

REVIEW

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Epidemiology and genetic diversity of *Taenia asiatica*: a systematic review

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Abstract

Taenia asiatica has made a remarkable journey through the scientific literature of the past 50 years, starting with the paradoxical observation of high prevalences of *T. saginata*-like tapeworms in non-beef consuming populations, to the full description of its mitochondrial genome. Experimental studies conducted in the 1980s and 1990s have made it clear that the life cycle of *T. asiatica* is comparable to that of *T. saginata*, except for pigs being the preferential intermediate host and liver the preferential location of the cysts. Whether or not *T. asiatica* can cause human cysticercosis, as is the case for *Taenia solium*, remains unclear. Given the specific conditions needed to complete its life cycle, in particular the consumption of raw or poorly cooked pig liver, the transmission of *T. asiatica* shows an important ethno-geographical association. So far, *T. asiatica* has been identified in Taiwan, South Korea, Indonesia, the Philippines, Thailand, south-central China, Vietnam, Japan and Nepal. Especially this last observation indicates that its distribution is not restricted to South-East-Asia, as was thought so far. Indeed, the molecular tools developed over the last 20 years have made it increasingly possible to differentiate *T. asiatica* from other taeniids. Such tools also indicated that *T. asiatica* is related more closely to *T. saginata* than to *T. solium*, feeding the debate on its taxonomic status as a separate species versus a subspecies of *T. saginata*. Furthermore, the genetic diversity within *T. asiatica* appears to be very minimal, indicating that this parasite may be on the verge of extinction. However, recent studies have identified potential hybrids between *T. asiatica* and *T. saginata*, reopening the debate on the genetic diversity of *T. asiatica* and its status as a separate species.

Keywords: Transmission, Geographical distribution, Genetic diversity, *Taenia asiatica*

Background: the journey of a new tapeworm

The journey of *Taenia asiatica*, as documented by scientific literature, started in Taiwan in the late 1960s. Several authors reported on the paradox of observing a high prevalence of *Taenia saginata*-like tapeworms in the native aboriginal population living in mountainous areas of Taiwan, while these populations restrained from beef consumption (reviewed by [1,2]), and meat inspection for bovine cysticercosis had been negative for some time [3]. Dr Ping-Chin Fan, a Taiwanese parasitologist, conducted various studies on this Taiwan *Taenia* in the late 1980s and early 1990s (reviewed by [1,4-6]).

Through observational and experimental studies, he and his team observed the morphology and researched the epidemiology of the Taiwan *Taenia*, which diverged from that of *T. saginata*. This led Fan to raise the possibility of the Taiwan *Taenia* being a new species [4].

Further experimental studies on *T. saginata*-like tapeworms from South Korea, Indonesia, Thailand, and the Philippines showed similar results, leading the authors to rename their Taiwan *Taenia* into Asian *Taenia*, denoting its more diverse geographical distribution [7-10].

In the early 1990s, a group of Korean parasitologists, led by Dr Keeseon Eom, performed various experimental infections using Korean specimens of the Asian *Taenia*. Their observation that the cysts of the Asian *Taenia* preferably develop in viscera of pigs, made them propose the name *Cysticercus viscerotropica* [11]. In 1993, they described the morphology of the Asian *Taenia*, and declared it as a new species, designated *Taenia asiatica* [12].

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With the advent of molecular techniques, it became clear that the Asian *Taenia* is genetically much more related to *T. saginata* than it is to *T. solium* [13-17]. This led the earlier protagonists to declare the Asian *Taenia* as a strain or subspecies of *T. saginata*, designated *Taenia saginata taiwanensis*, or, in line with its geographical distribution, *Taenia saginata asiatica* [18].

However, this purely molecular view was soon contrasted to an epidemiological and public health perspective. Galan-Puchades and Mas-Coma opened the debate, and made the case for *T. asiatica* as a separate species [19]. The debate continued, with different phylogenetic studies considering the Asian *Taenia* either as *T. saginata asiatica* [20,21] or *T. asiatica* [22-27], depending on the research group involved. The identification of *T. saginata/T. asiatica* hybrids in China and Thailand [28-30], may re-open this debate, as reproductive isolation has historically been an important criterion for considering *T. asiatica* and *T. saginata* as distinct biological entities [24]. Although the current literature seems to favor *T. asiatica* at the species level, it is clear that the taxonomy of the Asian *Taenia* remains as complex and controversial as it was two decades ago [31].

The remainder of this systematic review will provide an update of our current understanding of the transmission, risk factors, geographical distribution and genetic diversity of *T. asiatica*. For a review on the history, taxonomy and morphology of *T. asiatica*, we refer to Eom [32].

