unique motion sequence. In the stereo-microscopical examination for *Trichinella*, one "cannot but recognize it" (Große and Wüste 2006). This is illustrated by a sequence of single shots taken from a film of a DMS in typical motion in Fig. 2.

The metacercarial stage of *Alaria* spp. is a roundish, thin-walled, almost transparent vesicle of 0.4–0.7 mm length and 0.2 mm breadth with fine parallel lines on it (Hiepe 1985). In these cysts, one can recognize the whitish larva with a magnifying glass (Odening 1961b, 1963). The reserve bladder system is, as within most *Strigeata* larvae, strongly developed and covers large parts of the primary excretion system (Komiya 1938, Odening 1961a, Savinov 1954).

Life cycle

The complete life cycle of *Alaria* species, as schematically depicted in Fig. 3, had been worked out in the middle of the twentieth century (Petrov et al., 1950a, 1950b, Potekhina 1950, Savinov 1953a, b, Savinov 1954). The role of DMS in connection with the cycle of *A. alata* was recognized only at this time (Dollfus and Chabaud 1953, Stefański and Tarczyński 1953). While the members of the genus *Strigea* have an obligatory four-host life cycle, *Alaria* spp. develop in a three-host life cycle with an interjectional mesocercarial stage between the cercarial and the metacercarial stage. This life cycle can be extended by paratenic hosts. The term "hôtes d´attente" was first characterized by Joyeux and Baer (1934). The original description of this kind of life-cycle as well as the term "mesocercaria" was given by Bosma (1934). The mesocercarial stage is a kind of "resting stage" which is characterized morphologically by persistence of penetrating glands and a cyst which is solely formed by the host's connecting tissue. The mesocercaria can survive several host transitions unharmed. After breaking through the intestine wall of the new host, it behaves as in the preceding host (Bosma 1934, Hiepe 1985, Lutz 1933a, b, Lutz 1921, Odening 1963, Pearson 1958, Pearson 1956, Schnieder 2006). Adult flukes, residing in the intestines of the definitive hosts, pass unembryonated eggs through the feces of the host. After two weeks, these eggs hatch in water, releasing the miracidium. They

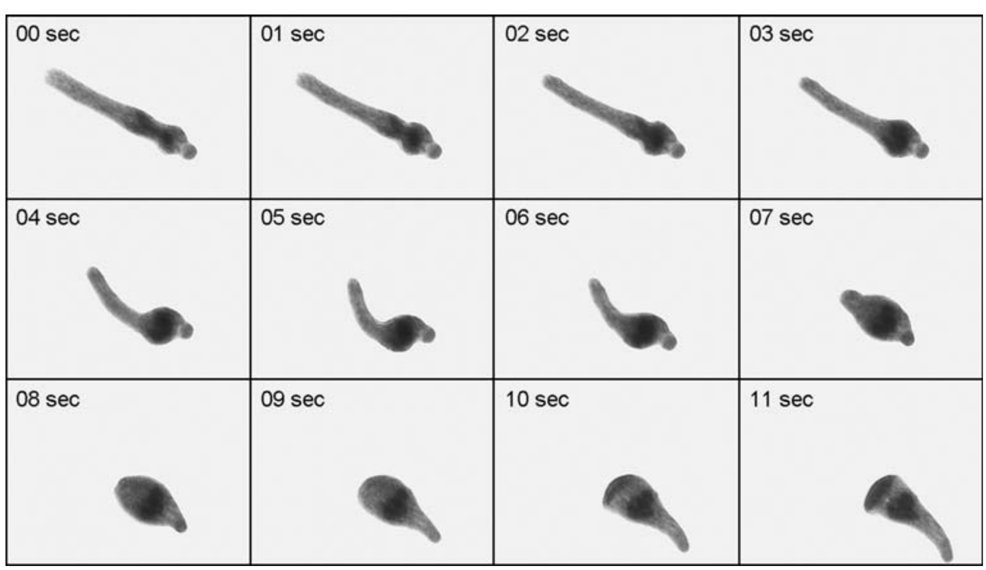

Fig. 2 *Alaria alata* from a film of *A. alata* mesocercaria in motion after HCL/Pepsin digestion

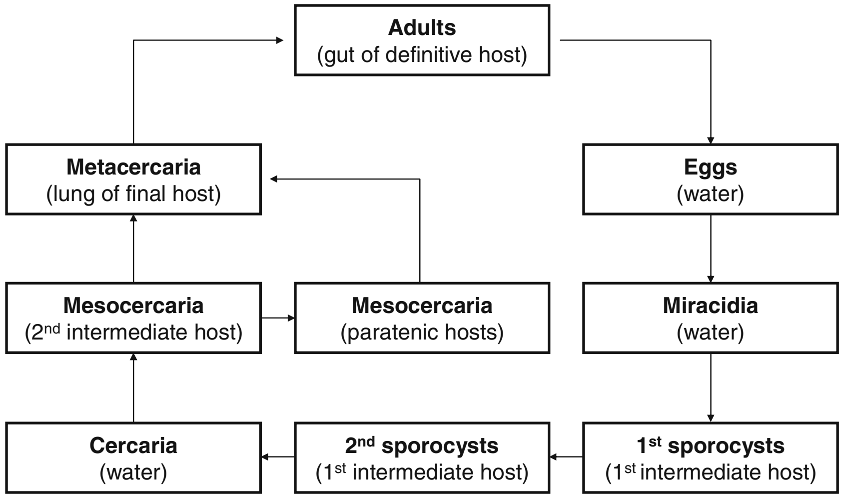

Fig. 3 Life cycle of *Alaria* species: developmental stages

actively penetrate and develop further in a snail host (*Planorbis*-, *Heliosoma*-, *Lymnea*- and *Anisus* species) (Bosma 1934, Cort and Brooks 1928, Nikitina 1986, Odlaug 1940, Pearson 1956, Potekhina 1951, Ruszkowski 1922, Wójcik 2001). In this first intermediate host the miracidiae reproduction starts and after nearly a year of maturation, daughter sporocysts release cercariae provided with a fork tail (furcocercariae). They show a high motility in the water until an appropriate second intermediate host is exposed to them. This host might be a tadpole, an adult frog or other amphibian in which the furcocercariae develop into mesocercariae. The spectrum of snails, frogs, and amphibians and their preference vary depending upon *Alaria* species as shown in Table 1.

In addition to the amphibian intermediate hosts, specified in Table 1, there are also paratenic hosts in the developmental cycle of *Alaria* spp., as already mentioned above. In this potential intermediate hosts, the larval parasites can survive when ingested, but they do not undergo any further development. They are also called “transport” or “auxillary intermediate” hosts (Wallace 1939, Baer 1951). These hosts may accumulate the mesocercariae with each transition, and they may also serve to pass over the infection from the aquatic to the terrestrial environment (Dönges 1969). While such hosts are not essential for the development of the parasite, they may be necessary for the completion of the life cycle for ecological reasons. For example, the intermediate host in which the larval stage develops obligatorily may not be included in the diet of the definitive host, whereas a paratenic host may be included. On the other hand, a paratenic host may be excluded from the diet of the definitive host in which case this host would be a “cul-de-sac” (Pearson 1956). The infection of these paratenic hosts takes place via the uptake of obligatory second intermediate hosts. Then the mesocercaria migrates through the intestine wall into the musculature of the anterior body section and/or settles at or in the different organs. The further development of the mesocercariae takes place in the body of the definitive hosts. According to Odening (1963), only members of the *canidae* can act as definitive hosts for *A. alata*. More recent studies point to the fact, however, that other carnivores (*felidae, mustelidae*) can also serve as definitive hosts for the parasite (cf. following chapter). After the oral uptake of an infected auxiliary or obligatory second intermediate host by a definitive host, the metacercariae perform a somatic migration. After reaching the lungs, the mesocercariae change into the metacercarial stage, are swallowed, and develop into adult worms in the host’s small intestines (Cuckler 1940, 1949, Odening 1963, Pearson, 1956, Schnieder 2006). Migration and reorganization of the mesocercariae through the metacercarial stage (syn.: *Diplostomulum*) to the adult worm are continuous processes with no intermediary stationary phase.

With the excretion of eggs into the intestine of the definitive host by adult trematodes and the entry of the eggs in the environment, the infection cycle starts again.

