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Biology and Life Cycles of Equine Parasites

Life cycles are the road maps that guide parasites to their ultimate goal – propagating a subsequent generation. Some parasites follow a single, direct path to grandma's house, while yet others may travel by convoluted routes, sojourn for protracted periods at some wayside convenience, or even pick up a passenger or two. These differences represent alternate strategies for coping with the vagaries of the environment and of their eventual hosts.

A thorough knowledge of life cycles is not emphasized merely to torment veterinary students. Rather, life cycle details reveal opportunities to control parasites through chemical or management interventions, to exploit unfavorable environmental conditions, or to promote natural enemies that might act as agents of biological control. Taking advantage of these potential control opportunities will be emphasized in individual chapters in this volume.

At the root of all life cycles is a fundamental principle that distinguishes helminth parasites from other infectious agents such as viruses, bacteria, fungi, and protozoa. Through various types of clonal expansion, the latter can all amplify their numbers within a host animal. Literally millions of individual organisms may arise from infective burdens that are orders of magnitude smaller. The reproductive products of nearly all helminths, however, are required to leave the host and undergo essential change in a different location. Defecation is the most common means by which reproductive products exit the host, but a notable exception includes immature parasitic stages that are ingested by blood-sucking arthropods (*e.g.*, *Onchocerca*, *Setaria*). Most parasitic products can become infective in the environment, whereas others require intermediate hosts or vectors. Regardless, all of these essential transformations occur "outside the definitive host". Indeed, dramatic biological change is mandatory before a parasitic organism is capable of infecting a new host animal or of reinfecting the original host.

Compared to those organisms that amplify their numbers through clonal expansion, helminth disease is a numbers game. Simply put, as the number of invading parasites increases, greater tissue damage or nutrient loss results, and the range and severity of clinical signs become more extensive.

In this chapter, we propose to describe the basic life cycles of the major helminth parasites of equids. Specific control opportunities may be mentioned in this overview, but these will be discussed more fully elsewhere in the volume.

Nematodes

Superfamily Strongyloidea

The members of the Strongyloidea ("strongyles") are moderately sized, stout worms with substantial buccal capsules.

Handbook of Equine Parasite Control, Second Edition. Martin K. Nielsen and Craig R. Reinemeyer.

The males have a copulatory bursa at the posterior end and females of all species produce eggs that are similar in appearance. Eggs of small strongyles cannot be differentiated microscopically from those of large strongyles, and the only practical method of differentiation (other than molecular approaches) is through coproculture. The strongyloids of horses all have direct life cycles; intermediate or paratenic hosts are never used (Figure 1.1).

Strongyloid eggs pass in feces and hatch in favorable environmental conditions of moisture, temperature, and