Search strategy

Evidence on the epidemiology and genetic diversity of *T. asiatica* was obtained through a systematic search of national and international peer-reviewed literature. Given the relatively limited number of papers on *T. asiatica*, a general search phrase was used consisting of the different synonyms of *T. asiatica*, i.e., *Taenia saginata asiatica*, Asian *Taenia* and Taiwan *Taenia*. Manuscript titles were retrieved through searching PubMed, Asia Journals OnLine (AsiaJOL), African Journals OnLine (AJOL), Latin American Journals OnLine (LAMJOL), WHO Global Health Library, and IndMED. The searches were performed on 20 September 2013.

In a second step, the retrieved titles were screened for eligibility by applying a set of inclusion/exclusion criteria to the titles and, if possible, to the abstracts and full texts. Papers were included if they provided authentic information on the transmission, geographic distribution and/or genetic diversity of *T. asiatica*. No restrictions were imposed on the publication year or on the language of the manuscript. Non-English manuscripts were translated through Google Translate (<http://translate.google.be/>).

In a third step, additional titles were retrieved by hand-searching the reference lists of the eligible documents initially retrieved. The same inclusion/exclusion

criteria as for the initial titles were applied to these new titles. The backward reference searches were repeated until no more new information could be retrieved.

In a fourth and final step, a narrative synthesis of each paper was made, serving as the basis for the current qualitative review of the epidemiology and genetic diversity of *T. asiatica*.

Figure 1 shows a flow diagram of the applied search strategy. In total, 162 relevant unique records could be identified, of which 15 had to be translated from Chinese (n = 14) or Korean (n = 1). Of the 162 unique records, 49 provided information on the transmission and risk factors of *T. asiatica*; 92 on its geographical distribution; and 42 on its genetic diversity. Several studies provided information on multiple aspects covered by this review.

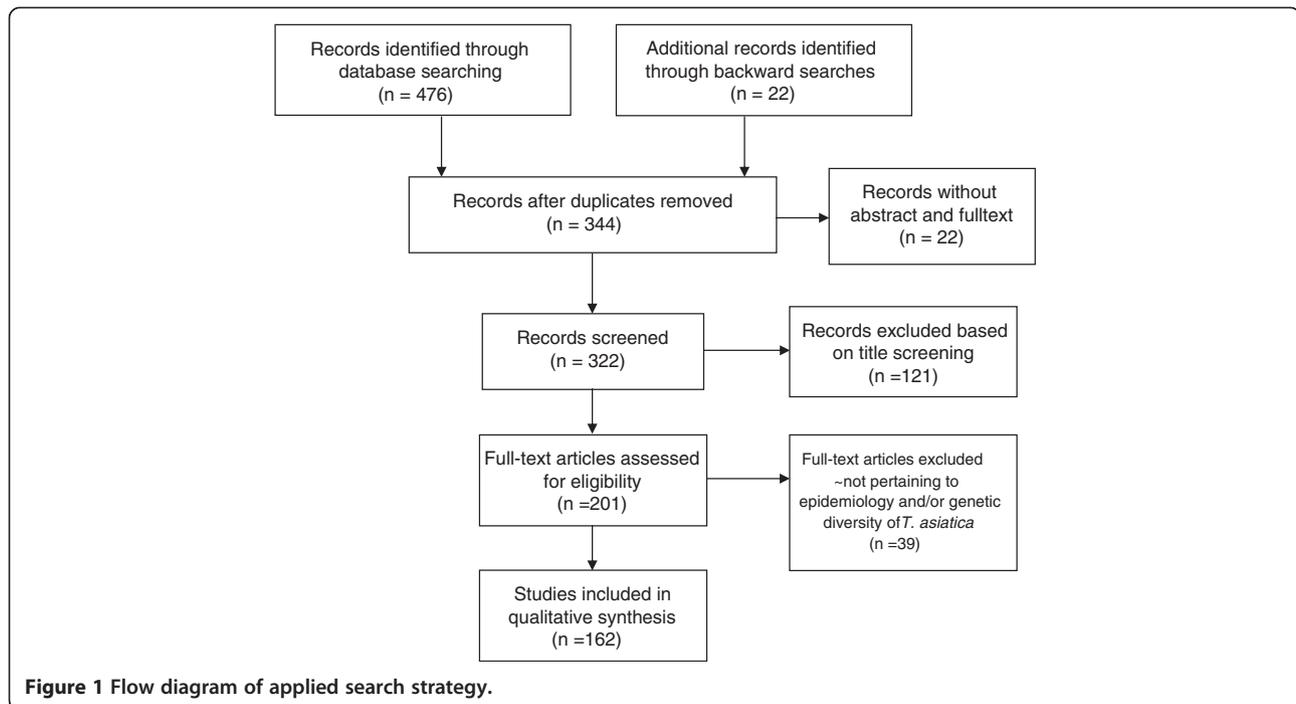
Review

Transmission and risk factors

The transmission and infectivity potential of *T. asiatica* has been extensively studied in the 1980s and 1990s through experimental studies [1,4,11,33]. Humans act as definite host, while pigs appear to act as natural intermediate hosts. However, other animals, such as cattle, goats and certain monkey species were also found to become infected [1,8-11,34]. Experimental infections with the eggs of Asian *Taenia* in cats, dogs, rabbits, rodents and baboons (*Papio hamadryas*), on the other hand, were not successful [1,35].