Hosts

The mesocercarial stage is particularly nonspecific toward its hosts. All *Alaria* species have a broad spectrum of paratenic hosts and almost all representatives of vertebrate animal classes may act as a carrier for the mesocercariae. Within the paratenic host, the parasite does not lose its infectivity toward the definitive host (Odening 1960,

Table 1 Second intermediate hosts of Mesocercariae of *Alaria* species according to literature

Alaria species	Host species (Infection, stage)	References
A. mustelae (Bosma, 1934)	*Rana palustris* (adult, N) [2], *Rana catesbiana* (adult, N) [2], *Rana clamitans* (adult, N) [2], *Rana clamitans* (tadpole, E) [2], *Rana pipiens* (adult, N) [2], *Rana pipens* (tadpole, E) [2], *Hyla regilla* (adult ,N, E) [10]	Andreas 2006 [1] Bosma 1934 [2] Bugge 1942b [3] Cort 1918 [4]
A. intermedia (Olivier and Odlaug, 1938)	*Rana pipiens* (adult, N) [12], *Rana pipens* (tadpole, E) [11]	Cort and Brooks 1928 [5] Cuckler 1941 [6]
A. marcianae (La Rue, 1917)	*Rana sp*. (tadpole, E) [5], *Rana pipiens* (adult, N) [6], *Rana pipens* (tadpole, N) [4], *Rana sphenocephala* (adult, N) [6], *Rana clamitans* (tadpole, N) [4]	Gastaldi 1854 [7] Goldberg et al., 2001 [8]
*A. alata (*Goeze, 1782)	*Rana esculenta* (N) [1,3,7], *Rana fusca* (N) [14], *Rana temporaria* (adult, N) [1, 3], *Rana temporaria* (tadpole, E) [14], *Pelobates fusca* (N) [14,16], *Rana arvalis* (adult, N) [1], *Bufo bufo* (adult, N), *Bufo calamita* (adult, N), *Bufo viridis* (adult, N) [15]	Goldberg et al., 1998 [9] Johnson et al., 1999 [10] Odlaug 1940 [11] Olivier and Odlaug 1938 [12]
A. arisaemoides (Augustine and Uribe, 1927)	*Bufo americanus* (tadpole, E) [13], *Rana sylvatica* (tadpole/adult, E) [13], *Rana pipiens* (tadpole/adult, E) [13]	Pearson 1956 [13] Potekhina 1951 [14]
A. canis (La Rue and Falis, 1934)	*Bufo americanus* (tadpole, E) [13], *Rana sylvatica* (tadpole, E) [13], *Rana pipiens* (tadpole/ adult, E) 13], *Pseudacis nigrita* (tadpole, E) 13]	Shimalov et al., 2000 [15] Timofeev 1900 [16]
Alaria sp.	*Rana pipiens* (adult, N) [8], *Rana catesbeiana* (adult, N) [9], *Rana chiricahuensis* (adult, N) [39], *Rana yavapaiensis* (adult, N) [9]	

N natural infection, *E* experimental infection

1961a, 1963). The wide range of potential paratenic hosts of *Alaria* species is demonstrated in Table 2.

There was a long-standing controversy whether fish could act as paratenic hosts for *Alaria* spp. Leiper (1920) maintained that encysted larvae as recovered from naturally infected fish (African butter catfish, lat. *Schilbe mystus*) developed into *A. alata* when fed to wolves. Pearson (1956) fed mesocercariae of *A. canis* to six goldfish to see whether this fish could act as a paratenic host. Three days p.i., all mesocercariae were found on the viscera in the body cavity in various stages of encapsulation. None was found within the viscera or musculature. Pearson concluded that the mesocercariae made their way into the body cavity of goldfish, where some survived for 2 days, but where all were dead and encapsulated by 3 days. So the observations of Pearson (1956) suggest that, at least, goldfish are unsuitable as paratenic hosts for the mesocercariae of *A. canis*.

Riis et al. (2006) found living encapsulated mesocerariae in the periocular tissues, cornea, sclera, and occasionally the iris of an oyster toadfish (*Opsanus tau*). Unfortunately, they could not identify the mesocercariae properly. It is, however, well-known, that larvae of the *Diplostomatidae* occasionally infest the lens and the vitreous body of fish eye (Ashton et al., 1969, Hoffmann 1976, Leibovitz et al., 1980). Whether this infestation of the eye can be due to an oral intake of the parasites is contentious.

Moreover, the spectrum of definitive hosts is very broad and includes, depending upon the *Alaria* species, a wide range of carnivores in the respective geographic range. In the literature, numerous descriptions of *A. alata* infections in different canides, felides, and mustelides can be found as summarized in Table 3.

Foster et al. (2008) demonstrated *A. marcianae* mesocercariae in the lungs of three freshly dead Florida panther neonates. The 11-, 12-, and 17-day-old neonates were presumably fed only on milk from the dam since birth. Milk was the only item found in the gastrointestinal tract of these whelps. Mesocercariae and diplostomula of *A. marcianae* were collected from the lungs of the three neonates, indicating a transmammary route of infection.

Table 2 Paratenic hosts of *Alaria* spp. mesocercariae following natural (N) and experimental infection (E) according to literature

Alaria species	Host species (Infection)	References
A. mustelae (Bosma, 1934)	Snakes (N), *Mus musculus* (House mouse, E),*Rattus rattus* (Rat, E), *Peromyscus leucopus* (White-footed Mouse, N), *Mustela vison* (Am. Mink, N), *Procyon lotor* (Raccoon, N) [1], *Martes pennanti* (Fisher, N) [10]	[1] Bosma 1931, [2] Bugge 1942a, [3] Bugge 1942b, [4] Burrows and Lillis 1965, [5] Castro et al., 2008,
A. intermedia (Olivier and Odlaug, 1938)	*Thamnophis sirtalis* (Garter snake, N) [7], *Mus musculus* (House mouse, E) [6, 15], *Rattus rattus* (Rat, E) [15], *Felis domestica* (Cat) [7]	[6] Cuckler 1940, [7] Cuckler 1941, [8] Cuckler 1949, [9] Cort 1918, [10] Dick and Leonard 1979,
A. marcianae (La Rue, 1917)	Snakes (E) [9], *Thamnophis sirtalis* (Garter snake, N) [10], *Thamnophis marcianae* (N), *Thamnophis eques* (N) [14], *Mus musculus* (House mouse, E), *Felis domestica* (Cat) [7, 8, 9], *Leopardus pardalis* (Ocelot, N) [18]	[11] Goüy de Bellocq et al., 2003, [12] Kimber and Kollias 2000, [13] La Rue 1917, [14] Morozov 1937,
A. alata (Goeze, 1782)	*Tropidonotus natrix* (Grass snake, N) [25], *Mustela putorius* (Ferret, N), *Mustela erminea* (Stoat, N), *Mustela lutreola* (Europ. Mink, N), *Mustela nivalis* (Weasel, N) [14], *Mustela lutreola* (Europ. Mink, N), *Martes martes* (Pine marten, N), *Martes zibellina* (Sable, N) [20], Pig (N), *Sus scrofa* (Wild boar, N) [2, 22], *Meles meles* (Badger, N) [3], Cattle (N), *Ursus arctos* (Brown bear, N) [21], *Talpa europaea L.* (Mole, N) [24], *Vipera berus* (Europ. adder, N) [23], *Apodemus sylvaticus* (Woodmouse, N) [11], *Felis domestica* (Cat) [5]	[15] Odlaug 1940, [16] Pearson 1956, [17] Pence and Dowler 1979, [18] Pence et al., 2003, [19] Poole et al., 1983, [20] Petrov and Dubnickij 1950a, [21] Staskiewicz 1947,
A. arisaemoides (Augustine and Uribe, 1927)	*Thamnophis sirtalis* (Garter snake, E), *Gallus gallus* (Chicken, E), *Mus musculus* (House mouse, E), *Peromyscus maniculatus* (Deer mouse, E) [16]	[22] Stefansky and
A. canis (La Rue and Falis, 1934)	*Felis domestica* (Cat, N) [4] *Thamnophis sirtalis* (Garter snake, E), *Anas boschas* (Duck, E), *Gallus gallus* (Chicken, E), *Mus musculus* (House mouse, E), *Peromyscus maniculatus* (Deer mouse, E), *Mustela putorius* (Ferret, E), *Lutra canadensis* (Otter, N) [16], Lontra canadiensis (North American river otter, N) [12]	Tarczynski 1953, [23] Shimalov et al., 2000c, [24] Shimalovet al., 2001b, [25] Timofeev 1900.
A. taxideae (Swanson and Erickson, 1946)	*Martes Americana* (Pine marten, N) [19], *Taxidea taxus* (American badger, N) [17]	

