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Review

# On the origin of *Anguillicoloides crassus*, the invasive nematode of anguillid eels

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## Abstract

The nematode *Anguillicoloides crassus* is one of the many threats hanging over anguillid eels, now known to infect six *Anguilla* species worldwide. It was first described in Japan, in 1974, and is commonly thought to natively stem from East Asia. Here our primary objective was to critically evaluate this long-held statement. We first retraced the factual history of this global invader, to later investigate the pros and cons for an East Asian origin. After exploring the alternative scenarios for the joint origin of the two anguillicolid parasites occurring in this area, we concluded that the geographic zone covering the natural range of the local eel *A. japonica* is still the most probable origin (in the absence of another identified candidate host and area). However, we cannot exclude that *A. crassus* may have been previously introduced along with exotic eel species, at some early stages of aquaculture in Japan. We call for caution when dealing with the native origin of this and other parasitic invaders *in provenance* of East Asia, a region to be regarded as a major crossroads for fish and parasites of the world. We finally identified the need for a possible resolution of the question, which includes a deeper sampling effort in the Indo-Pacific zone and the further development of molecular phylogeographic studies of all five anguillicolid species and their hosts.

**Key words:** *Anguilla; Anguillicola;* fish parasite; nativeness; aquaculture; world trade

## Introduction

*Anguillicoloides crassus* (Kuwahara, Niimi and Itagaki, 1974) is a histotrophic nematode, exclusively reproducing in the swimbladder of anguillid eels, *Anguilla* spp. In less than three decades, driven by intercontinental eel trade, it has spread over four continents, infecting six of the 20 eel species/subspecies described world-wide (Moravec 2006; Sasal et al. 2008; Froese and Pauly 2011). Its impact on the host population(s) as a whole is unclear (see Kirk 2003; Székely et al. 2009), however, there is increasing evidence that the induced swim-bladder degradation may compromise the eel's spawning migration and reproduction (Palstra et al. 2007; Sjöberg et al. 2009). Recently, it has been listed as one of the 100 "worst" exotic species that threaten European species and ecosystems (DAISIE 2008). As such, *A. crassus* meets the most stringent criteria of invasiveness (Davis and Thompson 2000; Colautti and MacIsaac 2004; ISSG 2011): i.e., its expansion was human-driven, it is critically harmful in its new environment, it is abundant and well-established far beyond its native home range. But what exactly do we know about its native distribution?

Nearly half of the articles published on *A. crassus* (or anguillicolosis, its disease) refers at some stages to its East Asian origin (according to conservative estimates, mentioned in about 200 references), and we, beside others, were among the ones who popularized this idea (e.g.,

Moravec and Konecny 1994; Lefebvre et al. 2002). What then is the scientific evidence justifying that statement? Here we retrace the factual history of *A. crassus*, critically evaluate both the pros and cons for an East Asian origin, explore alternative scenarios, and suggest possible lines of further investigations.

## Of parasites and men

The first unambiguous trace of *Anguillicoloides crassus* in the scientific literature dates back to 1974, in Japan, with its formal description by Kuwahara, Niimi and Itagaki, as *Anguillicola crassa* [1]. However, shortly thereafter, Egusa reported (*a posteriori* in Hirose et al. 1976) that he may have observed *A. crassus* much earlier in Japan (e.g., in Egusa et al. 1969), but at that time, having had mistaken it for the formerly described *Anguillicola globiceps* Yamaguti, 1935. Similarly, according to Nagasawa et al. (1994), the nematodes illustrated by Matsui (1972), and erroneously referred to as *Anguillicola japonica*, may actually correspond to *A. crassus* specimens. Moravec and Taraschewski (1988) also considered that specimens of *A. crassus* were present in the material sampled in China (which they had received from the collection of P. S. Wang and H. S. Wu), and noted that some of the drawings by Wu (1956, 1984) actually more closely resembled *A. crassus* than *A. globiceps* (see Moravec and Taraschewski 1988; Moravec 2006). Furthermore, Yamaguti (1935) illustrated its original description of *A. globiceps* with a drawing of a larval stage (L4), which Nagasawa et al. (1994) considered to possibly be *A. crassus*.

