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REVIEW ARTICLE

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Raw meat consumption and incidence of bovine cysticercosis in Ethiopia: A brief overview

YOSEF DENEKE, ABAY BESHAH, D. RAMESH, RAJIB DEB AND BLESSA SAILO

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Ethiopia has large number of livestock. However, its productivity remains marginal due to prevalent disease, malnutrition and management constraints. Parasitism represents a major set back to the development of the sub-sector. However, data on epidemiology, economic loss and relative hierarchy of individual parasitic infections are hardly available. For understanding these contexts, yield paramount importance to determine the type and scope of control intervention is to be envisaged (Jobire *et al*., 1996).

Among the parasites of livestock, *Bovine cysticercosis* affects the muscle of cattle. Its life cycle is entirely dependent on the link between man and cattle. Thus, any break in this links can result in the total elimination of the parasite (Urquhart *et al.*, 1996). *Bovine cysticercosis* is also known as beef measles. It is prevalent in most countries of the world (Frolova, 1982; Smyth; 1994, Urquhart *et al*., 1996). Financial losses can be considerable when large numbers of animals are affected, such as in feedlot. Most incidents arise as a result of direct exposure to proglottids shed from farm workers. There are also some reports of large scale outbreaks resulting from sewage contaminated feed or forage (Wayne, 2002). Hence, cysticercosis is an important public health and economic problem because of its consequences on human nutrition and economy of some countries (Wanzala *et al*., 2003).

Globally, carriers of bovine *taeniosis* are 77 million and about 40% of them live in Africa. In relation to developed countries even if the disease has a very low prevalence, the problem with removal and treatment facilities in their sewage system plays a role in the distribution of eggs (Lightowlers, 2003), since it is shown that the eggs can survive in sewage (Arundel and Adolph, 1980). The larvae of *T. saginata* still cause significant problems in many parts of the world.

In Ethiopia, the adult parasite in human and the cyst in cattle population is widespread nationwide but differ from region to region. The prevalence of *T. saginata* in human population indicated 64.2% in Hawassa (Fufa, 2006), 75.9% in East Showa (Hailu, 2005) and 89.11% in Addis Ababa (Tembo, 2001). *Bovine cysticercosis* prevalence in abattoir survey varied from region to region in cattle population. In Gonder the range was from 4.9% (Dawit, 2004) to 9.7% (Amsalu, 1989), 19.5% in Bahir Dar (Mulugeta, 1997), 21% in Nekemte (Ahmed, 1990), 17.5 % in East Shewa (Hailu, 2005) and 24.8% in local and 52.38% in cross-breed cattle in Hawassa (Fufa, 2006).

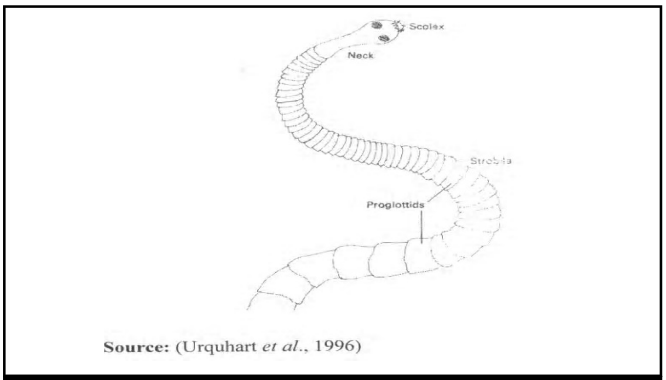
Morphology:

Adult worm:

T. saginata is ribbon- shaped flattened, multi-segmented and hermaphrodite. The body is divided into three distinct parts of scolex (head), neck and strobila. *T. saginata* measures 4 -8 meters in length and rarely measured up to 15m (Urqguhart *et al*., 1996).

The gravid segments are 10-20 mm long and are usually shaded singly and leave the host spontaneously or crawling about the body, clothes and beds of human beings self and cross- fertilization between proglottids is possible. The gravid proglottids are 15 to 35mm long and 5 to 7mm wide filled with eggs, which detach from the strobila singly and leave the host via anus. This implies that coprological examination has a limited value in the diagnosis of *T.*

saginata infection (Gebre Emanuel, 1997).