No mesocercariae, diplostomula, or mature *A. marcianae* were seen in the stomach or the small intestine. So the dam was assumed to be the definitive host. The probable paratenic host for the *A. marcianae* infection in the adult Florida panther is the raccoon (*Procyon lotor*). Several authors already reported about the possibility of a vertical transmission of *Alaria* mesocercarial stages (Pence et al., 1988, Shoop and Corkum 1983, 1984a, b, 1987, Shoop et al., 1990). Shoop and Corkum (1987) assume not-lactating and male cats to serve as definitive hosts for *Alaria* spp., whereas lactating dams would usually act as a paratenic host (Shoop and Corkum 1987). Yastrebov et al. (2005) demonstrated *A. alata* mesocercariae in the blood of stray cats and dogs. The results of these studies indicate a hematogenous spread of the mesocercarial stage of the parasite and simultaneously point to the fact that even definitive hosts can act as carriers of *Alaria* spp. mesocercarial stages.

Table 3 Prevalence (Prev. %) of carnivore hosts of *Alaria alata* as reported in literature

Host	Country or region	Prev. (%)	Number of parasites (min-max)	Reference
Canis lupus L. (European wolf)	Poland	2.2	n.g.	Popiołek et al., 2007
	Estonia	89.0	3–1533	Moks et al., 2006
	Belarus	17.3	2–150	Shimalov et al., 2000b
Canis lupus familiaris (dogs)	Greece	2.5	n.g.	Papazahariadou et al., 2007
	Turkey	5.0	n.g.	Umur 1998
	Sweden	0.4	n.g.	Jogeland et al., 2002
Vulpes vulpes L. (Red fox)	Denmark	15.4	n.g.	Saeed et al., 2006
	Germany	0.1	n.g.	Loos-Frank and Zeyhle 1982
	Finland	9.6	n.g.	Freeman 1966
	Sweden	40.6	n.g.	Persson and Christensson. 1971
	Denmark	26.0	n.g.	Guildal and Clausen 1972
	Wales	13.0	n.g.	Williams 1976
	Germany (West Berlin)	28.3	n.g.	Saar 1957
	Austria	18.4	n.g.	Hinaidy 1976
	Poland	88.0	n.g.	Kozlowska 1957
	Poland	76.5	n.g.	Furmaga and Wysocki 1951
	Yugoslavia	64.5	n.g.	Lozanić 1966
	Bulgaria	2.1	n.g.	Jančev and Ridjakov 1978
	Portugal	27.4	n.g.	Eira et al., 2006
	Netherlands	10.9	–18	Borgsteede 1984
	Belarus	42.6	2–600	Shimalov et al., 2003
	Germany (Schleswig-Holstein)	29.7	n.g.	Lucius et al., 1988
	Ireland	27.3	–308	Wolfe et al., 2001
Nyctereutes procyonoides (raccoon dog)	Danube delta	47.4	n.g.	Barbu 1972
	Armur-Primorsker-area	>10	n.g.	Judin 1977
	Germany (eastern)	69.2	n.g.	Schuster et al., 1993
	Volga delta	23.5	n.g.	Ivanov and Semenova 2000
	Belarus	42.9	4–800	Shimalov et al., 2002
	Germany (eastern)	70.0	n.g.	Schuster et al., 1993
Pseudalopex gymnocercus (Pampas fox)	Brasil	36.4	n.g.	Ruas et al., 2008
Cerdocyon thous	Brasil	50.0	n.g.	Ruas et al., 2008
Mustela erminea L. (Stoat)	Belarus	3.3	–500	Shimalov et al., 2001a
Mustela vison (American mink)	Belarus	6.0	–500	Shimalov et al., 2001c
Mustela nivalis L. (Weasel)	Belarus	3.2	–500	Shimalov et al., 2001a
Lutra lutra (European Otter)	Belarus	4.0	–500	Shimalov et al., 2000a
Lynx lynx (Eurasian lynx)	Poland	n.g.	n.g.	Szczęsna et al., 2008
Domestic cat	Uruguay	25	5	Castro et al., 2008

n.g.: not given

Prevalence

As stated above, *A. alata* is reported to be the species of European carnivores. However, recent studies revealed that DMS can also be found in South American carnivores (Castro et al., 2008, Ruas et al., 2008). *Alaria* species are distributed worldwide (Danijarow 1968, Ljubaschenko and Petrov 1962, Mehlhorn 2008, Schnieder 2006). Mehlhorn (2008) estimated that about 30% of the wild canides in Europe are carriers of *A. alata.* The results of various field studies are listed in Table 3. Variability of prevalence data is high, ranging, for example, in the red fox from 0.1% to

88% as shown in Table 3. *A. alata* is the most frequently described trematode of the raccoon dog (Thiess 2006) with prevalence data ranging from <10 to nearly 70% (Schuster et al., 1993). Moreover, the number of parasites that were found per individual animal varied strongly and ranged from 1 to 1.533 adult helminthes (e.g., Borgsteede 1984, Castro et al., 2008, Moks et al., 2006, Shimalov et al., 2000a, 2001a, b, c, 2002, 2003, Wolfe et al., 2001).

Although only the definitive host of the parasite excretes its contagious eggs, transition of mesocercariae between paratenic hosts is quite common (Odening 1963, Hiepe 1985). High infestation rates can therefore be found particularly in omnivores such as wild boars, which live in areas with high *Alaria* prevalence in the definitive hosts. This is because these animals, besides the obligatory second intermediate hosts, also feed on paratenic hosts such as rodents, reptiles, and amphibians (Dönges 1969).

Generally, a significant prevalence of *A. alata* mesocercariae in wild animal populations can be expected in water-rich areas in which the suitable host species (snails, amphibians, and definitive hosts) are present. Wojcik et al. (2001) demonstrated the dependency between the occurrence of suitable snail and amphibian hosts and the prevalence of *A. alata* mesocercariae in wild boars. The studies were conducted between 1999 and 2001 in two hunting regions. Larval alariosis was only revealed in the boars from one of the studied regions. In this region, the results of the parasitological studies revealed definitive (domestic dogs) and intermediate hosts (snails, *Planorbis planorbis* and *Anisus vortex* as well as frogs: *Rana temporaria* and *Rana terrestris*) to be carriers of *A. alata.* The lack of snail hosts in the other region was interpreted as a possible reason for the absence of the parasite in the boar (Wójcik et al. 2001).

In 2002, first incidental findings of *A. alata* during *Trichinella* inspection in the Perleberg abattoir (Brandenburg, Germany) were reported to one of the authors (KG). The parasite was found in carcasses of two wild boars which were finally judged fit for human consumption (personal communication to KG). Jakšić et al. (2002) demonstrated that 1.8% of 210 wild boar samples from Croatia were positive for *A. alata* mesocercariae. Positive carcasses were judged unfit for human consumption (Jakšić et al., 2002). Große and Wüste (2004, 2006) were the first to publish results on incidental findings of DMS in meat of wild boars during routine *Trichinella* inspection in certain areas of Germany (Brandenburg), indicating a potential health risk to consumers. Whereas the first finding of a mesocercarial stage (April 7, 2003) could not be confirmed by the BfR, the second finding of eight highly motile mesocercariae (October 12, 2003) was clearly identified as *A. alata* by the BfR. The carcasses were declared unfit for human consumption. In 2007, DMS was demonstrated in 0.24% of all *Trichinella* samples in Brandenburg. However, as samples were then pooled, the correct prevalence could not be exactly stated (Große and Wüste 2008). During the examination of other wild animals (reptiles, amphibians, birds, mammals) in Brandenburg, *A. alata* mesocercariae could be demonstrated in a badger (personal communication to KG). The isolated parasite is depicted in Fig. 4.

Detection

In the following, we will concentrate on the methods for detection of mesocercariae in paratenic hosts with respect to the human exposition risk.