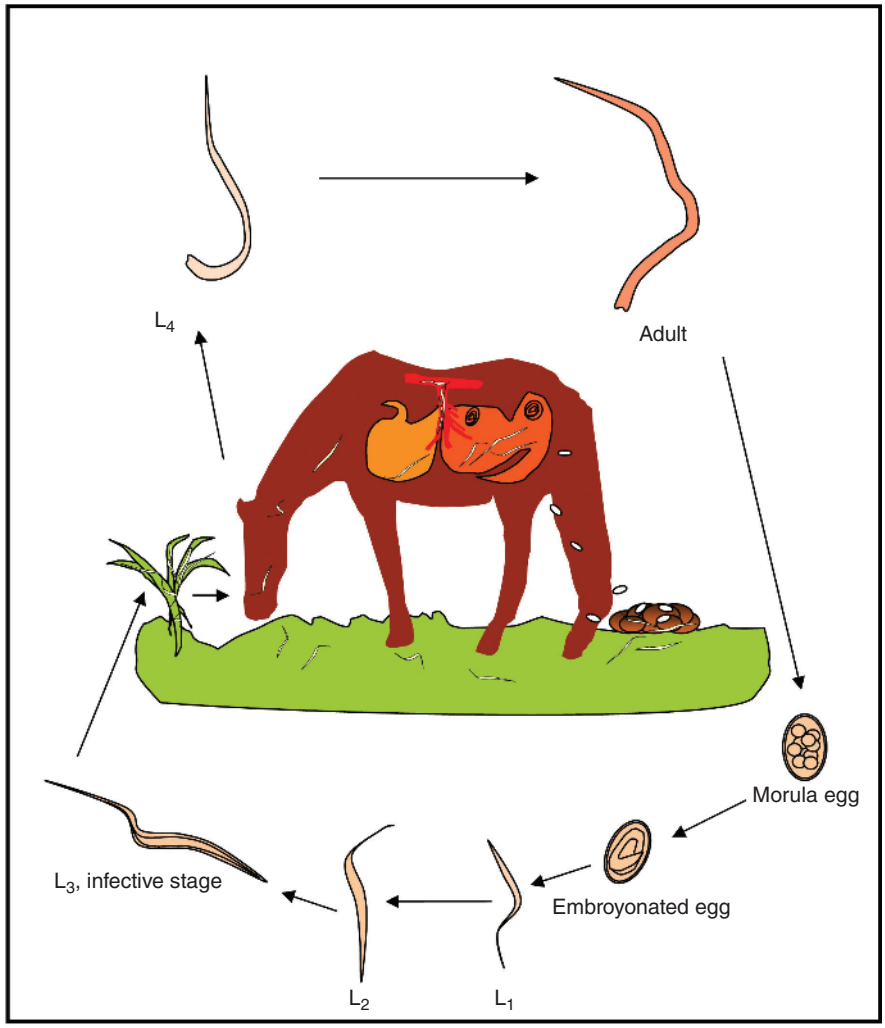

Figure 1.1 Strongyle life cycle. The life cycle of strongyle parasites. Parasitic stages can be seen above the horse and preparasitic stages below it. Fertilized eggs are shed by adult females in the cecum and colon, and excreted to the environment in the feces. Here, the eggs hatch and a first-stage larva (L_1) emerges. The L_1 then molts to L_2 in the feces. Another molt gives rise to the L_3, which retains its L_2 cuticle and thus has a double-layered sheath. The L_3 leaves the fecal pat and migrates on to forage, where it is ingested by a horse. Inside the horse, the L_3 exsheathes and invades the mucosa of the large intestine. Large strongyles (*Strongylus* spp.) undergo extensive migration in various organs of the horse, while cyathostomins encyst in the mucosal lining of the large intestine. After returning to the large intestinal lumen, the worms reach sexual maturity and start shedding eggs.

oxygenation. All species exhibit three sequential larval stages, first (L_1), second (L_2), and third (L_3). The L_1 and L_2 stages feed on organic material in the environment, but the third stage develops within the sheath of the L_2. This protective covering helps L_3s to resistant environmental conditions, but it has no oral opening, so third stage larvae are unable to ingest nutrients. The L_3 is the infective stage for all strongyloid nematodes of equids. Infection invariably occurs through inadvertent ingestion, whether while grazing or via oral contact with elements of the environment.

Apparently, horses never develop absolute immunity to strongyloids, so these are often the sole nematode parasites recovered from well-managed, mature equids. The Strongyloidea of horses are comprised of two distinct subfamilies, the Strongylinae and the Cyathostominae.

Strongylinae (large strongyles)

Members of the subclass Strongylinae tend to be larger, on average, than most genera that comprise the Cyathostominae. In addition, Strongylinae have large buccal capsules, adapted for attachment to, and even ingestion of, the gut mucosa. The larval stages of at least one strongylin genus undergo extensive, albeit stereotypic, migration within the host prior to returning to the gut to mature and begin reproduction.