In Europe also, first observations of the introduced anguillicolids (in the 1980s) lead to taxonomic difficulties in correctly identifying the sampled specimens (e.g., Paggi et al. 1982; Peters and Hartmann 1986), and it was pointed out that the original descriptions by Yamaguti (1935) and Kuwahara et al. (1974) were either incomplete or inadequate (Køie 1988). Actually, the first comprehensive and most inclusive taxonomic reference (based on the total set of then available material) was established by Moravec and Taraschewski (1988), with the description of two new species in the family Anguillicolidae. According to the current taxonomic standard (Moravec 2006), anguillicolids are divided into two genera comprising a total of five species, namely, *Anguillicola globiceps* Yamaguti, 1935, *Anguillicoloides australiensis* (Johnston et Mawson, 1940), *A. crassus* (Kuwahara et al., 1974), *A. novaezelandiae* (Moravec et Taraschewski, 1988), and *A. papernai* (Moravec et Taraschewski, 1988).

## The story of a worldwide expansion

Of all anguillicolids, *A. crassus* is, by far, the most invasive species, while the other four are mostly confined to only one eel host or continent (Moravec 2006; Taraschewski 2006; Sasal et al. 2008). It was first recorded out of Asia in 1982, from wild European eel specimens, in Northern Germany (Weser-Ems region, Neumann 1985). It then spread extremely rapidly throughout the continent, and today it almost entirely matches the geographical range of its new host, spanning from North Africa to Scandinavia to the sole exception of Iceland (Kristmundsson and Helgason 2007; Jakob et al. 2009; ICES 2011; A. Kristmundsson 2012, pers. comm. to FL). In the 1990s, *A. crassus* also invaded the American eel *A. rostrata*, starting in the USA (Fries et al. 1996) and now spreading North to South, from Canada to Mexico (Moravec 2006; G. Salgado-Maldonado 2010, pers. comm. to FL). While there is ample evidence of natural dissemination of the nematode, the recent global expansion of *A. crassus* was clearly driven by long-range jumps along existing trading routes of live eels (Belpaire et al. 1989; Koops and Hartmann 1989; Kennedy and Fitch 1990; Fries et al. 1996).

Recently, Wielgoss et al. investigated the genetic structure and phylogeography of worldwide populations of *A. crassus* and provided strong evidence that European nematodes derived from a Taiwanese source population from a single invasion event (Wielgoss et al. 2007, 2008; Laetsch et al. 2012). The finding well matches import data that documented the introduction of live eels in a single import from Taiwan into Northern Europe, in 1980, just prior to the time of the first observation of the nematode in that region (Neumann 1985; Koops and Hartmann 1989). For the American eel and continent, the population source of *A. crassus* most likely came from Japan rather than from a primary or secondary colonization from Taiwan or Europe (Wielgoss et al. 2008; Laetsch et al. 2012).

Since East Asian countries have long been the centre of intercontinental eel trade (with massive import and export of live eels for restocking,

consumption or aquaculture purposes, see for example Egusa 1979; FAO 2009), there seems to be little doubt that the primary infection source for the whole of Europe, North Africa and North America is of Asian origin. However, it remains unclear whether or not *A. crassus* as a species is originally native to East Asia.

**Pros and cons for an East Asian origin**

Arguments put forward to support a native East Asian origin for *A. crassus* revolve around the following ideas:

1 - first description in the Japanese eel;
2 - first description in Japan;
3 - wild occurrence in East Asian countries;
4 - moderate pathogenicity in the Japanese eel;
5 - high genetic structure in East Asian countries.