The life cycle of *T. asiatica* appears to be rather short compared to other human *Taenia* species. Approximately four weeks after ingestion of eggs, mature cysts become visible in the intermediate host [1,11]. *T. asiatica* cysts are mainly found in the liver of intermediate hosts, and more so in the parenchyma than on the surface. Other viscera, such as lungs, omentum, serosa and mesentery, may also harbor cysts [11,34,36]. These extrahepatic cysts are believed to have migrated from the liver surface [34]. Two to four months after ingestion of viable cysts by a human host, motile tapeworm segments may be excreted with the stool [33,37,38]. The number of proglottids released per day may vary from 0 to 35 [37,38]. Cases have been reported of carriers passing proglottids for more than 30 years [39,40], although it cannot be ascertained if this was due to the same tapeworm or due to reinfection.

Comparatively, the life cycle of *T. asiatica* closely follows that of *T. saginata*, with the exception of the natural intermediate host (pigs versus cattle), and the location in the intermediate host (liver versus muscle). A matter of debate remains whether *T. asiatica* may also infect humans as intermediate host, as is the case for the other human taeniid, *T. solium*. Experimental infections with *T. asiatica* eggs in primates remain inconclusive, as Fall et al. [35] were not able to infect



baboons, but other researchers did report successful infections in *Macaca cyclopis* and other unspecified monkey species [1,34]. Galan-Puchades & Fuentes [41,42] argue that, if *T. asiatica* were to cause cysticercosis, the location of the cysts would most likely be the liver, as in other intermediate hosts. Hepatic cysticercosis, if existing, would most probably not give rise to clinical symptoms, given the small size of the cysts. On the other hand, from a diagnostic point of view, cross-reactions in tests for the detection of other *Taenia* spp. would be very plausible, as cross-immunity and *in vitro* cross-reactions have been observed at various times [43-48].

The life cycle of *T. asiatica* indicates that the main transmission risk factors are raw pork viscera consumption (to infect the human host), and open defecation (to infect the intermediate host) [32]. As the consumption of (raw) pork viscera is generally less popular than that of (raw) pork meat, *T. asiatica* cannot efficiently spread within and between countries and acquire a true cosmopolitan status. However, social, cultural, and religious practices have preserved raw pork liver consumption in certain population groups, leading to high prevalences in these specific population groups, who often live in specific geographical areas. Indeed, observations from various countries demonstrate that transmission of *T. asiatica* is clearly ethnically and geographically associated. Table 1 gives an overview of the different ethno-geographical foci where *T. asiatica* has been studied. Remarkably, most of these foci were islands, which possibly facilitated the preservation of *T. asiatica* in these foci.

Earlier studies reported an increasing prevalence with age [1,50,52], while others reported a predominance in males [62]. However, these findings can probably be attributed to differential consumption patterns.

Geographical distribution

The current state of knowledge on the geographical distribution of *T. asiatica* is visualized in Figure 2. Most knowledge originates from the analysis of individual specimens and limited case series. Observational studies on *T. asiatica* remain largely lacking, mainly due to the difficulty in identifying tapeworm carriers and the subsequent collection and identification of tapeworm specimens. As a result, the true prevalence of *T. asiatica* taeniosis remains unknown.

To date, most observations originate from the countries where *T. asiatica* was initially studied, i.e., Taiwan and South Korea. In fact, high taeniosis prevalences have been reported from these countries since the beginning of the 20th century, although it is unclear to what extent these cases were due to *T. asiatica*. The first report from Taiwan is ascribed to Oi (1915; cited by [2]), while the first report from South Korea is ascribed to Matsumoto (1915; cited by [55]). Zarlenga *et al.* [13] were the first to confirm *T. asiatica* specimens at the molecular level in these countries, and several studies would follow (e.g., [15,29,57,66-69]). Interestingly, Jeon *et al.* [70] found that 51 out of 68 museum specimens, preserved since 1935–2005 and originating from different South Korean provinces, were in fact *T. asiatica*, whereas they were