Strongylus vulgaris

Strongylus vulgaris is widely acknowledged as the single most pathogenic nematode parasite of horses. Adult worms measure about 1.5–2.5 cm in length and the females are larger than the males. Adults are usually found attached to the mucosa of the cecum and the ventral colon (Figure 1.2). After ingestion from the environment, third stage larvae invade the mucosa of the distal small intestine, cecum, and colon. Here, they molt to the fourth stage (L_4) before penetrating local arterioles and migrating proximally beneath the intimal layer of local blood vessels. Migrating *S. vulgaris* L_4s leave subintimal tracts in their wake and congregate near the root of the cranial mesenteric artery. A portion of the infecting larvae may continue to migrate, even to the root of the aorta near the left ventricle. Migrating L_4s have been found in numerous vessels arising from the aorta, including the celiac artery, the renal arteries, and external and internal iliac arteries. The pathologic characteristics and consequences of these arterial lesions will be discussed in Chapter 2.

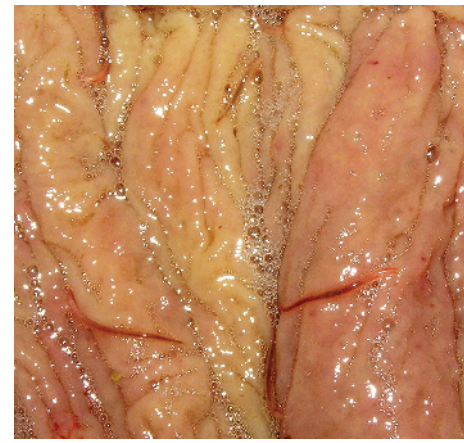

Figure 1.2 Adult *Strongylus vulgaris* attached to the cecal mucosa. (*Source*: Photograph courtesy of Dr. Tetiana Kuzmina).

Larvae reach the cranial mesenteric artery about two weeks post-infection. Here, they reside for about four months before returning to the large intestine. The final molt to the L_5 stage occurs about 90 days after infection, while larvae are still present in the artery. These L_5s (essentially young adults) characteristically retain their L_4 cuticle and thus appear with a double-layered cuticle just like the infective L_3 (Figure 1.3). Beginning approximately 120 days after infection, young adults migrate within the blood stream to the large intestine, where they are found within pea-sized nodules in the

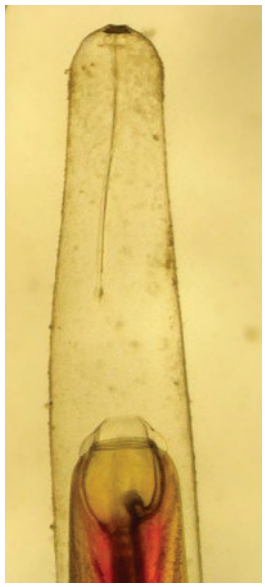

Figure 1.3 *Strongylus vulgaris* L_5 pre-adult collected from the cranial mesenteric artery. Note that this specimen characteristically has retained its L_4 cuticle.

submucosa of the ventral colon and cecum. Adult worms eventually emerge from these nodules and mature in the intestinal lumen for an additional 6 weeks. Females begin to lay eggs from 5.5 to 7 months after infection (Ogbourne and Duncan, 1985).

Strongylus edentatus

Strongylus edentatus is a larger worm than *S. vulgaris,* measuring about 2.5–4.5 cm in length, and apparently is also more prevalent. Adults are usually attached to the mucosa of the base of the cecum and the proximal ventral colon. The larvae undergo a complex and fascinating migratory route. Following ingestion of infective L_3 stages from the environment, larvae are carried by the portal system to the liver, where they molt to the fourth stage. Following migration within the parenchyma, larvae leave the liver via the hepatorenal ligament and migrate beneath the peritoneum to various locations in the flanks and ventral abdominal wall (hence, the common term, "flank worm"). Larvae are also commonly found in the perirenal fat. The majority of larvae are found on the right side of the body (*i.e.*, in the right ventral abdominal wall and around the right kidney), probably because the hepatorenal ligament attaches on the right side of the ventral midline (see Chapter 2).