All detections of *Alaria* mesocercariae in wild boar meat were incidental background findings during official *Trichinella* inspection, which was and is obligatory for meat of all potential *Trichinella* carriers to be introduced into the human food chain (64/433/EEC, 854/2004/EC). Only official methods for *Trichinella* detection which have been standardized and officially published may be applied (77/96/EEC, 2075/2005/EC). Currently, one reference method and three alternative methods exist which are all based in principal on (a) pepsin/HCl-digestion of muscle tissue, (b) concentration of the digest by sedimentation or filtration, and (c) microscopic examination (2075/2005/EC). A fourth method, the traditional compression method ("trichinoscopy"), where a small muscle sample compressed between to glass slides is directly examined under the microscope, may still be applied in an exceptional case s (2075/2005/EC). It is of some interest that this method, which has

Fig. 4 Four motile *Alaria* mesocercariae and two unspecified nematodes after HCL/pepsin digestion from muscle tissue of a badger (bar conforms 200 µm)

shown to be of significantly less sensitivity then the digestion methods, is apparently applied with relatively high frequency in some countries/areas of the European Union for *Trichinella* inspection of the meat of wild boars.

Samples for *Trichinella* inspection have to be "free of all fat and fascia" as stated *expressis verbis* in Annex I, Chapter I, No 2 b) and c) of the respective regulation, (EC/2075/2005). However, *Alaria* mesocerariae show "apparently a high affinity to the host's adipose tissue" (Odening 1961b). This high affinity to the adipose tissue was first described by Bugge (1942a). As can be seen from Table 4, *Alaria* mesocercariae were detected in all paratenic hosts—in most cases, exclusively (North American river otter, Kimber and Kollias (2000), raccoon and opossum, Shoop

Table 4 Anatomic localization of and detection methods for mesocercariae of *Alaria* spp. in several paratenic host species as described in literature

Alaria sp. / Host	Method	Anatomic location	Author
A. spp. / snakes	Direct	Adipose tissue ("fat body") – other anatomic locations are not specified by the authors	Cort 1918, Dick and Leonard 1979, Odening 1961b, Pearson 1956, Shoop and Corkum 1981, Shoop et al. 1990
A. canis / North American River Otters (*Lontra canadiensis*)	Direct	Subcutaneous mesenteric fat	Kimber and Kollias 2000
A. marcianae / Raccoon (*Procyon lotor*)	Direct	Subcutaneous mesenteric fat	Shoop and Corkum 1981
A. marcianae / Opossum (*Didelphis virginiana*)	Direct	Subcutaneous mesenteric fat, lungs	Shoop and Corkum 1981
A. marcianae / Domestic cat (*Felis*…)	H	Adult: adipose tissue of mammary gland (mesocercariae) Offspring: lungs (metacercariae), intestines (adult)	Shoop and Corkum 1983
A. marcianae / Mice	H	Adult: adipose tissue of mammary gland (mesocercariae)	Shoop and Corkum 1983
A. alata / wild boar (*Sus scrofa*…)	Direct	Accumulation in abdominal cavity followed by infestation of viscera and adipose tissue	Bugge 1942a
A. alata / wild boar (*Sus scrofa*…)	TC	Diaphragm (official *Trichinella* sample side according to 2075/2005/EC)	Jakšić et al., 2002
A. alata / wild boar (*Sus scrofa*…)	TDp	Diaphragm (official *Trichinella* sample side according to 2075/2005/EC)	Große and Wüste 2004, 2006
Alaria alata / Rhesus monkey (*Macaca mulatta*)	Direct	Adipose tissue of heart, pericard, between liver, diaphragm, mesentery between Arteria carotis and oesophagus, subcutaneous adipose tissue of the distal ribs, in the intramuscular connecting tissue of the ribs and in the tendons of shoulder, neck and throat musculature	Odening 1961b
A. marcianae / Primates (*Callithrix jaccus*)	H	Adult female: mammary glands (alveoli in proximity to the nipple), head and neck muscle, anterior body muscle, posterior body muscle, heart lungs Infants: head and neck muscle, anterior body muscle, posterior body muscle, liver, kidneys, heart, lungs, stomach, small intestine	Shoop et al., 1990
A. Americana / *Homo sapiens*	H	bronchial aspirate, lung tissue, ascitic fluid, liver, heart, kidney, pancreas, stomach, spleen, lymph nodes, fat, brain, spinal cord	Fernandez et al., 1976, Freeman et al., 1976
A. alata / skunk	Direct	Adipose tissue, heart, aorta, kidney, thyroid, below pleura, thoracic cavity, abdominal cavity	Sudarikov 1960
A. alata / hedgehog, wild canides	Direct	Subcutaneous mesenteric fat	Sudarikov 1960
A. alata / otter	Direct	Lungs	Sudarikov 1960
A. alata / mice	Direct	Diaphragm	Sudarikov 1960
A. alata / mole	Direct	Heart, lungs	Sudarikov 1960
A. alata / Domestic cat (*Felis*…)	Direct	Heart, intercostal muscle	Sudarikov 1960

TD Trichinella inspection by digestion, *TC* Trichinella inspection by compression, *Direct* visual inspection (particulary with the aid of a magnifying glass), *H* histological examination and Corkum (1981), hedgehog and wild canides, Sudarikov (1960), snakes (e.g. Cort 1918, Dick and Leonard 1979, Odening 1961b, Pearson 1956, Shoop and Corkum 1981, Shoop at al. 1990)—in adipose tissue.

It is highly questionable if a method as optimized for the detection of *Trichinella* in pure muscle tissue can reliably detect *Alaria* mesocercariae which obviously distributes quite differently in its host as shown in Table 4.

Up to 2005, *Trichinella* inspection was by way of derogation from the obligatory ruling—until a common harmonizing rule would be created for so-called "*Trichinella*-free areas"—not necessary in member states which applied for non-inspection on a national level (92/120/EEC). The extent of this derogation from *Trichinella* inspection of fattening pigs reached substantial orders of magnitudes in some member states (Lücker and Hartung 2006). It might be concluded that also a substantial number of wild boars remained unexamined for *Trichinella* and thus for DMS in some European member states. Today, derogation from the obligatory *Trichinella* inspection is possible in the context of so-called "*Trichinella*-freedom" which is under strict official control (i.e., "Trichinella-free" farms and "*Trichinella*-free" regions) and only applicable to fattening pigs (2075/2005/EC). For wild animal populations, derogation from obligatory *Trichinella* inspection will be possible, where "the competent authority has ascertained by risk assessment that the risk of *Trichinella* infestation of a particular farmed or wild species is negligible." Moreover, *Trichinella* inspection of wild game or wild game meat directly supplied to the final consumer or to local retail establishments directly supplying the final consumer falls within the responsibility of the member state s (2075/2005/EC). Thus, future development in *Trichinella* inspection might also contribute to a further increased underestimation of DMS in wild animal populations.

Pathogenicity

For a long time, it was assumed that DMS in wild boars would not imply any risk to consumers (Beutling 2004, Lerche et al., 1957, Ostertag and Schönberg 1955).

In contrast, Odening (1961b) demonstrated by experimentally infecting a primate that *Alaria* mesocercariae can cause severe damages within a paratenic host closely related to humans. Overall pathogenicity is correlated to high infestation densities, in particular, after repetitive intake of mesocercariae. The transition of the mesocercariae from one paratenic host to another fails to decrease infectivity of the parasite (Bosma 1934, Dönges 1969, Hiepe 1985, Lutz 1933a, b, Lutz 1921, Odening 1963, Pearson 1958, Pearson 1956, Schnieder 2006). Since 1973, several reports about human larval alariosis have been published as summarized in Table 5.

It is important that most infections with trematodes are found to be associated with eosinophilia and an increase of IgE (Löscher and Sonnenburg 2005), which means that a general anaphylactic reaction may arise from a repetitive oral intake of infected material. The symptoms of an anaphylactic shock range from tachycardia and drop in blood pressure to vasomotoric collapse and unconsciousness (Bork 1985, Egger 2005).

