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Invited Review

Beyond the raccoon roundworm: The natural history of non-raccoon *Baylisascaris* species in the New World

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ABSTRACT

A total of 10 species of *Baylisascaris*, a genus of ascaridoid nematodes, occur worldwide and 6 of them occur in the New World. Most of the *Baylisascaris* species have a similar life cycle with carnivorous mammals or marsupials serving as definitive hosts and a smaller prey host serving as paratenic (or intermediate) hosts. However, one species in rodents is unique in that it only has one host. Considerable research has been conducted on *B. procyonis*, the raccoon roundworm, as it is a well-known cause of severe to fatal neurologic disease in humans and many wildlife species. However, other *Baylisascaris* species could cause larva migrans but research on them is limited in comparison. In addition to concerns related to the potential impacts of larva migrans on potential paratenic hosts, there are many questions about the geographic ranges, definitive and paratenic host diversity, and general ecology of these non-raccoon *Baylisascaris* species. Here, we provide a comprehensive review of the current knowledge of New World *Baylisascaris* species, including *B. columnaris* of skunks, *B. transfuga* and *B. venezuelensis* of bears, *B. laevis* of sciurids, *B. devosi* of gulonids, *B. melis* of badgers, and *B. potosis* of kinkajou. Discussed are what is known regarding the morphology, host range, geographic distribution, ecoepidemiology, infection dynamics in definitive and paratenic hosts, treatment, and control of these under-studied species. Also, we discuss the currently used molecular tools used to investigate this group of parasites. Because of morphologic similarities among larval stages of sympatric *Baylisascaris* species, these molecular tools should provide critical insight into these poorly-understood areas, especially paratenic and definitive host diversity and the possible risk these parasites pose to the health to the former group. This, paired with traditional experimental infections, morphological analysis, and field surveys will lead to a greater understanding of this interesting and important nematode genus.

Contents

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1. Genus *Baylisascaris*

1.1. History and relationships within Ascarididae

Baylisascaris is a genus within the family Ascarididae, comprising mostly heteroxenous nematodes with carnivorous definitive hosts. *Baylisascaris procyonis,* the raccoon roundworm, is by far the most well-known and extensively studied member of the genus, primarily because of its association with severe neurologic disease in humans and numerous species of animals. As a consequence, many other *Baylisascaris* species are relatively poorly studied compared to *B. procyonis*. Here, we review the life history and current knowledge of non-raccoon *Baylisascaris* spp. in the Americas.

The genus *Baylisascaris* was officially described in 1968 and was named in honor of parasitologist H. A. Baylis of the British Museum of Natural History (Sprent, 1968). This genus united some previous members of *Ascaris* and *Toxascaris* and was mainly differentiated from other ascarid genera based on the presence of pericloacal rough patches and subventral postcloacal papillae (versus the absence of subdorsal postcloacal papillae as in *Toxascaris*) (Sprent, 1968). Former members of *Ascaris* reassigned into *Baylisascaris* include *B. devosi, B. columnaris, B. procyonis,* and *B. laevis,* while *B. transfuga* and *B. melis* were formerly within the genus *Toxascaris.* While *Baylisascaris* and *Toxocara* share biological similarities and are often discussed together in the context of zoonotic ascarids, they are in different subfamilies and are well-separated within Ascarididae (Nadler and Hudspeth, 2000). Molecular phylogenetic analyses of several genetic targets also support the separation of *Baylisascaris* from other ascarid genera (Zhu et al., 1998; Nadler and Hudspeth, 2000; Franssen et al., 2013; Tokiwa et al., 2014).

1.2. Life cycle characteristics

With the exception of *B. laevis,* all members of *Baylisascaris* utilize a carnivore definitive host. Most of these carnivore-infecting species also utilize a wide range of natural paratenic hosts (although there are some data to suggest these hosts are intermediate hosts, see below). Adult nematodes develop in the small intestinal lumen of the definitive host where they feed on host digesta. Females are remarkably fecund and can release >100,000 eggs/worm/day (primarily based on data from *B. procyonis*), which are shed in the feces (Snyder and Fitzgerald, 1987). Over a variable period of time (10–14 days under ideal conditions), the zygote within the egg develops into an infective-stage larva that may infect either definitive hosts in a direct cycle, or paratenic hosts in an indirect cycle (Fig. 1). However, it is likely that definitive hosts acquire some immunity to infection via the direct route with age; experimental infections show that egg inoculation can generally only establish infection in young definitive hosts (Kazacos, 1983; Berry, 1985). Like other ascarids, *Baylisascaris* spp. eggs are covered in an adhesive proteinaceous coat that confers a high degree of resilience to desiccation, freezing, heat (up to 62 C), and disinfectants, and may remain viable in the environment for years (Shafir et al., 2007; Kazacos, 2016).

When ingested by paratenic hosts, larvae hatch from eggs in the small intestine, penetrate the intestinal wall, and undergo tissue migration after entering circulation. The pattern of migration and the resulting larva migrans syndromes vary among *Baylisascaris* spp. and host species. In *B. procyonis,* three larva migrans syndromes are well-described: visceral larva migrans (VLM), ocular larva migrans (OLM), and neural larva migrans (NLM), the latter of which can cause severe neurologic disease with permanent sequellae and death (Kazacos, 2016). Migrating larvae often become encapsulated in paratenic host tissues and are infective to definitive hosts upon predation. Once ingested by the definitive host, it is presumed L3 larvae mature in the mucosa of the small intestine, returning to the lumen at the L4 stage and molting into adults, as has been shown with *Toxascaris*, although it is not clear whether further somatic and/or tracheal migration takes place within all definitive hosts (Sprent, 1954).

It is possible that the route of infection determines whether further migration occurs within the definitive host. Assuming that the stage within the egg is L2, after egg inoculation, migration out of the gastrointestinal tract may be required for advancement to L3. However, if infection occurs via the ingestion of L3 larvae in host tissues, somatic migration may not be necessary; maturation may occur solely in the intestinal wall and lumen without migration, as has been shown with *Toxascaris leonina* (Sprent, 1954). Phylogenetically, *Baylisascaris* forms a sister clade with other Ascarididae (e.g., *Toxascaris, Ascaris, Parascaris*) although within this group,