The final molt to the fifth stage occurs within retroperitoneal nodules about four months post-infection. Young adults migrate back to the large intestinal walls (primarily the ventral colon), where purulent nodules form and eventually rupture to release adult worms into the lumen. Altogether, this extensive migration results in a prepatent period of up to one year (McCraw and Slocombe, 1978).

Strongylus equinus

Strongylus equinus is another large strongyle with a prolonged life cycle and a prepatent period of 8–9 months from infection to egg production. The adult worms are of about the same size as *S. edentatus*. Larvae molt to the L_4 stage upon invading the mucosa of the caecum and colon. They then migrate across the abdominal cavity and through the pancreas to finally reach the liver, where they wander for several weeks. On the way back to the large intestine, larvae again migrate through the pancreas and large L_4s and L_5s can be found free in the peritoneal cavity (McCraw and Slocombe, 1984). The third stage larvae of *S. equinus* are very distinctive in coproculture. This nematode species has become exceedingly rare in domestic herds and is not detected in managed and regularly dewormed horses. *S. equinus* can be highly prevalent and abundant in feral horses, however, and has been reported in prevalence surveys of working equids in South America (Kyvsgaard *et al.*, 2011).

Strongylus asini

Strongylus asini is a common internal parasite of zebras and donkeys in Africa. It resembles *S. vulgaris* in many ways but genetically is more closely related to *S. edentatus* and *S. equinus* (Hung *et al.*, 1996). Adults occur in the cecum and colon, but larvae are found attached to the lining of hepatic and portal veins (Malan *et al.*, 1982). Fourth stage larvae migrate within the liver and hepatic cysts are reportedly found in zebras.

Triodontophorus spp.

Although they are technically "large strongyles", the several species of *Triodontophorus* are non-migratory. The larvae encyst within the lining of the large intestine and eventually emerge to become adults. The prepatent period is thought to be approximately 2–3 months (Round, 1969). *Triodontophorus brevicauda* and *T. serratus* are probably the most prevalent species of large strongyles in managed horses, presumably because of a shorter life cycle than *Strongylus* species. One study of naturally infected horses found that the presence of *Triodontophorus* larvae in coproculture was independent of the presence of *Strongylus* spp. (Cao, Vidyashankar, and Nielsen, 2013). This finding was attributed to a shorter life cycle, which is more similar in duration to that of cyathostomins.

Triodontophorus females apparently produce eggs that are significantly larger than those of the other strongylin and cyathostomin genera (Figure 1.4).

Other strongylinae

Craterostomum acuticaudatum, Oesophagodontus robustus, and *Bidentostomum ivaschkini*

These species have non-migratory life cycles and are only classified as Strongylinae on the basis of their large buccal capsules (see Table 1.1). The larvae derived by coproculture can be differentiated, but as the species prevalences are so

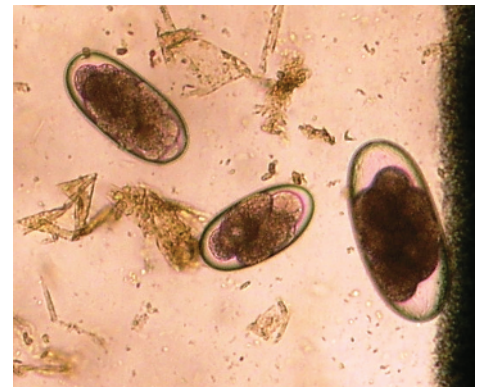

Figure 1.4 Most strongyle eggs are relatively uniform in size and shape. One exception is the eggs of *Triodontophorus* spp. (right), which are about twice the size of a typical strongyle egg. (*Source*: Photograph courtesy of Tina Roust and Maria Rhod).

Table 1.1 Examples of predilection sites of common cyathostomin species. Information from Tolliver (2000).