Human alariosis manifests in various clinical signs which range from low-grade respiratory and cutaneous symptoms to a diffuse unilateral subacute neuroretinitis (DUSN) (Bialasiewicz 2000, Hedges 2000) and to an anaphylactic shock with lethal consequence as mentioned above. Freeman et al. (1976) report on a 24-year-old Canadian male who complained of tightness in the chest and abdominal symptoms after several long hikes across eastern Ontario (Canada). Within 2 days of the initial illness, the patient developed flu-like symptoms like head-

Table 5 Cases of human larval alariosis according to literature

Year	Parasite	Location	N	Manifestation	Infestation route and vector	Author
1969	*Alaria* (?) mesocercariae (?)	CA, USA	1	Eye	(?), (?)	Byers and Kimura 1974, McDonald et al., 1994
1972	*Alaria* mesocercariae	Ontario, Canada	1	Eye	Smear infection with the preparation of frog legs	Shea et al., 1973
1975	*Alaria Americana* mesocercariae	Ontario, Canada	1	Generalized (see Table 3), lethal	NU (frog legs)	Freeman et al., 1976, Fernandez et al., 1976
1975	*Alaria* mesocercariae	LA, USA	1	Skin	NU (venison, raccoon (?))	Beaver et al., 1977
1988	*Alaria* mesocercariae	CA, USA	1	Eye	NU (venison) or frog legs (PSI)	McDonald et al., 1994
1990	*Alaria Americana* mesocercariae	CA, USA	1	Eye	NU (venison) or frog legs (PSI)	McDonald et al., 1994
1993	*Alaria Americana* mesocercariae	Manitoba, Canada	1	Respiratory tract, skin	NU (wild goose (?))	Kramer et al., 1996

N: cases; (?): unconfirmed, unknown; PSI: possible smear infection; NU: nutritional aches, fever, faintness, and cough, and on the third day, showing severe dyspnea and hemoptysis, he was admitted to a local hospital. On the fourth day, the patient became comatose, and skin petechiae were evident. The tentative diagnosis was viral pneumonia, and he was treated with broad-spectrum antibiotics. After the treatment failed, biopsy of a skin lesion and an open-lung biopsy were performed. The tissue sections of fixed lung tissue contained lengthwise sections of a fluke which was tentatively identified as *Alaria* spp. mesocercaria. By the ninth day, after initial symptoms, the patient died in the hospital. At autopsy, practically all viscera showed extensive local or diffuse hemorrhage. Several thousand mesocercariae were estimated to have been present within the viscera and nearly all organs. The cause of death was asphyxiation from extensive pulmonary hemorrhage, probably due to immune-mediated mechanisms, after repetitive oral intake of *Alaria Americana* mesocercariae. The possibility that the infective dose of mesocercariae might have been ingested with drinking water was investigated and ruled out. The authors concluded that the victim ate uncooked or more likely inadequately cooked frog legs heavily infected with mesocercariae; however, relatives denied that.

Risk assessment and conclusion

In accordance with the recent assessment of the BfR (2007), which concluded that current methodology and data are insufficient, a sound analysis of consumer exposition risk to *Alaria* mesocercariae is impossible for the time being. However, there is no question about the high potential pathogenicity of this parasite as shown in the previous chapter. Jakšić et al. (2002) and Große and Wüste (2004, 2006) pointed out, that the parasite represents a potential source of infection for both humans and animals and that consumption of wild boar meat can be an important factor for the epidemiology of this zoonosis.

Both alimentary and occupational exposition must be taken into account. As to the latter, the Swiss Federal Office for the Environment (FOEN) categorized *A. alata* as a stage 2 risk (Z) for parasites with zoonotic potential (Anonymous 2003) as pertaining to occupational health risks.

Up to now, only few reports on human larval alariosis exist, and none have been reported in Germany. Keeping the possibly high non-inspection rate of wild boars for *Trichinella* as well as the methodological deficiencies in mind, we must balance this against a presumably low level of awareness of this zoonosis in general and particularly against more or less uncharacteristic symptoms of low level infections. A tendency can be noted for European official meat inspection to treat DMS positive meat of wild boars as unfit for human consumption, at least on a provisional basis and in favor of consumer protection (BfR 2007, Jakšić et al. 2002).

In conclusion, we can state that the high potential pathogenicity of *Alaria* spp. mesocercariae and their presence in wild game should initiate further studies. They must concentrate on (1) the optimization and/or development of methods of DMS detection, (2) the distribution of the mesocerariae within paratenic hosts (so-called predilection sites), (3) their prevalence in sylvatic populations of wild animals and in the food chain. Further, their tenacity within the paratenic host and meat as pertaining to food technological treatments has to be elucidated. Moreover and in close connection with the parasites' pathogenicity and tenacity, the question whether *Alaria alata* might split up into different species should be elucidated.

Following the publications of incidental findings of *Alaria* mesocercariae in wild boar meat (Große and Wüste 2006) and the statement on the DMS problem by the BfR, the Federal Ministry of Nutrition, Agriculture and Consumer Protection (BMELV, Germany) consequently initiated and funded a study on the detection and prevalence of *Alaria* mesocercariae in wild animal populations. We will present first results of this study in a following paper. They support the conclusions of this review strongly and will supply further prevalence data as well as first results of a preliminary method for the detection of *Alaria* mesocercariae in adipose tissue.

Acknowledgement We gratefully acknowledge the funding of parts of this work by the Federal Ministry of Food, Agriculture and Consumer Protection (BMELV, Germany).

For their valuable technical assistance in the present study, we would like to thank Lia Kieker, Heiko Wellner, Lutz Gumpert, Carolin Gladis, and TÄ Katrin Zetzsche. Further, we would like to express our gratitude for helpful scientific input made by Dr. Walentina Holthaus, Dr. Viktor Dyachenko, Dr. Ronald Schmäschke, and in particular Dr. Karsten Nöckler.

References

Andreas K (2006) Helminthen einheimischer Froschlurche. Vet Diss FU Berlin. Journal-Nr. 3048

Anonymous (2003) Einstufung von Organismen. Parasiten. Herausgegeben vom Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern

Department of the Environment, Transport, Energy, and Communications, Federal Office for the Environment (FOEN) http://www.umwelt-schweiz.ch/imperia/md/content/stobobio/biotech/12.pdf

Ashton AN, Brown N, Easty P (1969) Trematode cataract in fresh water fish. J Small Anim Pract 10:471–478

Baer JG (1951) Ecology of animal parasites. Univ. of Illinois Press, Urbana III, 1951

Barbu P (1972) Beiträge zum Studium des Marderhundes, *Nyctereutes procynoides ussuriensis* (Matschie, 1907), aus dem Donaudelta. Säugerk Mitt 20:375–405

Beaver PC, Little MD, Tucker CF, Reed RJ (1977) Mesocercaria in the skin of man in Louisiana. Am J Trop Med Hyg 26(3):422–426

Beutling DM (2004) Lehrbuch der Schlachttier und Fleischuntersuchung. Parey Verlag Stuttgart 2004;ISBN 3-8304-4098-7:22

BfR (2007) Bundesinstitut für Risikobewertung Wildschweinfleisch kann den gefährlichen Duncker´schen Muskelegel enthalten. Stellungnahme Nr. 027/2007 des BfR vom 1. Juli 2007

Bialasiewicz AA (2000) Neuroretinitis. Ophthalmologie 97:374–391

Borgsteede FHM (1984) Helminth parasites of wild foxes (*Vulpes vulpes* L.) in the Netherlands. Z Parasitenkd 70:281–285

Bork K (1985) Kap.12 Soforttyp-Reaktionen. In: Arzneimittelnebenwirkungen an der Haut: Klinik- Diagnostik zur Erkennung der auslösenden Medikamente- Pathogenese- Therapie. 2. Auflage, Schattauer

Bosma NJ (1931) *Alaria mustelae* sp. nov., a trematode requiring four hosts. Science 74:521–522

Bosma NJ (1934) The life history of the trematode *Alaria mustelae* sp. nov. Trans Amer Micr Soc 53:116–153

Bugge G (1942a) Das sogenannte Muskeldistomum, Agamodistomum suis, ein Bewohner der Bauchhöhle des Schweines. Tierärztl Rdsch 48:146–151

Bugge G (1942b) Der Muskelegel Dunckers beim Frosch. Zschr Fleisch-Milchhyg 54:73–76

Burrows RB, Lillis WG (1965) Trematodes of New Jersey dogs and cats. J Parasitol 51(4):570–574

Byers B, Kimura SJ (1974) Uveitis after death of a larva in the vitreous cavity. Am J Ophthalmol 77(1):63–66

Castro O, Venzal JM, Felix ML (2008) Two new records of helminth parasites of domestic cat from Uruguay: *Alaria alata* (Goeze, 1782) (Digenea, *Diplostomatidae*) and *Lagochilascaris major* (Leiper, 1910) (Nematoda, *Ascrididae*). Vet Parasitol . doi:10.1016/j.vetpar.2008.11.019

Cort WW (1918) The excretory system of *Agamodistomum marcianae* (LaRue), the agamodistome stage of a fork-tailed cercaria. J Parasitol 4:130–134

Cort WW, Brooks ST (1928) Studies of the holostome cercariae from Douglas Lake, Michigan. Trans Am Microscop Soc 47:179–221

Cuckler AC (1940) Studies on the migration and development of *Alaria* spp (Trematoda: *Strigeata*) in the definitive host. J Parasitol Suppl 26:36

Cuckler AC (1941) Morphological and biological studies on certain strigeid trematodes of mammals. Ph.D. Thesis, Univ. of Minnesota, Minneapolis, Minn.