However, these arguments are circumstantial evidences which do not constitute definite proofs and have to be understood in a broader evolutionary and socio-economic context:

1 - While some specimens used in the original description were indeed collected from Japanese eels, the official 'type host' of *A. crassus* in fact is the European eel (see Kuwahara et al. 1974), which has been imported into Japan for aquaculture evaluation.

2 - The country of first description is of no help regarding the native origin of a given species, and more caution is warranted particularly in the case of invasive species. The taxonomic literature abounds in examples of first description outside the native range of the species. For instance, the brown rat, *Rattus norvegicus* (Berkenhout, 1769), was first described in England (from specimens thought to come with Norwegian ships), but natively originates from Asia (Wilson and Reeder 2005).

3 - In East Asia, *A. crassus* was frequently recorded in natural populations of *A. japonica*, outside any aquaculture grounds (Nagasawa et al. 1994; Moravec 2006; Han et al. 2009; also see Figure 1 and Appendix 2). But 'natural' does not mean 'native'. Occasionally, *A. crassus* can be been found, in natural waters of East Asia, in the introduced European eel (Egusa 1979; Nagasawa et al. 1994).

4 - Epidemiological data in wild Japanese eels indicate that *A. crassus* prevalence values hardly reach 50% and mean intensities rarely exceed 10 worms per infected eel (review in Nagasawa et al. 1994), which indeed resembles the situation which has been described for other anguillicolid species in their supposedly indigenous eel hosts (e.g., *A. australiensis* in the eel *A. reinhardtii*, see Kennedy 1994; *A. novaezelandiae* in the eel *A. australis*, see Lefebvre et al. 2004; *A. papernai* in the eel *A. mossambica*, see Taraschewski et al. 2005). Also, physiological studies demonstrated a lower susceptibility, a higher humoral immunity, a lower stress response, and overall moderate pathologies in the Japanese eel (in comparison to the European eel) when infected by *A. crassus* (Knopf and Mahnke 2004; Nielsen and Esteve-Gassent 2006). However, these are comparative data, and the lower virulence currently documented in the Japanese eel may also be explained by a slightly longer exposure to *A. crassus* (in the 1960-70s, and possibly earlier, *versus* in the 1980s), and/or previous experience with other anguillicolid nematodes (e.g., *A. globiceps*).

5- One of the best supports for an East Asian origin derives from molecular studies and from inferences based on the phylogeographic principle, i.e., highest genetic diversity expected in the native area (Wielgoss et al. 2008). Genetic markers indeed indicate that *A. crassus* is more structured and differentiated in East Asian countries (Japan and Taiwan) than in any European, North African or North American countries (Wielgoss et al. 2008; Laetsch et al. 2012). Moreover, within East Asia, a more ancient origin for Japanese populations is supported (Wielgoss et al. 2008; Laetsch et al. 2012), which well matches the known epidemiological history (i.e., first records ever in Japan). However, one cannot fully exclude that the Japanese *A. crassus* populations had been originally founded by several independent invasion waves from unknown sources (as a result for instance of repeated imports of other Indo-Pacific eels for aquaculture evaluation in Japan) which after mixing could have led to the observed -inflated- genetic diversity.

In conclusion, we can trace back the history of *A. crassus* to Taiwan and Japan, but there is not enough hard data yet to definitely conclude a native East Asian origin. This commonly held statement may come from misleading or circumstantial arguments (as exposed above), and from a mix-up of ideas between the population source of an introduction, and the native origin of the concerned species. The initial confusion was no doubt exacerbated by the difficulties for European authors to access and appreciate the very first works on anguilli-