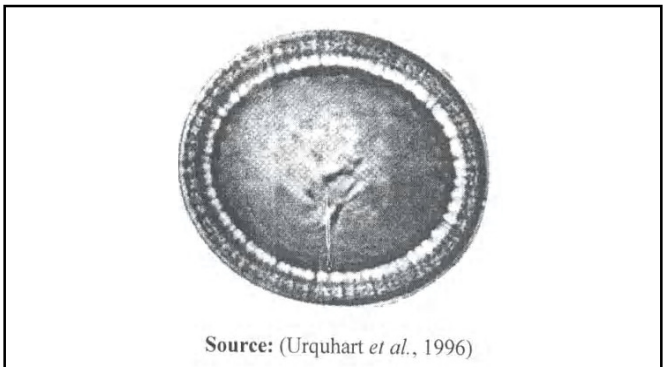


Source: (Urquhart *et al.*, 1996)

Fig. 1 : Morphology of adult worm

Egg:

Taenid egg passed in the faeces or discharged from ruptured gravid segment are sub-spherical to spherical in shape. The egg consists of hexacanth (six looked) embryo (oncosphere), thick, dark brown to yellow in color. There is an outer oval membranous coat, the true egg shell, which is voided in the faeces. Inside the inner envelope, develops into the embryophere, which is made of "keratin" blocks and gives the egg its characteristic radiated appearance (WHO, 1983).



Source: (Urquhart *et al.*, 1996)

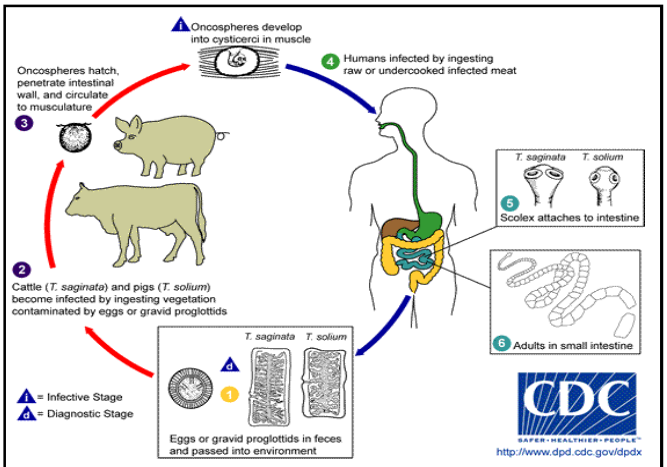
Fig. 2 : Morphology of the egg

Larvae:

Over a period of 3-4 months, the cysticercoids are formed after the egg is ingested and may remain viable in the intermediate host for up to 9 months or even up to the entire life of the host (WHO, 1983). The larval stages or metacestods are found in striated mussels of the intermediate host (Dunn, 1978). *C. bovis* is small (pea sized) oval in shape (OIE, 2001). *C. bovis* is grayish white, about 1cm in diameter and filled with fluid in which the scolex is often clearly visible (Urquhart *et al.*, 1996 and Smyth, 1994)

Life cycle:

The life cycle of *T.saginata* is indirect where the definitive host is human and intermediate host is cattle (Urquhart *et al.*, 1996). Human is infected by the ingestion of raw or under cooked parasititzed meat (Biru, 1984 and WHO, 1983). An infected person can shed as many as 1million eggs each day. Ingesting contaminated pasture infects bovine. The tape worm thrives in the small intestine of humans. As it matures it produces segments that each contains about 100 thousand eggs. The segments break off and move to the outside either in the faces or by migration through the anus (Fig. 3).



Source: http://www.dpd.cdc.gov/dpdx

Fig. 3 : Life cycle of *T. saginata*

Epidemiological distribution of the adult and cyst parasite:

Infection of the intermediate host is affected by many factors. These include the level of environmental contamination, age of the host, egg dispersion rate, egg survival, immune response of the host and heterogeneous infection (Minozzo *et al.,* 2002).

The prevalence of *C. bovis* in cattle population of Africa was 33.02% in Kenya (Onyango, 1996), 22.3% in Zaire and 6.67% in Chad (Gracey, 1992), 10.2% in Nigeria (Frolova, 1982), 10% in Sudan (Mosienyane, 1986), 15% in Rwanda (Pagot, 1992).