Table 1 Ethno-geographical foci of *Taenia asiatica* transmission

Country	Region	People	Food habits	References
Taiwan	Mountainous areas of northern and eastern Taiwan	Bunun, Atayal	Habit of eating viscera, especially liver and blood, of fresh-killed animals, including wild boar, but excluding cattle	Fan 1988 [1]; Chung <i>et al.</i> 1990 [39]; Fan <i>et al.</i> 1990 [49]; Fan <i>et al.</i> 1992a [40]; Ooi <i>et al.</i> 2013 [2]
Taiwan	Orchid island, Lanyu Township, Taitung County, southeastern Taiwan	Tao (originally known as Yami)	Habit of eating viscera, especially liver and blood, of fresh-killed animals, including wild boar, but excluding cattle	Fan <i>et al.</i> 1992b [50]; Eom <i>et al.</i> 2009 [51]; Ooi <i>et al.</i> 2013 [2]
Indonesia	Ambarita village, Samosir Island, northern Sumatra	Batak (Christian)	" <i>Sang-sang</i> ": traditional dish with minced pork, viscera and blood; during preparation, uncooked meat and viscera are sometimes eaten	Fan <i>et al.</i> 1989 [7]; Fan <i>et al.</i> 1992c [52]; Suroso <i>et al.</i> 2006 [53]; Wandra <i>et al.</i> 2006 [54]
South Korea	Jeju Island (Jeju-do) and mainland South Korea	<i>Not minority people as seen in other countries</i>	Habit of eating liver and other viscera of pigs at " <i>Churyum</i> ", a common rural practice of slaughtering pigs at home during weddings, funerals and other special occasions	Fan <i>et al.</i> 1992b [50]; Eom <i>et al.</i> 1992 [11]; Eom & Rim 2001 [55]; Galan-Puchades & Fuentes 2001 [56]
China	Luzhai County, Guangxi Zhuang Autonomous Region, southern China	Zhuang	Habit of eating raw pork and pig liver, unseasoned or mixed with sour sauce and salted garlic; consumption of raw beef is uncommon	Eom <i>et al.</i> 2002 [57]; Eom <i>et al.</i> 2009 [51]
China	Yajiang (Nyagqu) County, Garzê Tibetan Autonomous Prefecture, Sichuan Province	Kham Tibetans	Habit of eating raw pork and beef	Li <i>et al.</i> 2006 [58]; Li <i>et al.</i> 2013 [59]
Thailand	Thong Pha Phum District, Kanchanaburi Province, west-central Thailand, Thai-Myanmar border	Karen	Habit of eating raw or under cooked beef, pork, or pig viscera and fresh blood	Anantaphruti <i>et al.</i> 2007 [60]; Anantaphruti <i>et al.</i> 2010 [61]; Anantaphruti 2013 [62]
Japan	Kanto region, central Honshu	<i>Not minority people as seen in other countries</i>	Serving of pig liver " <i>sashimi</i> " (raw slices) at " <i>yakitori</i> " or " <i>yakiniku</i> " restaurants	Eom <i>et al.</i> 2009 [51]; Michelet & Dauga 2012 [63]; Yamasaki 2013 [64]
Nepal	Morang & Sunsari district, southeastern Nepal	Dum	Frequent pork consumption; habit of eating undercooked meat and viscera of home raised <i>Hurra</i> piglets during certain religious and social festivities	Devleesschauwer <i>et al.</i> 2012 [65]