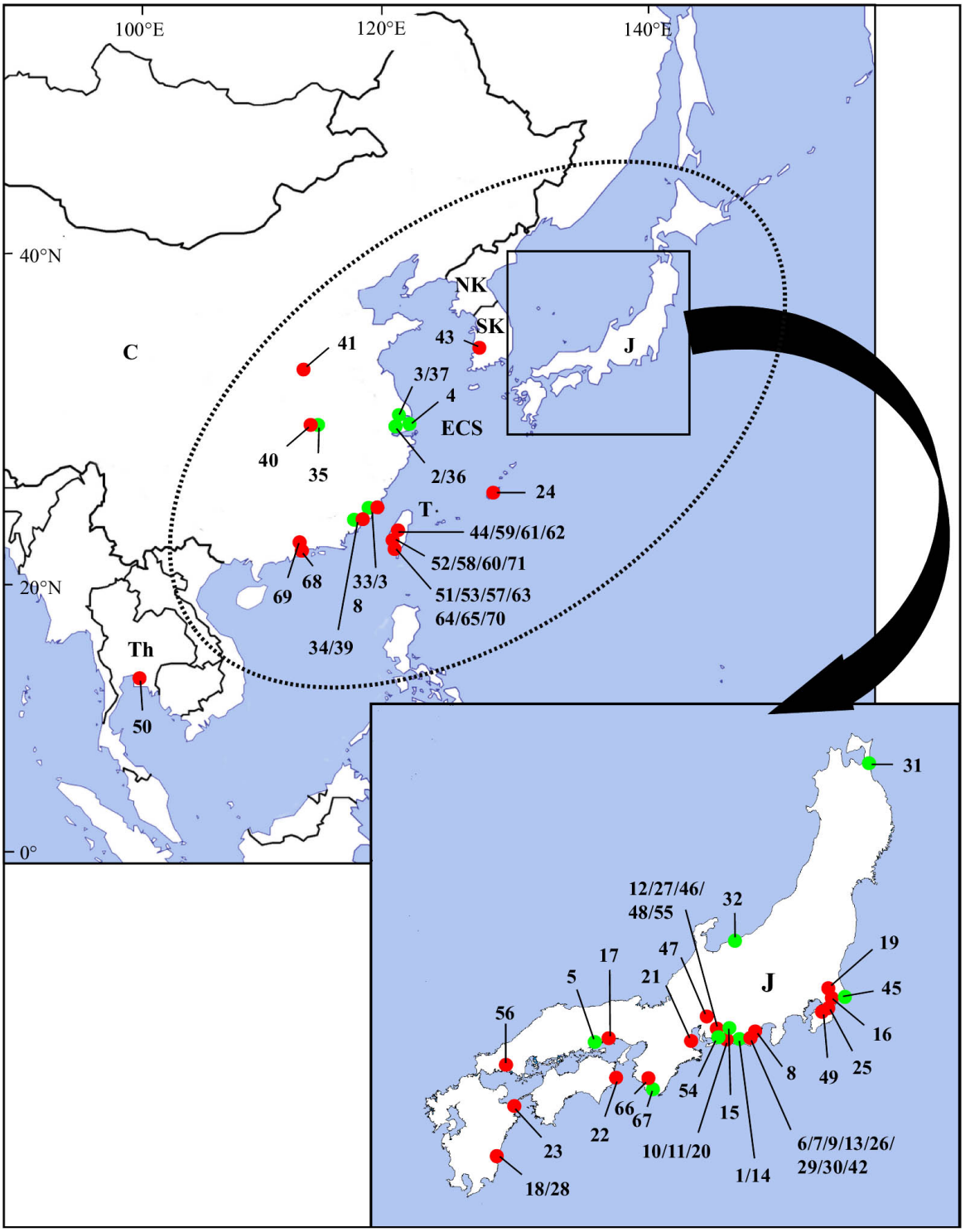


**Figure 1.** Map of the northwestern part of the Pacific Ocean showing the localities where *A. crassus* (red spots) and *A. globiceps* (green spots) have been recorded so far (see Appendix 2 for details). The dotted line indicates the natural range of the Japanese eel host *A. japonica* (from Froese and Pauly 2011). The East Asia zone (as referred to in the text) covers all the neighbouring countries of the East China Sea (ECS), i.e., China (C), Taiwan (T), Japan (J), North Korea (NK) and South Korea (SK).

colid nematodes, mostly written in Japanese, Chinese, Korean, and/or published in Asian based journals [2]. Then, the intuitive idea of the nematode's East Asian origin (because imported from there) had such an appeal that it instantly swept to fixation in the scientific literature, basically unchallenged until today (with a dynamic of spread similar to "memes", cultural analogues to selfish genes according to the working concept originally coined by Dawkins, 1976).