Public health importance:

The fact that man is only definitive host has simplified the epidemiology of this infection on the other hand, the varies relationships between man, his animals and the environment make complex factors affecting the function of this parasite in most general terms transmission from man to cattle may be direct or indirect. Direct transmission is usually uncommon but it can occur when hands

contaminated with eggs feed and handle calves. Oncosphers have been found in finger nails; dirty water transmission is accomplished by the contamination of pasture, fodder and water with egg (WHO, 1983). Once infected, individual as a source of infection is able to excrete daily in to environment up to 5 million eggs. Thus, the average number of discharge oncosphers constitutes 1-1.5 million. Thus, intensive environment contamination by the infective material takes place (Frolova, 1982).

At present, the epidemiological role of each infected individual as infection source has increased significantly in large scale fattening complexes. Epidemiological investigations of out break in such feed lots showed that one employee alone infects with beef tape worm was the source of an out break in each complex. Urban citizen can also play definite epidemiological role. That is due to that the modern system of sewage cultures are growth for cattle use. Developed countries, the movement of people in the form of camping and tourism provide opportunities for the spread prognostics and feces in cattle and man (FAO, 2004).

Transmission between animals and man depends on etiological factors such as human habits and religion. They influence the type of food that man consumes and the manners and the manner of preparation. Some of these practices are based on the hundred years of tradition. Example of this could be eating of raw meat in the from of ', Kitfo', Lebileb' and Kurt in Ethiopia. In Egypt, Turkey and middle east, a beef dish known as counters " basterm" or kebaba – like fishes " basterma" or semi-raw meat used as staffing for regional; dishes are responsible for transmitting taeniosis (WHO, 1983). Cyst development takes 3-5 months, and the majority remains viable and infective for about 1-2 years. Man is infected by ingesting raw in adequate cooked beef harboring the viable cyst (Ginsberg, 1960; Lightowlers, 2003).

Status of cysticercosis in Ethiopia:

In Ethiopia the rural communities mainly raise cattle under extensive husbandry practices. Existence of high population density, raw meat consumption, low awareness, poor hygiene and sanitary infrastructures may facilitate transmition of the disease between animals and human beings in the rural areas. The prevalence reports of cysticercosis in Ethiopia showed variable results with localities. Relatively lower prevalence of 2.93% in Jimma (Getachew, 2008), 3.1% in central Ethiopia (Tembo, 2001), 4.9% at Gondar (Dawit, 2004) and 7.5% in Addis Ababa (Nigatu, 2004) were reported. At Asmara 5.95% out of 996 examined (Foad, 1986), 9.7% out of 1168 at Gondar (Amsalu, 1989), while others reported as high as 16.25 in Kombolch Elfora export abattoir (Yimam, 2008), 22.75% in Debre zeit Elfora export abattoir (Natnael, 2008), 17.5% in East Shoa (Hailu, 2005), 21% in Nekemt (Ahmed, 1990) and 26.25% (Fufa. 2006).

In Ethiopia, the prevalence of *T. saginata* egg positive in human varied from place to place. In Hawassa, the prevalence was 64.2% (Fufa, 2006), 79.5% in East Shewa (Hailu, 2005), 89.41% in Addis Ababa (Tembo, 2001) (Table 2).

Risk factors of *T. Sagninata* and *cystiercus bovis:*

Environmental factors:

Emphasis has been placed on the environmental factors that affect the free living egg, the infective pattern of taeniids in their intermediate host is determined by complex interaction of parasite and host – related factors. Many of theses have been examined but particularly emphasis placed on environmental factors that affect determining the infective pattern. (WHO, 1983).