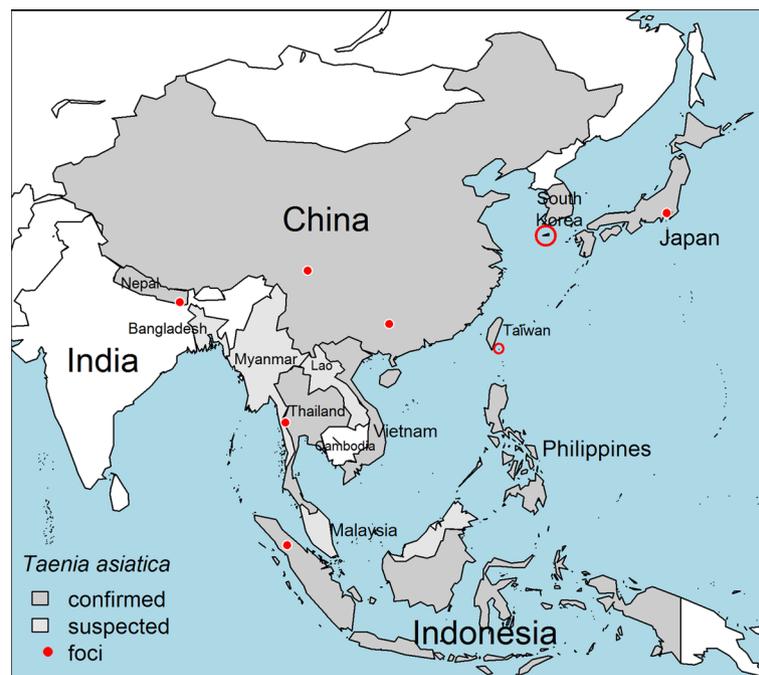


Figure 2 Country-level geographical distribution of *Taenia asiatica*. In China, *T. asiatica* has so far only been identified in the south-central provinces Yunnan, Guangxi, Guizhou and Sichuan. The ethno-geographical foci refer to, from west to east: Morang & Itahari district (Nepal); Thong Pha Phum district (Kanchanaburi province; Thailand); Samosir Island (North Sumatra, Indonesia); Yajiang (Nyagqu) County (Garzê Tibetan Autonomous Prefecture, Sichuan Province, China); Luzhai County (Guangxi Zhuang Autonomous Region, China); Orchid island (Lanyu Township, Taitung County, Taiwan); Jeju Island (Jeju-do, South Korea); and Kanto region (Honshu, Japan).

initially labeled as *T. saginata*. Current knowledge on taeniosis and *T. asiatica* in Taiwan and South Korea is reviewed by, respectively, [2], and [55,71].

Fan *et al.* identified in their original studies the presence of *T. asiatica* in Indonesia, Thailand and the Philippines based on morphological characteristics [7,9,10]. These findings were later confirmed by molecular characterization of individual specimens originating from these countries. *T. asiatica* has so far mainly been identified on Sumatra [29,72]. During 2003–2005, an epidemiological survey on 240 local people identified six *T. asiatica* tapeworm carriers (2.5%), using mitochondrial DNA analysis [53,54]. The presence of *T. asiatica* on Bali, on the other hand, remains controversial. No human *T. asiatica* taeniosis cases have been confirmed [54,73,74], but in 1998, 146 of 638 pigs (22.9%) at a slaughter-house in Bali were found to have cysts in the liver [31], and more recently, one cyst originating from Bali was identified as *T. asiatica* by multiplex Polymerase Chain Reaction (PCR) [67]. The current knowledge on taeniosis and cysticercosis in Indonesia has recently also been reviewed by Wandra *et al.* [75]. In Thailand, different *T. asiatica* cases, including one triple infection and one co-infection with *T. solium*, have been identified in the Myanmar-bordering Kanchanaburi province [29,60,61]. The current status of taeniasis in Thailand is further reviewed by Anantaphruti [62]. In the Philippines,

finally, different authors identified individual *T. asiatica* specimens [29,68,69], but no epidemiological studies appear to have been performed.

McManus & Bowles [15] report the first confirmation of *T. asiatica* from mainland China, but without providing details on the exact origin of the examined specimen. Further research identified *T. asiatica* cases in four south-central provinces of China, i.e., Yunnan, Guangxi, Guizhou and Sichuan. Zhang *et al.* [36] were the first to identify *T. asiatica* in Yunnan province, based on morphological characteristics of adults and cysts. To date, specimens have been molecularly confirmed from three Yunnan counties, i.e., Lanpin, Dali and Baoshan [20,76–78]. Eom *et al.* [57] identified six cases from the Zhuang minority in Guangxi province. Other specimens have been confirmed from Luzhai and Binyang county in Guangxi [68,79]. Furthermore, cases have been confirmed from Duyun and Congjiang county in Guizhou province [20,76,80,81], and from Yajiang and Danba county in Sichuan province [30,58,82].

More recently, it has become clear that the geographical distribution of *T. asiatica* is more widespread than originally thought, as cases have been confirmed in Vietnam, Japan and Nepal. In 2003, a case report was published on a patient from Ha Tay province, Vietnam, suffering from taeniosis [83]. DNA analysis revealed that

the causative species was *T. asiatica*. Somers et al. [84] confirmed 36 out of 65 human tapeworm cases in North Vietnam as *T. asiatica*. In 2010, the *Infectious Agents Surveillance Report* of the Japanese National Institute of Infectious Diseases dedicated a section to the detection of several *T. asiatica* cases in Kanto region (reviewed by [64,85]). These were the first and so far only case reports from Japan, although two museum samples had earlier been molecularly characterized as *T. asiatica* [51,72]. In Nepal, several *T. asiatica* tapeworm carriers were identified among the Dum, an indigenous community living along the Nepal-India border [65]. So far, this is the most western location where *T. asiatica* has been found.