## Additional considerations, before going any further

Figure 1 and Appendix 2 present the known historical records of both *A. crassus* and *A. globiceps* in East Asia. From this, we can outline the following five trends:

1 - Data on abundance and geographic distribution of the two anguillicolid species in East Asia are very patchy and only based on sporadic sampling efforts, as no systematic survey on fish parasites has been done in these countries since Yamaguti's time (i.e., for around 80 years). On the several eel species naturally occurring in this area (i.e., *A. japonica*, *A. marmorata*, *A. bicolor*, *A. breviceps* and *A. nigricans*; see Froese and Pauly 2011), epidemiological data are almost inexistent for all but *A. japonica* (Kennedy 2007; see Nagasawa et al. 2007 for an extensive review in Japan).

2 - Both *A. globiceps* and *A. crassus* were first observed and formally described in the Shizuoka Prefecture (see Yamaguti 1935; Kuwahara et al. 1974), a region known to be the most eel productive of all Japan until the 1980s, with nearly 70% of the market at that time (Egusa 1979).

3 - In East Asia, the two anguillicolid nematodes are parasitic in wild and cultured Japanese eels *A. japonica* (exclusive host for *A. globiceps*), but they have rarely been found co-occurring together in the same eel swimbladder (Moravec 2006; H. Taraschewski pers. comm.), to the possible exception of a few old records (e.g., in the Chinese province of Fujian, by Wang and Zhao 1980; also see Moravec and Taraschewski 1988, and Nagasawa et al. 1994).

4 - There is great overlap in the known distribution of the two species (without any temporal scale). However, outside Japan, *A. crassus* tends to show a southernmost distribution, with records in the inter-tropical zone (± 23°N), e.g., in Thailand, southeast mainland China and Taiwan (there observed in the native Japanese eel, but also in the imported eels *A. anguilla* and *A. rostrata*). On the contrary, *A. globiceps* is only known from mainland China and Japan, and has never been recorded south of 25°N.

5 - The population of *A. globiceps* appears to be contracting in East Asia as of late. At the time of its original description, *A. globiceps* was reported to be common in Japan (see Yamaguti 1935). Later, Wu (1956) reported prevalence of 61%, and Wang and Zhao (1980) of 39%, both in China (in Moravec 2006). Nowadays, *A. globiceps* seems to have almost disappeared from East Asia (Egusa 1992; Hirose et al. 1998; Moravec 2006; Wielgoss et al. 2007; H. Hirose, H. Taraschewski and P. Nie pers. comm. to FM).

Also, it is worth recalling here that eels have long been of high economic value on the Asian markets, and that Japan always constituted the most important eel market in the world (Ringuet et al. 2002; FAO 2009). In 1979, Egusa (p 51) wrote "commercial eel culture in Japan started about 80 years ago and grew steadily" (according to other sources, it started even earlier; e.g., in the 1860s for Ringuet et al. 2002; in the 1820s for Willoughby 1974). And because of surging prices and short supply in elvers of the local Japanese eel, millions of exotic young eels were shipped to Japan for aquaculture purposes (Egusa 1979). Altogether, over 10 species of eels from more than 17 countries have been imported to Japan, for the only documented period between 1968 and 1975 (Kawatsu 1974; Tabeta et al. 1978; Usui 1991).

## Possible alternative scenarios

The putative origin of *A. crassus* cannot be further apprehended without considering its closest relative in the area of their oldest records, i.e., *A. globiceps*. We here envisage four possible evolutionary scenarios for the joint origin of the two nematodes in East Asia. Indeed, since *A. crassus* and *A. globiceps* differ sufficiently with regard to their morphology, hence their taxonomic separation into two distinct genera (see Moravec 2006 and footnote [1]), one might not dismiss the possibility they could also differ with regard to their native host and origin.