Egg out put and dispersal in the system:

The biotic potential of micro-climatic effects of the environment, the egg put of *T. saginata* worms have been

Table 1 : Prevalence of cysticercosis in Ethiopia

Sr. No.	Study areas	Species	Number of animal examined	Prevalence(in %)	References
1.	Gondar	Bovine	1168	9.7	Amsalu(1989)
2.	Jimma	Bovine	512	2.93	Getachew(2008
3.	Asmera	Bovine	996	5.9	Foad(1986)
4 .	Kombolcha Elforaexport abattoir	Bovine	325	16.2	Yimam(2008)
5.	Debrezeit Elforaexport abattoir	Bovine	400	22.75	Natnael(2008)
6.	Nekemt	Bovine	2,250	21	Ahmed(1990)
7.	East shoa	Bovine	1292	17.5	Hailu(2005)
8.	Awassa	Bovine	400	26.25	Fufa(2006)
9.	Addis Ababa	Bovine	743	7.5	Nigatu(2004)
10.	North Gondar	Bovine	2023	4.9	Dawit(2004)
11.	Addis Ababa	Bovine	1026	3.1	Tembo(2001)

earlier described in this paper. Daily out put runs into several hundred thousand eggs. The important epidemiological aspects with both species are the ways in which the enormous number of eggs dispersed following the expulsion in ptoglottids and feces, so that they become readily available to the intermediate hosts (OIE, 2001).

The primary sites of egg deposition determine the movement and defecation habit of the definitive host. How every, evidence is accumulating, the considerable dispersion occurs almost immediately after defection. Eggs have been shown to disperse up to 80 meters within 10 days and there are indications that small numbers travel much further. Intermediate hosts, such as cattle and sheep generally avoid grazing areas contaminated with feces. Thus, dispersal increases the chances the being ingested (Cabaret *et al*., 2002).

Egg longevity and duration of infectivity:

It will be very important to define factors that are lethal to the eggs because it will give us an over view of the epidemiological significance of the process and some other factors on the duration o infectivity. In damp temperate climates, the oncosphere of the beef tape worm can withstand desiccation in the environment of about 10 months are viable for 130 days in pure water. In summer, solar radiation destroys the oncosphress on soil surface within tow days. However, under the protection of a plant cover, they can survive up or 40 days (Smyth, 1994).

Temperature:

Under laboratory conditions, the viability of isolated eggs of *T. saginata* in much higher when compared with those inside a prognostic. At temperatures 19-37^{0}C longevity varies from 27-29 hours to 2-3 days, at 40^{0}C, it is about 62-64 days, with regards to humidity, the eggs of *T. sagnata* do not survive *in vitro* in the absence of surface moisture (WHO, 1983).

Prevalence of *C. bovis* in cattle population:

In Ethiopia, prevalence of *C. bovis* in cattle population of different regions was conducted by meat inspection survey in abattoirs. It showed that *C. bovis* was prevalent and widespread throughout the country with national average of 13.7%. However, the prevalence distribution varied from place to place. In Gonder the range was from 4.9% (Dawit, 2004) to 9.7% (Amsalu, 1989), 19.5% in Bahir Dar (Mulugeta, 1997), 21% in Nekemte (Ahmed, 1990), 17.5 % in East Shewa (Hailu, 2005), 13.8% in Debre Zeit (Getachew, 1990) and 24.8% in local and 52.38% in cross-breed cattle in Hawassa (Fufa, 2006). Using serology by ELISA, a prevalence of 7.5% (Nigatu, 2004) and by meat inspection 3.11% (Tembo, 2001) was reported in Addis Ababa. Little work has been done and nothing is known whether the prevalence of *C. bovis* varies in different cattle breeds. Fufa (2006) reported that the prevalence of the disease is high (52.38%) in cross-bred cattle and low (24.8%) in local breeds. Among the local cattle breeds, Arsi breed had 29.03%, 25.03% in Wolayta and 21% in Borana breed (Fufa, 2006) (Table 2).

Prevalence of *C. bovis* in body tissues/organs in cattle:

The most infected tissues/organs varied from localities to localities. The prevalence in tongue was 41.27% in North Gonder (Dawit, 2001), 45.8% in Bahir Dar (Mulugeta, 1997), 52.2% in Gonder (Amsalu, 1989) and 28.5% in Debre Zeit (Getachew, 1990). According to Fufa (2006), heart (11.25%) was the highly infected organ in Hawassa while shoulder muscle (30.98%) was in Nekemte (Ahamed, 1990). In general, the rank order of *C. bovis* prevalence in organs from highest to lowest in Ethiopia was tongue > shoulder > heart > masseter > neck > thigh > liver > inter-coastal > diaphragm > kidney > lung > hump. The type of organ targeted by the cyst for its distribution and the quantity of cyst per organ/tissue varies from tissue to tissue and from region to region. At Nekemte shoulder muscle was largely infected whereas it was tongue at Bahr Dar and heart at Hawassa (Table 3).