Cuckler AC (1949) Morphological and biological studies on certain strigeid trematodes of mammals. Summaries of Ph.D. Theses, Univ. of Minnesota, Minneapolis, Minn. 4:45–47

Danijarow IA (1968) Veterinärenzyklopädie Bd. 1 (russ.). Moskau

Dick TA, Leonard RD (1979) Helminth parasites of Fisher, *Martes pennanti* (Erxleben), from Manitoba, Canada. J Wild Dis 15 (3):409–412

Dönges J (1969) Entwicklungs- und Lebensdauer von Metacercarien. Z Parasitenk 31:340–366

Dollfus RPh, Chabaud AG (1953) *Distomum musculorum suis* (HJC Duncker, 1896), mésoceraire d´*Alaria alata* (JAE Goeze, 1782) (Trematoda *Strigeata*) chez un sanglier (*Sus scrofa* L., 1758, Fera). Ann Parasitol humaine et comparée 28:352–364

Duncker HCJ (1881a) Distomeen im Schweinefleisch. Zschr mikr Fleischschau 2(3):23–24

Duncker HCJ (1881b) Muskel-Distomeen. Zschr mikr Fleischschau 2 (4):141

Duncker HCJ (1884) Distomeen im Schweinefleisch Zschr mikr Fleischschau 3:39–42

Duncker HCJ (1896) Die Muskel-Distomeen. Berl tierärztl Wschr 24:279–282

Duncker HCJ (1897) Die Muskel-Distomeen. Zschr Fleisch-Milchhyg 7:197–198

Egger G (2005) Kap 2 Zellen der unspezifischen Abwehr. In: Die akute Entzündung: Grundlagen, Pathophysiologie und klinische Erscheinungsbilder der unspezifischen Immunität. Springer

Eira C, Vingada J, Torres J, Miquel J (2006) The helminth community of the Red Fox (*Vulpes Vulpes*), in Duans de Mira (Portugal) and its effects on host condition. Wildl Biol Pract 2(1):26–36

Fernandez BJ, Cooper JD, Cullen JB, Freeman RS, Ritchie AC, Scott AA, Stuart PE (1976) Systemic infection with *Alaria Americana* (Trematoda). Can Med Assoc J 115:1111–1114

Foster GW, Kinsella JM, Sheppard BJ, Cunningham MW (2008) Transmammary Infection of free-ranging Florida Panther neonates by *Alaria marcianae* (Trematoda: *Diplostomatidae*). J Parasitol 29:1

Freeman RS (1966) Helminth parasites of the red fox in Finland. Proc Int Congr Parasitol Rome (1964):482

Freeman RS, Stuart PE, Cullen SJ, Ritchie AC, Mildon A, Fernandes BJ, Bonin R (1976) Fatal human infection with mesocercariae of the trematode *Alaria Americana*. Am J Trop Med Hyg 25:803–807

Furmaga S, Wysocki E (1951) Of the helminthofauna of foxes in the Lublin voivodships territory. Ann Uni M Curie-Sklodowska Sectio DD 6:97–123

Gestaldi B (1854) Cenni sopra alcuni nuovi Elminti della *Rana esculenta* con nuove osservatione sul *Codonocephalus mutabilis* (Diesing). Tesi per aggregazione al Collegio della Facolta delle Scienze Fisiche e Mathemetiche nella R Univ di Torino:25-36

Goldberg SR, Bursey CR, Cheam H (1998) Helminths of two native frog species (*Rana chiricahuensis*, *Rana yavapaiensis*) and one introduced frog species (*Rana catesbeiana*) (Ranidae) from Arizona. J Parasitol 84(1):175–177

Goldberg SR, Bursey CR, McKinnell RG, Tan IS (2001) Helminths of northern leopard frogs (*Rana Pipiens, Ranidae*) from North Dakota and South Dakota. West N Am Naturalist 61(2):248–251

Goüy de Bellocq J, Sarà M, Casanova JC, Feliu C, Morand S (2003) A comparison of the structure of helminth communities in the woodmouse, *Apodemus sylvaticus*, on islands and the western Mediterranean and continental Europe. Parasitol Res 90:64–70

Große K, Wüste T (2004) Funde des Duncker'schen Muskelegels bei der Trichinenuntersuchung mittels Verdauungsverfahrens. DVG 45. Arbeitstagung des Arbeitsgebiets "Lebensmittelhygiene" 28.09-01.10.2004;Garmisch Partenkirchen

Große K, Wüste T (2006) Der Dunker'sche Muskelegel Funde bei der Trichinenuntersuchung mittels Verdauungsverfahren. Fleischwirtschaft 4:106–108

Große K, Wüste T (2008) Duncker'scher Muskelegel—Risiko für den Verbraucher? 8. Fachtagung Fleisch- und Geflügelfleischhygiene für Angehörige der Veterinärverwaltung 04.03-05.03.2008, Berlin

Guildal JA, Clausen B (1972) Endoparasites from one hundred Danish red foxes (*Vulpes vulpes*). Norwegian J Zool 21:329–330

Hedges TR (2000) Diffuse unilateral subacute neuroretinopathy. Principles and practice of ophthalmology clinical practice 3:2167–2171

Hiepe TH (1985) Lehrbuch der Parasitologie Bd 3: Veterinärmedizinische Helminthologie. Fischer, Stuttgart, Jena

Hinaidy HK (1976) A further contribution to the parasite fauna of the red fox, *Vulpes vulpes* (L.), in Austria. Zentralbl Veterinarmed B 23(1):66–73

Hoffmann GL (1976) Parasites of North American freshwater fishes. University of California Press, Berkeley and Los Angeles, CA, USA

Ivanov VM, Semenova NN (2000) Parasitological consequences of animal introduction. Russ J Ecol 31(4):281–283

Jakšić S, Sunčica U, Vučemilo M (2002) Nachweis von Mesozerkarien des Saugwurms *Alaria alata* im Wildschweinfleisch. Z Jagdwiss 48:203–207

Jančev J, Ridjakov N (1978) Helminth fauna of the fox (*Vulpes vulpes crucigera*, Bechstein) in north western Bulgaria. Chelminthologija, Sofia 4:73–96

Jogeland M, Raue H, Petersson U (2002) Inventering av invartesparasiter hos hundar i Skane 1999–2000. [Inventory of internal parasites in dogs in Skane 1999–2000]. Svensk Veterinartidning 54(13):635–637

Johnson PTJ, Lunde KB, Ritchie EG, Launer AE (1999) The effect of trematode infection on amphibian limb development and survivorship. Science 284(5415):802–804

Joyeux Ch, Baer JG (1934) Les hôtes d´attente dans le cycle evolutif des helmintes. Biol Med Paris 24(9):482–506

Judin VG (1977) Enotovidnaja sobaka Primorja i Priamurja (russ.). Izd Nauka, Moskva

Kimber KR, Kollias GV 2nd (2000) Infectious and parasitic diseases and contaminant-related problems of North American river otters (Lontra canadensis): a review. J Zoo Wild Med 31(4):452–472