*Scenario 1: both* A. crassus *and* A. globiceps *native*

According to the most commonly held opinion, the two anguillicolids are native to East Asia, and have evolved in the Japanese eel. From an evolutionary perspective, it first seems rather unlikely for two closely related parasites, exploiting exactly the same niche (feeding on host tissues, and reproducing in the swimbladder lumen), to inhabit the same host species in the same area (competitive exclusion). However, there is now convincing evidence that speciation does occur in sympatry given markedly differing ecological preferences (Barluenga et al. 2006; Pérez-Tris et al. 2007; Morand et al. 2008), such as different tolerance/preference to water salinity or temperature, or most obviously different intermediate hosts. Also, both species could have existed until quite recently in strict allopatry considering the large geographic range of the Japanese eel (natively found in eight countries according to Froese and Pauly 2011). Strikingly, two other global invaders, the monogeneans *Pseudodactylogyrus anguillae* and *P. bini*, are supposedly both native to the Japanese eel and it is suspected that they have both been imported along with *A. crassus* from East Asia to Europe (Taraschewski 2006; Nagasawa et al. 2007).

*Scenario 2:* A. crassus *invasive;* A. globiceps *native*

Under this scenario, *A. globiceps* would be native to East Asia and *A. crassus* would have been introduced along with the import of 'exotic' eel species for cultivation purposes (pioneering idea in Moravec 2006, p 517). Then, the more competitive *A. crassus* would have progressively replaced it in that region. In that sense, the case of *A. crassus* would present striking similarities with the early epidemiological history of the monogenean *Gyrodactylus nipponensis*, which was first described at almost the same time from cultured eels in Japan (Ogawa and Egusa 1978), and which is now strongly suspected to have been introduced with imported eels from somewhere else (Hayward et al. 2001; Nagasawa et al. 2007).

*Scenario 3:* A. crassus *native;* A. globiceps *invasive*

At the time of its formal description, *Anguillicola globiceps* was reported to "cause considerable thickening of the bladder wall" of the Japanese eel (Yamaguti 1935, p 362; also see Nagasawa et al. 1994), which is similar to the situation found in the European eel after its first contact with *A. crassus*. This would indicate that *A. japonica* was not yet adapted to resist *A. globiceps*, thus suggesting a recent host-parasite association at that time (first half of the past century). Under this scenario the introduced *A. globiceps* would not have succeeded in outcompeting the native and well-established *A. crassus* populations. The epidemiological history of *A. globiceps* would then closely resemble that of *Gyrodactylus nipponensis*, which was supposedly introduced to East Asia but is now disappearing probably due to competition with native *Pseudodactylogyrus* spp. (Kennedy 2007; Nagasawa et al. 2007).

*Scenario 4: both* A. crassus *and* A. globiceps *are invasive*

Under this scenario, both anguillicolids would have been introduced to East Asia along with 'exotic' eel species, at some early stages of aquaculture in Japan. It should be indeed questioned how such conspicuous worms (macroscopic and dark-brown) inhabiting a transparent organ (i.e., the swimbladder), in one of the most valuable fish in East Asia may not have been observed and described earlier if really native to these countries. It is somehow surprising, at least, that Ishii who described and named so many fish parasite species in Japan between the 1915 and 1931 (including other eel nematodes, such as *Philometroides anguillae*, see for review Nagasawa et al. 2007) did not mention these swimbladder worms in the Japanese eel. This scenario could have been replayed later on, in short, in Italy (Lake Bracciano), where the newly introduced *A. crassus* replaced the previously introduced *A. novaezelandiae* [4].