Clinical signs:

In human:

Taenia saginata like all other human helminthes may provoke symptoms or may not reveal symptoms. The most frequently observed symptom of *T. saginata* infection is the discharge of proglottids. In addition to this, some infected individuals may show abdominal pain (35.6%), nausea (34.4%), weakness (24.8%), losses of weight (21.0%), increased appetite (17.0%), headache (15.5%), constipation (9.4%), dizziness (8.2%), diarrhea (5.9%), pruritis (4.5%) and excitation (3.4%) (Pawlowski and Schultz, 1972).

In cattle:

Under natural conditions, the presence of *cysticerci* in the muscle of cattle is not associated with clinical signs (Urquhart *et al.*, 1996). However, heavy infection in cattle may rarely result in fever and muscle stiffness (FAO, 2004).

Diagnosis:

In human:

Since there is no characteristics clinical picture of

Table 2 : Prevalence of *T. saginata* cyst in cattle and egg in humans in different regions of Ethiopia

Study area	Origin/breed of the animals	Municipal Abattoir	Diagnostic technique	Cyst prevalence in cattle	Adult/egg prevalence in human	References
North Gondar		Gondar	Meat inspection	4.9%		Dawit (2004)
Bahir Dar		Bahir Dar	Meat inspection	19.5%	63,217 stool 525 patient	Mulugeta (1997)
Nekemte		Nekemte	Meat inspection	21%		Ahmed (1990)
Godar		Gondar meat factory	Meat inspection	9.7%		Amsalu (1989)
Debre Zeit	Nazareth, Meki, Zeway, Wallita, Ambo, Gojam, Arsi	Debre zeit	Meat inspection	13.8%		Getachew (1990)
Hawassa	Arsi			29.03%		
	Borana			21%		
	Wolayta			25.03%	64.2%	
	local breed	Hawassa	Meat inspection	24.8%		Fufa (2006)
	cross breed			52.38%		
East Shoa			Meat inspection	17.5%	75.9%	Hailu (2005)
Debre Zeit		Elfora				
Modjo		Modjo				
Dukem		Luna				
Addis Ababa		Addis Ababa	ELISA on serum	7.5%		Nigatu (2004)
Addis Ababa		Addis Ababa	Meat inspection	3.11%	89.41%	Tembo (2001)

Table 3 : Prevalence of *C. bovis* in body tissues/organs in cattle of different regions

Prevalence and cyst number	Organ or tissue infected												Study area	References
	Tongue	Shoulder	Heart	Masseter	Neck	Thigh	Inter costal	Liver	Diaphragm	Lung	Kidney	Hump		
Prevalence in tissue%	12.12	30.98	22.1	9.91	4.95	8.98	0.72	2.08	5.02	3.07		0.03	Nekemet	Ahemed (1990)
Cyst No.	367	938	669	300	150	272	22	63	152	93		1		
Prevalence in tissue%	45.8	31.2	8.1	2.1		36	0.8	1.7	0.4				Bahir Dar	Mulugeta (1997)
Cyst No.	143	96	21	14		102	2	5	1					
Prevalence in tissue%	3.25	9	11.25	0.5	0.5				1.75	0.75		0.25	Hwassa	Fufa (2006)
Cyst No	46	113	151	120				16	29	11	14			
Prevalence in tissue%	27.5	24.7	29.3	138				3.1		1.5			East Shoa	Hailu (2005)
													D/Zeit	
													Mojo	
													Dukem	
Prevalence in tissue%	41.27	15.87	31.75	30.16		3.17		3.17	1.59				North Gondar	Dawit (2004)
Prevalence in tissue%	52.2	41.6	43.5	1.8	48.7			11	2.7	1.8			Gondar	Hamsalu (1989)
Prevalence in tissue%	28.5	12.7	10.3	5	2.8		0.7	1	0.7		0.7		Debre Zeit	Getachew (1990)

Tania saginata infection, diagnosis in man is based on laboratory findings. Examination of the faces and anal swabs will help to find out whether a tape worm infection exists. However, the exact species identification of *Taenia saginata* is made by examination of the scolex or proglottids that show typical species characteristics (Pawloski and Schultz, 1972; Smyth, 1994).