For other South-Asian and South-East-Asian countries, i.e., Bangladesh, Myanmar, Malaysia, Lao PDR, and Cambodia, there is considerable uncertainty regarding the presence of *T. asiatica*. Amin et al. [86] reported a case of a symptomatic tapeworm carrier from rural Bangladesh. As the patient reportedly had not consumed undercooked beef, but possibly undercooked pork, the case was ascribed to *T. asiatica*. Nevertheless, as no morphological or molecular identification was performed, this diagnosis remains questionable. No cases have been confirmed from Myanmar, but Anantaphruti [62] identified *T. asiatica* in a Karen immigrant who recently moved from Myanmar to Kanchanaburi province, Thailand, and was passing segments in stool before migration. McManus & Bowles [15] identified one specimen from Malaysia as *T. asiatica*, and Conlan et al. [74] mentioned the finding of *T. asiatica* in one of 590 pig livers sampled in Lao PDR, but further evidence for these countries remains lacking. In Cambodia, finally, the only identification study conducted so far could not identify *T. asiatica* among 21 tapeworm carriers [87].

Genetic diversity

Since the 1990s, various researchers have developed and applied molecular methods for distinguishing *T. asiatica* from other *Taenia* spp., and, subsequently, for studying the relationship of *T. asiatica* with other *Taenia* spp., in particular *T. saginata*, and for examining the genetic variability within *T. asiatica*. The availability of the complete mitochondrial genome of *T. asiatica* [27], and the access to published sequences through GenBank, has greatly contributed to the understanding of the genetic diversity of *T. asiatica*.

Molecular tools for *Taenia asiatica* identification

Different tools have been developed to differentiate *T. asiatica* from other *Taenia* species based on the genetic information available in proglottids, cysts and eggs. Table 2 gives an overview of the different molecular tools and markers developed so far. To date, the most common method for molecular identification of *Taenia*

tapeworms has been PCR coupled with nucleotide sequencing of the amplified PCR product. Different mitochondrial (e.g., cytochrome c oxidase subunit I [*COX-1*], cytochrome b [*COB*], NADH dehydrogenase subunit I [*NAD-1*], and 12 s ribosomal RNA) and nuclear (e.g., ribosomal RNA (i.e., 18S rRNA, 5.8S rRNA, internal transcribed spacer 2 [*ITS-2*], and 28S rRNA), elongation factor-1-alpha [*ef1*], and ezrin/radixin/moesin-like protein [*elp*]) genes have been used as markers in such analyses (Table 2). By aligning the obtained sequences with published ones, the identity of the specimens can be determined [21]. Other assays for the differential diagnosis of *Taenia* tapeworms include PCR [13,69,93], PCR coupled with Restriction Fragment Length Polymorphism analysis (PCR-RFLP; [13,15,84,93,94]), Random Amplified Polymorphic DNA analysis (RAPD; [20,57]), Base Excision Sequence Scanning Thymine-base analysis (BESS T-base; [66]), multiplex PCR [67,68,93], and Loop-Mediated Isothermal Amplification (LAMP; [28]).

Genetic relatedness of *Taenia asiatica*, *Taenia saginata* and *Taenia solium*

With the availability of the mitochondrial genome of the different human taeniids, their genetic relatedness has become clearer [25-27]. The mitochondrial genomes of *T. asiatica*, *T. saginata* and *T. solium* measure 13,703 bp, 13,670 bp, and 13,709 bp, respectively. They consist of 36 genes, i.e., 12 protein-coding genes, 22 tRNA genes, and 2 rRNA genes. There is an overall nucleotide difference of 4.6% between *T. asiatica* and *T. saginata*, and of 11% between *T. saginata* and *T. solium*. The nucleotide difference in the *COX-1* gene is 4.6% for *T. asiatica*/*T. saginata*, 12.3% for *T. saginata*/*T. solium*, and 12.0% for *T. asiatica*/*T. solium*. These results thus indicate that *T. asiatica* is more closely related to *T. saginata* than it is to *T. solium*.

Similar conclusions are obtained from sequence comparisons of nuclear genes. The 18 kDa/HP6 protein-encoding gene shows a similarity of 95.5% between *T. asiatica* and *T. saginata*, but a similarity of merely 61.5% between *T. saginata* and *T. solium* [91]. The 18S rRNA genes of *T. asiatica* and *T. saginata* appeared to be 99.2% identical [78].

Studies on the diversification times of the different *Taenia* species indicate that *T. asiatica* fully diverged from a common *T. saginata/asiatica* ancestor in the late Pleistocene, ~40,000 years ago. This diversification might have co-occurred with the arrival of *Homo sapiens* in Asia, and the introduction of new wild boar populations and/or new breeding and husbandry practices in this region [63,95]. Again, these results indicate a closer relatedness of *T. asiatica* with *T. saginata* than with *T. solium*.