All these scenarios need to render account, at some stages, for the documented spread of *A. crassus* and the concomitant decrease in *A. globiceps* population size. How it occurred, either *via* direct competition or *via* environmental changes, is still a matter of speculation. But we know that *A. crassus* demonstrated the potential to do so; its invasiveness was already observed on several independent occasions (e.g., in Europe, then in America), and its competitiveness has been documented already (see footnote [4]). Possibly, the replacement took place at the favour of drastic environmental changes

that were initiated in the past century (e.g., massive expansion of aquaculture, accidental escape of exotic eels to the wild, decline of the local eel *A. japonica*; H. Taraschewski pers. comm. to FL), and under which *A. crassus* would have found potential grounds to express its competitive superiority. In this regard, the demonstrated tolerance of *A. crassus* towards intermediate/paratenic hosts could have been a key component of its success (reviewed in Kirk 2003; Thielen et al. 2007).

## Lines for further investigations

As parasites, anguillicolid nematodes have no commercial record of translocation (only indirectly *via* their eel hosts), and being soft invertebrates there is likely no fossil record either to help fix the question of their origin. However, biological inference can provide a framework to address some general clues. For instance, if, as it seems, *A. crassus* is better adapted to freshwater than to saltwater (e.g., low osmoregulation capacity, freshwater crustacean as main hosts, higher mortality and lower infectivity of free living stages in saline waters; De Charleroy et al. 1989), then the parasite probably evolved in inland habitats. Moreover, since egg hatching and development are impeded by low temperatures while optimal around 15-30°C (Kim et al. 1989; Knopf et al. 1998), *A. crassus* likely comes from inter-tropical areas. This would support the statement of Taraschewski (2006) according to which anguillicolids must have evolved in one of the founding eel species, somewhere in the Indo-Pacific region (see Minegishi et al. 2005).

Cross-infection experiments may also help to resolve the matter in targeting the most likely native combinations in this anguillid-anguillicolid system. Higher host susceptibility, higher parasite reproductive size and pathogenicity are in fact expected in new host-parasite associations while the same parameters are generally lower in native systems (Combes 2001; Taraschewski 2006; Kennedy 2007). Works are already under way in this direction (Weclawski 2012).

In any case, a deeper research effort in field sampling is critically needed, primarily as *A. globiceps* is apparently disappearing. It would thus be very informative to check for the current occurrence and abundance of *A. globiceps* in localities from where it was reported in the past (see Figure 1 and Appendix 2). Also, it would be worth sampling particularly in Southeast Asia (e.g., Malaysia, Indonesia, Philippines, Vietnam), where other eel species of the Indo-Pacific zone are likely infected with (other) anguillicolid nematodes.

All in all however, molecular genetics is our best tool to help retrace the host co-evolutionary history of *A. crassus* and the anguillicolids. A robust phylogenetic framework would inform us about the possible origin of the anguillicolid clade [4], through the identification of the most basal anguillicolid species. Also, the topology of the tree would clarify the phylogenetic relationships among the anguillicolids in general, and between *A. crassus* and *A. globiceps* in particular. If then both species are each other's closest relative (i.e., monophyletic sister species), we could already assume that they have evolved in the same host, and then diverged from one another, that means both can be either native to East Asia by co-evolving with *A. japonica* or invasive. On the contrary, if both species each have a different closer anguillicolid relative (i.e., the pair is paraphyletic), it is then likely that they have evolved in different hosts, and one of the species (or the two) must have been invasive to *A. japonica* (at some point of time in the past). According to the last released phylogenetic investigation on the subject [4], *A. crassus* would form alone a basal sister group to the other four anguillicolids (Laetsch et al. 2012), hence giving support to the hypothesis of a distinct origin for *A. crassus* and *A. globiceps*.