In cattle:

The diagnosis of bovine *cysticercosis* in many countries is mainly based on carcass inspection through incision of master, tongue, heart, triceps; intercostals muscles and the diaphragm (Urquhart *et al*., 1996). Many different serological tests have also been introduced in order to replace the current "knife and eye" method of diagnosis at the slaughter house, which detects only a small fraction of cattle infected with cysticerci (Greerts *et al*., 1992).

Differential diagnosis:

In man:

Man is the final host for three *Taenia* species such as *T. saginata, T. solium* and Asian /Taiwan/*Taenia* (*T.saginata asiatica*). All of which parasitize the human intestine. Differentiation of the *Taenia* species is important in order to relate infection to particular species and hence correctly determine the prevalence and incidence rates associated with each species (Smyth, 1994).

More precise differentiation methods have emerged with the development of molecular biological techniques and use of DNA probes. Accurate identification is now possible (Gottstein *et al.,* 1991). Identification of *Taenia* species using multiple PCR yielded differential products unique to *T .saginata*, *T. solium* and *T. saginata asciatica* with different molecular size of 817 base pair (bp), 269bp and 720bp, respectively (Yamasaki *et al.,* 2004).

In animal :

The metacestodes found in cattle should be differentiated from:

– *Cystcercus dromedaries* (*C. camel*); the larval form of taenia hyaenae. The identification of *C. camel* is by double rows of hooks on the lateral invaginated scolex and its length being twice as larger *C. bovis* measuring 12 to 18mm in length and pearly white in colour (Urquhart *et al.*, 1996)

– *Sarcocysitis bocitelis* (*Sarcocysitis hivusta*): which is a soft bradizoite cyst, very large and visible to the naked eye with whitish streaks running in the direction of the muscle fibres. The cyst ranges from 0.1mm to 5mm in length, localized in the esophagus, heart and indifferent muscular tissues (Urquhart *et al.*, 1996; Minozzo *et al*., 2002).

– Onchocercadki: measures 3mm to 6mm in diameter, from intoro muscular and subcuneous nodules that are firm to touch and reveal worms surrounded by pus when sectioned (CAT,1981)

Economic impact :

The cost implication can be broken down in to those involved in treating human *teaniasis* and cattle carcasses (cost of freezing, boiling) or condemnation, as well as the costs involved in the inspection procedures amount to millions of dollars (Mann, 1984). Annual losses due to treatment in USA were u.s.$ 100,000 (Robert, 1995), in south Africa u.s.$ 428 million (Fan, 1997).

In Ethiopia there is a wide usage of both traditional and modern taeniacidal drugs (Fesseha, 1995), which is an indication of the economic importance of the drugs in each house hold. The total dose of niclosamide and diclorphene production in two drug factories in this country between 1996 and 2000 was 31,814,833. The annual expenditure for the modern drug in three selected areas of Shoa (Akaki, Debre Zeit and Nazareth) was estimated to be 1,471,281 Ethiopia birr during the year 2000 (Tembo, 2001).

Treatment:

The most widely used systemic drugs for the treatment of *T. saginata* in Ethiopia are Neclo samid and paraziquantel. In addition, most people especially rural in habitants of this county use different types of traditional herbal drugs described in Table 5 as routine self-deworming (Feseha, 1995). For the treatment of the taeniosis are a number of taenicidal drugs available in the marks. However, the drugs of choice in treating taeniosis are Niclosamide (Niclosamide Yomesan). Adult dose rate of 200 mg is effective in damaging the worm to such an extent that a purge following therapy often procedures the scolex. (WHO, 1983).