Komiya Y (1938) Die Entwicklung des Exkretionssystems einiger Trematodenlarven aus Alster und Elbe, nebst Bemerkungen über ihren Entwicklungszyklus. Parasitol Res 10(3):340–385

Kozlowska J (1957) On the knowledge of the helminth fauna of wild and bred foxes. Acta Parasitol Pol 5:181–192

Kramer MH, Eberhard ML, Blankenberg TA (1996) Respiratory symptoms and subcutaneous granuloma caused by mesocercariae: a case report. Am J Trop Med Hyg 55:447–448

Leibovitz L, Riis RC, Georgi M (1980) Digenetic trematode infection. J Americ Vet Med Ass 177:40–42

Leiper RT (1920) Exhibition of lantern-slides illustrating the experimental transmission of some helminth infections. Proc Zool Soc London III(XXIX):438

Lerche M, Goerttler V, Rievel H (1957) Lehrbuch der tierärztlichen Lebensmittelüberwachung. Verlag M&H Schaper, Hannover

Ljubaschenko CJ, Petrov AM (1962) Krankheiten der Pelztiere, Moskau

Loos-Frank B, Zeyhle E (1982) The intestinal helminths of the red fox and some other carnivores in southwest Germany. Z Parasitenkd 67(1):99–113

Löscher T, v Sonnenburg F (2005) Parasitosen. In: Therapie innerer Krankheiten von Gustav Baumgartner., 11. Auflage, Springer

Lozanić BM (1966) Contribution a la cannaissance de la faune des helminthes chez le renard de nos regions (*Vulpes vulpes*). Acta vet Beogr 16:301–304

Lucius R, Böckeler W, Pfeiffer AS (1988) Parasiten der Haus-, Nutz- und Wildtiere Schleswig-Holsteins: Parasiten der inneren Organe des Rotfuchses (*Vulpes vulpes*). Z Jagdwiss 34:242–255

Lücker E, Hartung J (2006) Zum Problem der Risikobewertung so tenanted Trichinellen-freier Betriebe und Trichinellen-freier Gebiete. Proceedings 46. DVG Arbeitstagung des Arbeitsgebietes "Lebensmittelhygiene" 2005, Garmisch- Partenkirchen, DVG Service GmbH, Gießen, ISBN 3-938026-37-5:251-254

Lutz A (1921) Zur Kenntnis des Entwicklungszyklus der Holostomiden. Zbl Bakt I Orig 86:124–129

Lutz A (1933a) Zur Kenntnis des *Distoma tertracystis* (Gestaldi) und ähnlicher Formen, die fälschlich als Agamodistomum bezeichnet werden. Mem inst Oswaldo Cruz 27:50–60

Lutz A (1933b) Beobachtungen über Brasilianische Dicranocercarien. Mem inst Oswaldo Cruz 27:377–402

Marshall A (1972) Textbook of Zoology: Invertebrates. Elsevier, New York

McDonald HR, Kazacos KR, Schatz H, Johnson RN (1994) Two cases of intraocular infection with *Alaria* mesocercaria (Trematoda). Am J Ophtalmol 117:447–455

Mehlhorn H (2008) Encyclopedia of parasitology. Third edition. Springer, Heidelberg

Moks E, Jõgisalu I, Saarma U, Talvik H, Järvis T, Valdmann H (2006) Helminthologic survey of the wolf (*Canis lupus*) in Estonia, with an emphasis on *Echinococcus granulosus*. J Wildl Dis 42 (2):359–365

Morozov FN (1937) Discovery of encysted trematodes in the internal organs of polecats (russ.). Trudy Gor´kovsk Gosudarst Pedagog Inst 1:115–120

Nikitina EN (1986) Trematode larvae in snails of Lake Glubukoe. Hydrobiologia 141:139–141

Odening K (1960) Studien an Trematoden aus Schlangen, Vögeln und Säugetieren. Monatsbericht der Deutschen Akademie der Wissenschaften zu Berlin 2(7):437–455

Odening K (1961a) Zur Kenntnis des Exkretionssystems einiger Digenetischer Trematoden (Unterordnungen *Plagiorchiata, Brachylaemata, Strigeata*). Z Parasitenkd 204:440–456

Odening K (1961b) Der „Dunckersche Muskelegel" kann experimentell auf den Affen übertragen werden. Monatshefte für Veterinärmedizin 16:395–399

Odening K (1963) Zur Diagnostik der Mesocercarie von *Alaria alata*, eines möglichen Parasiten des Menschen in Europa, an Hand experimenteller Befunde beim Affen. Mber Dtsch Akad Wiss Berlin 5:385–390

Odlaug TO (1940) Morphology and life history of the trematode *Alaria intermedia*. Trans Am Microscop Soc 59:490–510

Olivier L, Odlaug TO (1938) A new mesocercaria (Trematoda: *Strigeata*) with a note on its further development. J Parasitol 24:369–374

Ostertag R v, Schönberg F (1955) Lehrbuch der Schlachttier- und Fleischuntersuchung. Enke, Stuttgart

Papazahariadou M, Founta A, Papadopoulos E, Chliounakis S, Antoniadou-Sotiriadou K, Theodorides Y (2007) Gastrointestinal parasites of shepherd and hunting dogs in the Serres Prefecture, Northern Greece. Vet Parasitol 148(2):170–173

Pearson JC (1956) Studies of the life cycles and morphology of the larval stages of *Alaria arisaemoides* (Augustine and Uribe, 1927) and *Alaria canis* (LaRue and Fallis, 1936) (Trematoda: *Diplostomatidae*). Can J Zool 34:295–387

Pearson JC (1958) Observations on the morphology and life cycle of *Strigea elegans* (Chandler & Rausch, 1947) (Trematoda: *Strigeidae*). J Parasitol 45(2):155–174

Pence DB, Dowler RC (1979) Helminth parasitism in the Badger (*Taxidea taxus*) from the western Great Plains. USA Proc Helminthol Soc Wash 46:245–253

Pence DB, Knowlton FF, Windberg LA (1988) Transmission of *Ancylostoma caninum* and *Alaria marcianae* in coyotes (*Canis latrans*). J Wildl Dis 24(3):560–563

Pence DB, Tewes ME, Laak LL (2003) Helminths of the Ocelot from Southern Texas. J Wildl Dis 39(3):683–689

Persson L, Christensson D (1971) Endoparasites of foxes in Sweden. Zool Revy 33:17–28

Petrov AM, Dubnickij AA (1950b) Die Metazerkarien-Alariose der Zobel (russ.). Trudy vsesojuznogo Instituta Gel´mintologii im Akad K I Skrjabina 4:20–22

Petrov AM, Dubnickij AA (1950a) Sables–metacercarial alariosis (russ.). Karakulevodstvo I Zverovodstvo 3:70–71

Poole BC, Chadee K, Dick TA (1983) Helminth parasites of Pine Marten, *Martes Americana* (Turton), from Mantitoba, Canada. J Wildl Dis 19(1):10–13

Popiołek M, Szczesna J, Nowaka S, Mysłajeka RW (2007) Helminth infections in faecal samples of wolves *Canis lupus* L. from the western Beskidy Mountains in southern Poland. J Helminthol 81 (4):339–344

Potekhina LF (1951) The life cycle of *Alaria alata* and alariosis in foxes and dogs (russ.). Doklady Akad Nauk SSSR 76:325–327

Riis RC, Georgi ME, Leibovitz L, Smith JS (2006) Ocular metacercarial infection of the oyster toadfish, *Opsanus tau* (L). J Fish Dis 4(5):433–435

Roberts L, Janovy Jr J (2000) Foundations of Parasitology (sixth edition). New York (2000), McGraw-Hill

Ruas JL, Müller G, Farias NA, Gallina T, Lucas AS, Pappen FG, Sinkoc AL, Brum JG (2008) Helminths of Pampas fox, *Pseudalopex gymnocercus* (Fischer, 1814) and of Crab-eating fox, *Cerdocyon thous* (Linnaeus, 1766) in the South of the State of Rio Grande do Sul, Brazil. Rev Bras Parasitol Vet 17(2):87–92

Ruszkowski J (1922) Die postembryonale Entwicklung von *Hemistomum alatum* Dies. auf Grund experimenteller Untersuchungen. Bull Intern Acad Polon Sci Classe Sci Math Nat Sér B, pp 237–250