Cecum
Coronocyclus coronatus
Cyathostomum alveatum
Cylicocyclus elongatus
Cylicostephanus calicatus
Petrovinema poculatum
Ventral colon
Coronocyclus labiatus, Cor. labratus,
Cyathostomum catinatum, Cya. pateratum (also dorsal colon), *Cya. tetracanthum,*
Cylicocyclus auriculatus, Cyc. brevicapsulatus, Cyc. radiatus, Cyc. leptostomum Cyc. nassatus, Cyc. ashworthi, Cyc. ultrajectinus (also dorsal colon)
Cylicodontophorus bicoronatus
Cylicostephanus asymetricus, Cys. minutus
Dorsal colon
Cyathostomum pateratum (also ventral colon)
Cylicocyclus insigne, Cyc. ultrajectinus (also ventral colon)
Cylicostephanus goldi, Cys. longibursatus
Parapoteriostomum euproctus, Par. mettami
Poteriostomum imparidentum, Pot. ratzii

low, larvae are more likely to be mistaken for similar, but more common, genera. None of these species has been associated with any distinct pathology.

Cyathostominae

The Cyathostomins (also known as small strongyles, cyathostomes, or trichonemes) comprise numerous genera, including *Cylicocyclus*, *Cyathostomum*, *Cylicostephanus*, *Coronocyclus*, *Cylicodontophorus*, *Gyalocephalus*, *Poteriostomum*, *Petrovinema*, and *Parapoteriostomum* in North America and world-wide. Lesser-known genera, such as *Hsiungia*, *Tridentoinfundibulum*, *Skrjabinodentus*, *Caballonema*, and *Cylindropharynx*, have been recovered from indigenous equids in Africa and Asia (Lichtenfels, Kharchenko, and Dvojnos, 2008). The majority (>80%) of cyathostomins recovered from horses belong to just a handful of species: *Cylicocyclus nassatus*, *Cylicostephanus (Cys.) minutus*, *Cys. longibursatus*, *Cyathostomum catinatum*, and *Cys. calicatus* (Reinemeyer, Prado, and Nielsen, 2015) (Figure 1.5). The common term "small redworms" is misleading as adult cyathostomins are all pale white in appearance. The L_4 and early L_5 stages of *Cylicocyclus insigne* are the only cyathostomin specimens that appear red in color. *C. insigne* is a relatively large species, however, so these L_4s are easily visible in a fresh fecal sample or on a rectal palpation sleeve.

The basic life cycle of all cyathostomins is virtually identical, with development to the infective third stage in the environment. Once ingested by a horse, however, L_3 cyathostomins do not migrate systemically. (In this handbook, migration is consistently defined as leaving one organ and entering another.) Rather, incoming larvae invade the mucosa or submucosa of the cecum and ventral colon, or, to a lesser extent, the dorsal colon. Cyathostomins never encyst in the lining of the descending colon or rectum. Some species apparently invade no deeper than the mucosa, whereas others encyst within the submucosa. In addition, species may prefer certain alimentary organs or even sites within an organ for encystment.

Cyathostomins first invade the large intestinal lining as early third stage larvae (EL_3). These are basically infective larvae that have shed their protective integument. Early L_3s are very small (<1 mm) and most genera contain only eight intestinal epithelial cells. Soon after they enter the mucosa, a fibrous capsule of host origin forms around the EL_3, and from this stage forward, these tissue larvae are referred to as "encysted" (see Chapter 2). The EL_3 is transient if the worm progresses steadily through all the larval stages to adulthood. Alternatively, individual worms may undergo arrested development and persist as EL_3s for more than a year or two.

With progressive development, the EL_3 molts into a late L_3 stage (LL_3), which is significantly larger, features a tubular buccal cavity, and has more than eight intestinal cells. The LL_3 remains within the cyst and ultimately molts into an L_4 stage, which has a distinct, goblet-shaped buccal capsule. The L_4 grows within the cyst, and eventually the cyst wall ruptures and the L_4 enters the lumen of the large intestine. This stage of emergence is also termed "excystment", which is the chief pathologic event during the cyathostomin life cycle (Chapter 2).