## Conclusion

From the available data we can track the epidemiological history of *A. crassus* back to Japan, at some uncertain stages in the past century (possibly as early as 1927-1935, but with certainty only from its formal observation and description in 1972-1974). Before that, all evolutionary scenarios are almost equally plausible. In particular, there is no definite proof that the invasive nematode *A. crassus* is native to the Japanese eel in East Asia (nor is there conclusive evidence against it), thus one should be at least more critical of this long held view. More generally speaking, East Asia is often reported as the cradle of an overwhelming number of fish pathogens (e.g., in Blanc 2001; Taraschewski 2006), but maybe this region of intensive aquaculture was only a stepping stone in the migration pathway of many ichthyo-parasitic invaders.

In the case of *A. crassus* and anguillid eels, the resolution of the native origin is likely possible but would require accumulating specimens and comparative data from all known species in the group. We therefore ask the ichthyo-parasitologist community to send every collected specimen, especially from the Indo-Pacific zone, to Prof. H. Taraschewski and fellow workers in Karlsruhe, Germany (in alcohol or preferably in RNAlater® to allow both genome and transcriptome sequencing; E. Heitlinger pers. comm. to FL). Since anguillicolid nematodes are strictly specific to the eel genus *Anguilla*, the detailed understanding of the historical epidemiology and population genetic structure of the parasite could serve as proxy for inference of the host's own phylogeography and ecology (Nieberding and Olivieri 2007; Wielgoss et al. 2010). A better understanding of the natural history of *A. crassus* is also critically timely as the nematode is increasingly cited as a textbook species of parasitic invaders able to threaten already endangered hosts (e.g., Combes 2001; Taraschewski 2006; DAISIE 2008).

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**Appendix 1.** Footnotes.

| Ref. N° | Footnote details |
|---|---|
| 1 | For long, commonly referred to as *Anguillicola crassus* (sub-genus *Anguillicoloides* Moravec et Taraschewski, 1988), until a recent systematic revision transferred it to the genus *Anguillicoloides* (see Moravec 2006). According to current taxonomic standards, might be given as *Anguillicoloides crassus* (Kuwahara et al., 1974) Moravec et Taraschewski, 1988. However, new phylogenetic investigations may soon shake up our understanding of the inter-relationships between anguillicolid species and call for further taxonomic revision (D. Laetsch and E. Heitlinger pers. comm. to FL). |
| 2 | The inherent difficulties of understanding between the two worlds (Asia and Europe in first place) are purposely illustrated by the citations of the work by Puqin Wang and Yuru Zhao (1980), published in Chinese in *Acta Zoologica Sinica*, on the biology of *A. globiceps*. Because of confusion between the given and family names of the two authors, this pioneering work is found cited either as Puqin and Yuru 1980 or Wang and Zhao 1980; sometimes the two forms being cited altogether as two different articles! The correct citation is Wang and Zhao 1980 (see reference section below). According to rough estimates, nearly one out of three papers on anguillicolids cites this reference wrongly. |
| 3 | In Lake Bracciano, the species *A. novaezelandiae* (first erroneously identified as *A. australiensis* and *A. globiceps*) was introduced *via* the importation of short-finned eels *Anguilla australis* (Paggi et al. 1982; for taxonomic re-evaluation see Moravec and Taraschewski 1988). In this Italian lake, *A. crassus* was first observed in 1993 and progressively out competed and replaced the then well-established population(s) of *A. novaezelandiae* (Moravec et al. 1994; K. Dangel and B. Sures 2012, pers. comm. to FL).. |
| 4 | While the higher taxonomic ranks involving Anguillicolidae have already been put to rigorous molecular phylogenetic tests (Wijova et al. 2006), there existed until recently no reliable phylogeny among anguillicolid species, to the sole exception of an inconclusive study comprising only two species (Hirose et al. 1998). Phylogenetic hypotheses involving all five anguillicolid species are now available thanks to the works of H. Taraschewski and fellow students (Laetsch 2010; Laetsch et al. 2012). |

**Supplementary material**

The following supplementary material is available for this article.

**Appendix 2.** Historical records of anguillicolid species in the definitive host in East Asia.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2012/Supplements/AI_2012_Lefebvre_etal_Supplement.pdf