Saar C (1957) Parasitologische Untersuchungen beim Rotfuchs (*Vulpes vulpes*) im Raum von West-Berlin. Vet Diss FU Berlin (1957)

Saeed I, Maddox-Hyttel C, Monrad J, Kapel CM (2006) Helminths of red foxes (*Vulpes vulpes*) in Denmark. Vet Parasitol 139(1–3):168–179

Savinov VA (1953a) Die Besonderheiten der Entwicklung von *Alaria alata* (Goeze, 1782) im Körper des End- und des Reservewirtes (russ.). Raboty po Gel´mintologii k 75-letiju Akad K I Skrjabina, pp 611–616

Savinov VA (1953b) Die Entwicklung von *Alaria alata* (Goeze, 1782) im Körper der Hunde (russ.). Trudy vsesojuznogo Instituta Gel´mintologii im Akad K I Skrjabina 5:63–64

Savinov VA (1954) Zu Frage einiger Besonderheiten der Stadienentwicklung der *Strigeata* und der Rolle der verschiedenen Wirte in dieser Entwicklung (russ.). Učen Zap vologodsk ped Inst 15:245–306

Schnieder T (2006) Veterinärmedizinische Parasitologie, Begr. v. Josef Boch u. Rudolf Supperer. 6. Auflage, Parey bei MVS

Schuster R, Schierhorn K, Heidecke D, Ansorge H (1993) Untersuchungen zur Endoparasitenfauna des Marderhundes *Nyctereutes procynoides* (Gray, 1834) in Ostdeutschland. Beitr Jagd Wildforschung 18:83–87

Shea M, Maberley AL, Walters J, Freeman RS, Fallis AM (1973) Intraretinal larval trematode. Trans Am Acad Ophthalmol Otolaryngol 77(6):784–791

Shimalov VV, Shimalov VT, Shimalov AV (2000a) Helminth fauna of otter (*Lutra lutra* Linnaeus, 1758) in Belorussian Polesie. Parasitol Res 86(6):528

Shimalov VV, Shimalov VT, Shimalov AV (2000b) Helminth fauna of the wolf (*Canis lupus* Linnaeus, 1758) in Belorussian Polesie. Parasitol Res 86(2):163–164

Shimalov VV, Shimalov VT, Shimalov AV (2000c) Helminth fauna of Snakes (Reptilia, Serpentes) in Belorussian Polesie. Parasitol Res 86:340–341

Shimalov VV, Shimalov VT, Shimalov AV (2001d) Helminth fauna of the stoat (*Mustela erminea* Linneaus, 1758) and the weasel (*M. nivalis* Linnaeus, 1758) in Belorussian Polesie. Parasitol Res 87 (8):680–681

Shimalov VV, Shimalov VT, Shimalov AV (2001a) Helminth fauna of the European mole (*Talpa europaea* Linnaeus, 1758) in Belorussian Polesie. Parasitol Res 87(9):790–791

Shimalov VV, Shimalov VT, Shimalov AV (2001b) Helminth fauna of the American mink (*Mustela vison* Schreber, 1777) in Belorussian Polesie. Parasitol Res 87(10):886–887

Shimalov VV, Shimalov VT, Shimalov AV (2001c) Helminth fauna of toads in Belorussian Polesie. Parasitol Res 87(10):84

Shimalov VV, Shimalov VT, Shimalov AV (2002) Helminth fauna of the racoon dog (*Nyctereutes procyonoides* Gray, 1834) in Belorussian Polesie. Parasitol Res 88(10): 944–945

Shimalov VV, Shimalov VT, Shimalov AV (2003) Helminth fauna of the red fox (*Vulpes vulpes* Linnaeus, 1758) in southern Belarus. Parasitol Res 89(1):77–78

Shoop WL, Corkum KC (1981) Epidemiology of *Alaria marcianae* mesocercariae in Louisiana. J Parasitol 67(6):928–931

Shoop WL, Corkum KC (1983) Transmammary infection of paratenic and definitive hosts with *Alaria marcianae* (trematoda) mesocercariae. J Parasitol 69(4):731–735

Shoop WL, Corkum KC (1984a) Transmammary infection of newborn by larval trematodes. Science 223(4640):1082–1083

Shoop WL, Corkum KC (1984b) Pathway of mesocercariae of *Alaria marcianae* (Trematoda) through the mammary glands of lactating mice. J Parasitol 70(3):333–336

Shoop WL, Corkum KC (1987) Maternal transmission by *Alaria marcianae* (Trematoda) and the concept of amphiparatenesis. J Parasitol 73(1):110–115

Shoop WL, Font WF, Malatesta PF (1990) Transmammary transmission of mesocercariae of *Alaria marcianae* (Trematoda) in experimentally infected primates. J Parasitol 76 (6):869–873

Staskiewicz RBS (1947) Studia nad *Agamodistomum muscolorum suis*. Med Weterynar (Poland) 31:28–31

Stefański W, Tarczyński S (1953) Sur le développement de l´ *Agamodistomum suis* Duncker, 1881. Acta Parasitol Polonica 1:149–154

Sudarikov WE (1960) In: Skrjabin KI Trematodes of animals and man, essentials of trematodology. Ac Sci USSR Helm Lab, Moskow (1960), Israel program f. sci. transl. (1965)

Thiess A (2006) Untersuchungen zur Helminthenfauna und zum Vorkommen von *Trichinella* sp. beim Marderhund (*Nyctereutes procyonoides*) in Brandenburg. Vet Diss FU Berlin

Timofeev NE (1900) Les trématodes des amphibiens et reptiles des environs de Kharkov. Trav soc naturalistes Univ imp Kharkov 24:137–166

Umur Ş (1998) Bir köpekte *Alaria alata* olgusu. Tr J of Veterinary and Animal Sciences 22:89–92

Wallace FG (1939) The life cycle of *Pharyngostomum cordatum* (Diesing) Ciurea (Trematoda: Alariidae). Trans Am Microscop Soc 58:49–61

Williams BM (1976) The intestinal parasites of the red fox in south west Wales. Br Vet J 132(3):309–312

Wirkerhauser T (1980) Trichinellose, ein altes Problem in neuem Gewand. Veterinärstation:3-4

Wójcik AR, Grygon-Franckiewicz B, Zbikowska E (2001) The studies of the invasion of Alaria alata (Goeze, 1782) in the Province of Kuyavia and Pomerania. Wiad Parazytol 47(3):423–426

Wojcik AR, Grygon-Franckiewicz B, Zbikowska E (2002) Current data of *Alaria alata* (Goeze, 1782) according to own studies. Medycyna Weterynaryjna 58(7):517–519

Wolfe A, Hogan S, Maguire D, Fitzpatrick C, Vaughan L, Wall D, Hayden TJ, Mulcahy D (2001) Red foxes (*Vulpes vulpes*) in Ireland as hosts for parasites of potential zoonotic and veterinary significance. Vet Rec 149:759–763

Yastrebov VB, Gorokhov VV, Shestakov AM (2005) To the detection of the trematode mesocercariae alaria alata in the blood of domestic dogs and cats (russ.). Medicina Moskva 4:48–51

Cited legal texts

77/96/EEC Opinion of the Scientific Committee on Veterinary Measures relating to public health—Detection of *Trichinella spiralis* in pork with a pooled sample digestion method using a magnetic stirrer and two separatory funnels—22 June 1998. Off. J. Eur. Commun. N L026 of 31/01/1977:0067

64/433/EEC Council Directive 64/433/EEC of 26 June 1964 on health problems affecting intra-Community trade in fresh meat. Off. J. Eur. Commun. N B121 of 29/07/1964:2012

92/120/EEC Council Directive 92/120/EEC of 17 December 1992 on the conditions for granting temporary and limited derogations from specific Community health rules on the production and marketing of certain products of animal origin. Off. J. Eur. Commun. N L062 of 15/03/1993:0086

2075/2005/EC Commission Regulation (EC) No 2075/2005 of 5 December 2005 laying down specific rules on official controls for *Trichinella* in meat.

854/2004/EC Regulation (EC) No 854/2004 OF THE EUROPEAN PARLAMENT AND OF THE COUNCIL of 29 April 2004 laying down rules for the organisation of official controls on products of animal origin intended for human consumption