Praziqantel 5 to 15 mg/kg is effective alternatively, a single 2 gram dose of niclosamide is given as 4 tablets (5000mg each that are chews one at a time and swallowed with a small amount of water (0.5 g is the dose of children 2 to 5 years old, 1 g for old children) both have cure rates of about 90%. Treatment can be considered successful when no proglottides are passed again within 4 months (CTA, 1981). In Ethiopia, the majority of the rural inhabitants use traditional herbal dugs in routine self-deworming as a taenichal herb, as has been topic for researches in Ethiopia (Fesha, 1995)

Table 4 : Some characteristics differentiating *Taenia saginata*, *Taenia saginata asiatica* and *Taenia solium*

Characteristics	*Taenia saginata*	*Taenia saginata asiatica*	*Taenia solium*
Intermediate host	Cattle, reindeer	Pig and wild boar, cattle, goat, monkey	Pig, wild boar
Development site	Muscle	Mainly liver	Skin muscle
Scolex			
Suckers	4	4	4
Rostellum	Absent	Present	Present
Hooks	Absent	Present	Present
Mature proglottids			
Ovary	2 lobes	2 lobes	3 lobes
Vaginal sphincter	Present	Present	Absent
Egg size	40 x 50 micrometer	33 x 28 micrometer	40 x 50 micrometer
Cysticercus size	10 mm by 6mm	1,320 micrometer x 3,219 micrometer	20 mm by 10 mm
Gravid proglottids uterine branches	23(14-32)	17(12-26)	8(7-11)
Passing of proglottids	Spontaneously, singly	Spontaneously, singly	Passively, in groups

Source: (Smyth, 1994)

Table 5 : Major taenicidal herbal drugs used in Ethiopia arranged in decreasing order of potency (Berhanu and Ermias, 1978, Desta, 1995 and Feseha, 1995)

Local name	Scientific name	Parts used
Bisana	*Croton macrosat chuys*	Bark
"	"	Seeds
Enkoko	*Embelio schimperi*	Fruits
Duba fire	*Cucurbita pepo*	Seeds
Tosigne	*Thymus serrucatus*	Dn #
Kechema	*Myrsine africana*	Dn#
Keleum	*Maesa lanceolta*	Dn#
Serdo	*Cynadon dactylon*	Dn#
Dendera	*Echinaps gignontean*	Dn#
Mettene	*Glinus lattoides*	Dn#
Gorrteb	*Plantago lanccleolota*	Dn#

Source: (Fufa, 2006)
Dn# = Do not known

Prevention and control strategies for Bovine cysticercosis:

In order to determine whether prevention or control programme should be introduced in countries affected by the disease, priority should be given to the surveillance of both *taeniasis* and *cysticercosis.* Prevention and control methods should be geared towards either to avoid or reduce the risk factors associated with the transmission of *taeniasis* and *cysticercosis.* Measures employed in the control of *taeniasis* and *cysticercosis* include diagnosis and treatment of *Taenia* carriers, education of the mass to use latrines, avoid the contamination of raw meat, serological testing of cattle and post – mortem inspection of carcasses for the presence of *Cysticercos bovis* (Cabaret *et al.*, 2002; Wanzala *et al.*, 2003). Generally, *T.saginata taeniasis* and *bovine cysticercosis* can be easily controlled by cooking meat at 56^0C or by freezing carcasses at -18^0C for 5days, or at -10^0C for 10 days (Urquhart *et al.,* 1996).

Immunity to taeniids is predominantly antibody mediated. It has been reported that highly effective vaccines have been developed against cysticercosis in sheep and cattle caused by *Taenia ovis*, *T. saginate*, and *T. solium* have been developed and they are highly effective both under laboratory and field conditions (Lightowlers, 2003).

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Address for correspondence :
YOSEF DENEKE
Division of Animal Biotechnology,
Genetic Engineering of Bioteriology,
Indian Veterinary Research Institute,
Izatnagar, BAREILLY (U.P.) INDIA
Email : yosefdeneke@yahoo.com

Authors' affiliations :
ABAY BESHAH
Department of Biomedical Sciences
Jimma College of Agriculture and Veterinary Medicine,
Jimma University, ETHIOPIA

D. RAMESH
Division of Animal Biochemistry,
Indian Veterinary Research Institute,
Izatnagar, BAREILLY (U.P.) INDIA

RAJIB DEB
Division of Animal Biotechnology,
Indian Veterinary Research Institute,
Izatnagar, BAREILLY (U.P.) INDIA

BLESSA SALIO
Division of Veterinary Public Health,
Indian Veterinary Research Institute,
Izatnagar, BAREILLY (U.P.) INDIA