Within the lumen of the large intestine, an L_4 grows in size and eventually molts into the L_5 stage. Fifth stage larvae (L_5s) are basically prepubertal, non-reproductive teenagers; the transition from L_5 to adult is a gradual one, involving only maturation of the reproductive organs and an increase in body size. The L_5 develops within the sheath of the L_4 stage and individual worms that are beginning the penultimate stage of development will exhibit the buccal capsule and other cephalic features of the adult, positioned

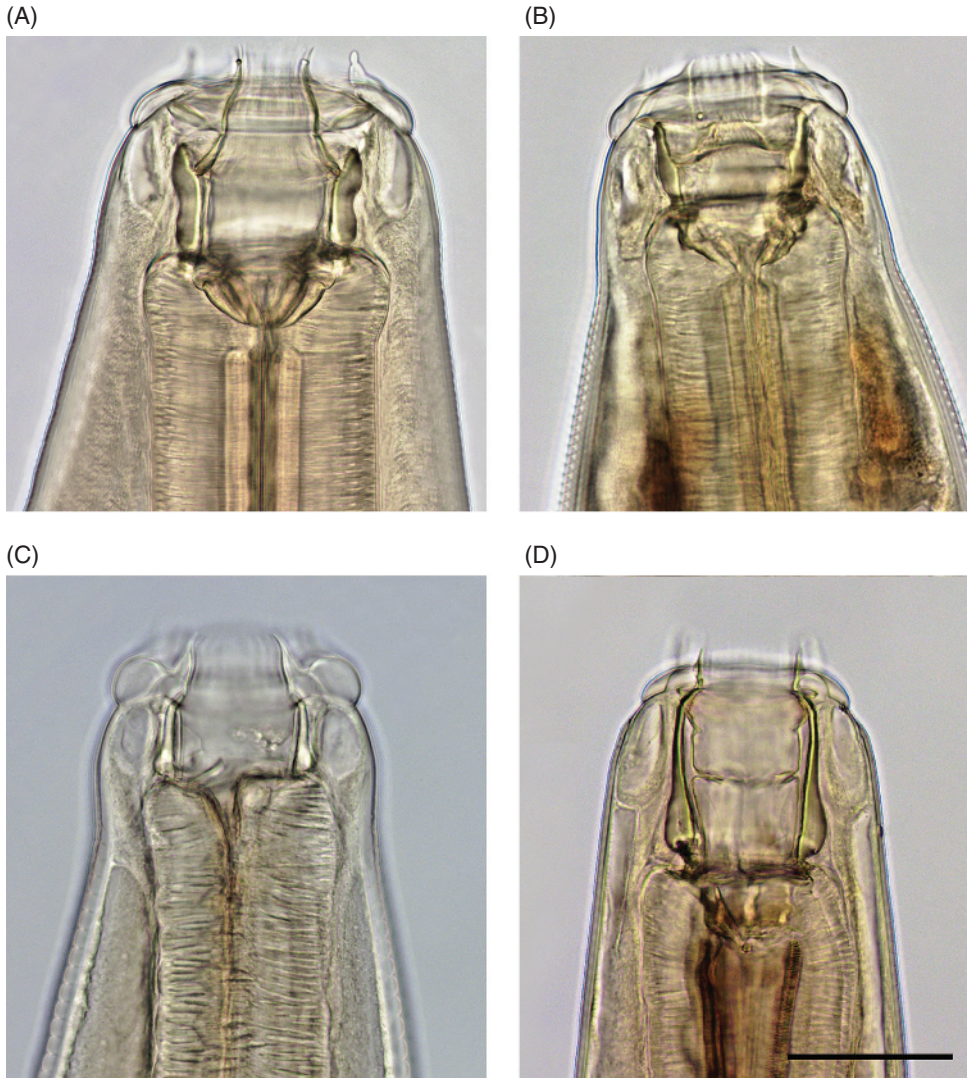

Figure 1.5 Common adult cyathostomin species. (A) *Coronocyclus coronatus,* (B) *Cyathostomum catinatum*, (C) *Cylicocyclus leptostomum*, and (D) *Petrovinema poculatum*. Size bar = 50 μm. (*Source*: Photograph courtesy of Jennifer L. Bellaw).

just beneath the remnants of the L_4 stage, which are about to be shed and discarded.