Genetic variability within *Taenia asiatica*

Several studies have indicated little or no genetic variation within *T. asiatica*. The nucleotide diversity found

Table 2 Molecular tools for *T. asiatica* identification

Method marker	Restriction enzymes	References
<i>Nucleotide sequencing</i>		
mt-COX-1	–	McManus & Bowles 1994 [15]; Bowles & McManus 1994 [16]; McManus 1997 [17]; Gasser <i>et al.</i> 1999 [88]; Wang & Bao 2003 [76]; Yamasaki <i>et al.</i> 2005 [89]; Jeon <i>et al.</i> 2008 [70]; Okamoto <i>et al.</i> 2010 [29]; Jeon <i>et al.</i> 2011a [87]; Jeon <i>et al.</i> 2011b [72]; Yang <i>et al.</i> 2012 [79]
28S rDNA	–	McManus & Bowles 1994 [15]; Bowles & McManus 1994 [16]; McManus 1997 [17]
mt-NAD-1	–	Gasser <i>et al.</i> 1999 [88]
5.8S rDNA/ITS-2/28S rDNA	–	Eom <i>et al.</i> 2002 [57]; Jeon <i>et al.</i> 2008 [70]
mt-COB	–	Le <i>et al.</i> 2003 [90]; Yamasaki <i>et al.</i> 2005 [89]
HDP2	–	Gonzalez <i>et al.</i> 2010 [69]
<i>ef1</i>	–	Okamoto <i>et al.</i> 2010 [29]
<i>elp</i>	–	Okamoto <i>et al.</i> 2010 [29]
18 kDa/HP6	–	Gonzalez <i>et al.</i> 2011 [91]
mt-12S rDNA	–	Liu & Yang 2011 [77]
18S rDNA	–	Yan <i>et al.</i> 2013 [78]
<i>PCR</i>		
Ribosomal DNA	–	Zarlenga <i>et al.</i> 1991 [13]; Zarlenga 1991 [14]; Morakote <i>et al.</i> 2000 [92]
HDP2	–	Gonzalez <i>et al.</i> 2004 [93]
HDP2	–	Gonzalez <i>et al.</i> 2010 [69]
<i>PCR-RFLP</i>		
Ribosomal DNA	<i>Bam</i> HI	Zarlenga <i>et al.</i> 1991 [13]; Zarlenga 1991 [14]
mt-COX-1	<i>Msp</i> I	McManus & Bowles 1994 [15]; Bowles & McManus 1994 [16]; McManus 1997 [17]
rDNA ITS-1	<i>Msp</i> I, <i>Cfo</i> I, <i>Rsa</i> I	McManus & Bowles 1994 [15]; Bowles & McManus 1994 [16]; McManus 1997 [17]
Mitochondrial DNA	<i>Eco</i> RI, <i>Hind</i> III, <i>Bgl</i> II, <i>Xba</i> I, <i>Bam</i> HI, <i>Pvu</i> II, <i>Ava</i> I, <i>Hae</i> III, <i>Hind</i> II, <i>Eco</i> RV, <i>Hpa</i> II	Zarlenga & George 1995 [94]
HDP2	<i>Bcl</i> I or <i>Bgl</i> I	Gonzalez <i>et al.</i> 2004 [93]
12S rDNA	<i>Dde</i> I, <i>Hin</i> fI	Somers <i>et al.</i> 2007 [84]; Devleesschauwer <i>et al.</i> 2012 [65]
<i>RAPD analysis</i>		
3 random primers: OPA-03, OPA-08, OPA-20	–	Eom <i>et al.</i> 2002 [57]
13 random primers: OPA-03, OPA-08, OPA-20, L-01, L-02, L-05, L-06, L-08, L-09, L-12, L-15, L-18, L-19	–	Zhang <i>et al.</i> 2006 [20]
<i>BESS T-base analysis</i>		
mt-COX-1	–	Yamasaki <i>et al.</i> 2002 [66]
mt-COB	–	Yamasaki <i>et al.</i> 2002 [66]
<i>Multiplex PCR</i>		
mt-COX-1	–	Yamasaki <i>et al.</i> 2004 [67]
HDP2	–	Gonzalez <i>et al.</i> 2004 [93]
mt-Valine tRNA, mt-NAD-2, mt-NAD-1	–	Jeon <i>et al.</i> 2009 [68]; Jeon <i>et al.</i> 2011a [87]
<i>LAMP</i>		
mt-COX-1	–	Nkouawa <i>et al.</i> 2009 [28]; Nkouawa <i>et al.</i> 2012 [82]
cathepsin L-like cysteine peptidase [<i>clp</i>]	<i>Hin</i> fI	Nkouawa <i>et al.</i> 2009 [28]

in the mitochondrial *COX-1* gene of specimens from different regions ranged between 0 and 0.2% [16,26,67]. *T. saginata*, on the other hand, appears to show an important genetic polymorphism, with mitochondrial *COX-1* gene diversity ranging from 0.2 to 0.8% [26]. In an analysis of *COX-1* gene sequences of 30 *T. asiatica* specimens from seven countries, only two haplotypes could be identified, with the major haplotype comprising 29 out of 30 samples. *T. saginata*, on the other hand, was found to be much more polymorphic, with eight haplotypes and a ten times higher haplotype diversity (0.70 versus 0.07; [96,97]).