In addition to the larval stages, adult cyathostomins also exhibit distinct site preferences (Table 1.1). Although it is not unusual for each organ of the large intestine to harbor at least some specimens of any species, the majority of individuals of any species are usually recovered either from the cecum, ventral colon, or dorsal colon. No species occupies the descending colon or rectum as a preferred niche, so specimens recovered from those locations are considered to be exiting the host.

Female cyathostomins can begin to lay eggs as soon as 5 weeks after infection (Round, 1969), but due to arrested development, some may not complete maturation until more than two years after

initial ingestion by the host (Gibson, 1953). Cyathostomins can remain in arrested development longer than any other nematode group and spend their entire parasitic life cycle in the alimentary tract. The reasons for this strategy are unclear, but the evolutionary advantages are obvious. If climatic conditions did not permit prolonged environmental survival of infective stages, it would be very beneficial for the parasite if the host could carry new sources of contamination and infection wherever it went. Similarly, the same strategy would be useful if nomadic horses returned to grazing areas after intervals longer than the maximum persistence of infective stages in the environment.

Encysted cyathostomin larvae are not 100% susceptible to any known anthelmintic regimen. For this reason, it is impossible to clear a horse of all its cyathostomins. If a horse were dewormed heroically and then transferred to a sterile environment with no hope of fecal/oral reinfection, that animal would eventually begin to pass strongyle eggs again at some point in the future. As demonstrated by Smith (1976a, 1976b), if the horse were held in such an environment for a prolonged period and dewormed repeatedly, it may require more than 2 years before the sources of such episodic contamination would be permanently exhausted.

The duration of survival of adult cyathostomins has not been determined with certainty, but is thought to be on the order of three to four months.

Ascaridoidea

The superfamily Ascaridoidea is comprised of very large, stout nematodes with three prominent lips surrounding the oral opening. Some ascarid species have the most complicated life cycles of any nematode of veterinary importance, but the ascarid of horses has the simplest of all.

Parascaris spp.

Few veterinarians are aware that two species of *Parascaris* have been reported to infect horses. *Parascaris univalens* is described as a cryptic equine ascarid species that appears morphologically identical to the better-known *P. equorum*. Characteristically, specimens of *P. univalens* have only one pair of chromosomes, whereas *P. equorum* has two pairs. To date, karyotyping remains the only established technique for differentiating these two species. Both species had been described by the late 1800s, and it is an interesting item of biological trivia that the phenomenon of mitosis was first observed in the eggs of *P. univalens*. For unknown reasons, *P. univalens* has faded into obscurity, and it is rarely mentioned in veterinary textbooks. However, cell biologists and cytogeneticists have used the parasite for decades as a model for studying chromatin diminution, whereby the parasite eliminates a large proportion of its DNA during the first mitotic cell cycle (Muller and Tobler, 2000).

Contrary to prevailing wisdom, available evidence suggests that *P. equorum* may be very rare and that *P. univalens* is the more common species of equine ascarid. One study performed in Italy in the late 1970s identified over 2000 worm specimens to species level and found over 90% to be *P. univalens*, with the remainder either *P. equorum* or hybrids (Bullini *et al*., 1978). A more recent karyotyping study performed in central Kentucky identified 30 worm specimens and 17 of 25 egg isolates to be *P. univalens*, while *P. equorum* was not identified (Nielsen *et al*., 2014). A study of the population structure among about 200 equine ascarid parasite specimens collected in Sweden, Norway, Germany, Iceland, Brazil, and USA concluded that all specimens were genetically homogenous, and thus essentially the same species (Tyden *et al*. 2013). One isolate examined in this study was collected from a parasitology research

population and subsequently identified as *P. univalens* by karyotyping. This strongly suggests that all 200 specimens from six different countries on three continents were indeed *P. univalens*. It remains possible that *P. equorum* still occurs in certain equid populations, but these need to be identified and characterized. The practical implications of these findings are currently unknown, but they may be limited to just substituting one name with another. For now, the most appropriate nomenclature to be applied for equine ascarids is "*Parascaris* spp.", unless karyotyping has been carried out to identify the specimens to species level.