The limited amount of genetic variation within *T. asiatica* has also been observed for other genes. Indeed, sequence divergences of 0.1 to 2.1% were found in *T. asiatica* HDP2 fragments [69], while no divergence was found in the 18 kDa gene sequence [91].

In contrast with this low genetic diversity is the recent identification of potential hybrids between *T. asiatica* and *T. saginata*. Nkouawa et al. [28] identified two specimens, one from China and one from Thailand, that were identified as *T. saginata* based on the mitochondrial *COX-1* gene, but as *T. asiatica* based on the nuclear cathepsin L-like cysteine peptidase gene. It is therefore possible that these specimens were hybrid parasites with *T. saginata* mitochondrial DNA and *T. asiatica* nuclear DNA. Likewise, a discrepancy between the mitochondrial and nuclear DNA was found in two tapeworm specimens from Thailand [29]. While the specimens had sequences typical of the *T. saginata* *COX-1* gene, both were homozygous for *T. asiatica* typical alleles of the *elp* gene, and one was additionally homozygous for *T. asiatica* typical alleles of the *ef1* gene. A similar mitochondrial/nuclear discordance was observed in China, where one tapeworm with *T. asiatica* mitochondrial DNA was heterozygous for *T. saginata* typical alleles of the *elp* and *ef1* genes, while a second tapeworm, with *T. saginata* mitochondrial DNA, was heterozygous for *T. asiatica* typical alleles of the *ef1* gene [30].

Conclusions

In the past 50 years, *T. asiatica* has made a remarkable journey through the scientific literature, from epidemiological paradox to mitochondrial genome. The studies performed in the 1980s and 1990s have provided us with the basic understanding of its transmission and risk factors. Nevertheless, several critical questions remain unanswered. As studies on the *T. asiatica* transmission risk factors so far mainly focused on pork liver consumption, other important factors, such as pig husbandry and slaughter practices, remain unaddressed. Furthermore, the potential of *T. asiatica* to cause human cysticercosis needs to be clarified. If this would be the case, then *T. asiatica* could be an important cause of cross reactions

in serological assays, but, more importantly, of human illness, making this indeed the most neglected of all neglected tropical diseases [98]. Finally, more needs to be done to understand if and how *T. asiatica* can protect against *T. solium*, through density-dependent and/or immune-mediated processes [99]. Indeed, as humans may become infected with three different *Taenia* species, i.e., *T. asiatica*, *T. saginata* and *T. solium*, the presence of one tapeworm species might physically reduce the likelihood of a second species to develop. Likewise, as pigs can become infected with three *Taenia* species, i.e., *T. asiatica*, *T. solium* and *T. hydatigena*, cross-immunity may interfere with the establishment of cysts of other species. If such interspecific competition could be proven to play an important role in moderating *T. solium* transmission, *T. asiatica* would indeed be a parasite to treasure and to save from extinction [100].

With increasing access to molecular tools, the geographical distribution of *T. asiatica* has been shown to be much more widespread than initially thought. Indeed, the recent confirmation of *T. asiatica* in Nepal shows that its distribution is not restricted to South-East-Asia, as was thought so far. Further studies are warranted to identify the true spread of this parasite.

Over the last 20 years, genetic studies have provided important insights into the past, present and future of *T. asiatica*. The limited genetic diversity of *T. asiatica* specimens may be a signal that *T. asiatica* is an endangered species [96,97]. Indeed, as its transmission is rooted in often ancient sociocultural habits, the gradual disappearance of these habits along with global development and globalization, may lead to the spontaneous extinction of *T. asiatica*. Such a scenario is certainly not unrealistic, as it happened for *T. solium* in Europe [101] and observations from Indonesia and South Korea indicate that with changing habits, taeniosis prevalences decrease [102]. Finally, the significance of putative hybrids needs to be clarified, and more studies are needed to ascertain whether or not hybridization between *T. asiatica* and other species still occurs today.

Abbreviations

BESS T-base: Base excision sequence scanning thymine-base; COX-1: Cytochrome c oxidase subunit I; COB: Cytochrome b; *ef1*: Elongation factor-1-alpha; *elp*: ezrin/radixin/moesin-like protein; ITS-2: Internal transcribed spacer 2; LAMP: Loop-mediated isothermal amplification; NAD-1: NADH dehydrogenase subunit I; PCR: Polymerase chain reaction; RAPD: Random amplified polymorphic DNA; RFLP: Restriction fragment length polymorphism; rRNA: ribosomal ribonucleic acid.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

AA and BD performed the systematic literature review. AA and BD conceived and wrote the review with assistance from BV, NP, SG, NS, and PD. All authors read and approved the final manuscript.

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