Parascaris spp. is the largest intestinal nematode parasite of horses, and mature females can reach 50 cm × 1–2 cm in size (Figure 1.6) and produce approximately 200,000 eggs per day. As adults, equine ascarids reside in the small intestine, with small numbers occasionally recovered from the stomach or cecum. Females lay distinctive eggs that are passed in the feces. Under favorable environmental conditions, eggs can become infective within 2 weeks. The infective stage is a larvated egg containing a coiled, third stage larva.

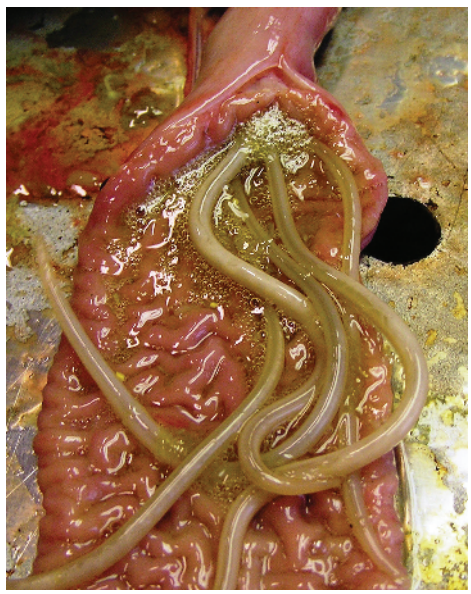

Figure 1.6 Adult *Parascaris* spp. in the small intestine of a weanling. (*Source*: Photograph courtesy of Dr. Tetiana Kuzmina).

Horses are infected by ingesting infective ascarid eggs from the environment. The eggs are covered by a sticky, protein coating, which enables them to adhere to vertical surfaces and even to the haircoat or udder of a mare. Foals and weanlings are most commonly infected by ascarids; and transmission is greatly assisted by the tendency of juvenile horses to investigate their environments orally. Interestingly, up to 10% of ascarid eggs appearing in equine feces lack their protein coating (Donoghue *et al.*, 2015). It remains unknown whether these decorticated eggs are equally viable and able to develop into the infective stage in the environment.

When a larvated ascarid egg is ingested from the environment, the egg loses its protective coating after passing through sequential acidic and basic conditions in the stomach and small intestine, respectively. A larva emerges from the egg shell in the small intestine and penetrates the gut lining. Migrating larvae enter the lymphatics or venules draining the small intestine and are carried passively to the liver. After infection, most larvae are found in the liver within 2 to 7 days post-infection. Larvae migrate within the hepatic parenchyma, which may result in inflammatory lesions and fibrous migratory tracts. Focal, white, fibrotic lesions are often seen just below the capsule of the liver, equivalent to the condition caused in swine by migrating *Ascaris suum* (see Chapter 2).

Migrating third stage larvae are found in the lungs, beginning about two weeks after infection. Here, they exit the pulmonary venules and capillaries, and rupture alveolar membranes to enter the airways. Migrating ascarid larvae usually reside within the lungs for about two weeks. Eventually, the larvae migrate

proximally in the pulmonary tree or are coughed up into the pharynx. Regardless of the mechanism, they are swallowed and return to the stomach and small intestine within 4 weeks post-infection. Once in the small intestine, the worms grow progressively, and eggs appear in the feces from 90 to 110 days post-infection (Lyons, Drudge, and Tolliver, 1976).

Adult ascarids continue to grow and may persist within the gut for several months. Ultimately, the majority of horses develop very strong immunity to *Parascaris* and egg shedding eventually ceases, even without benefit of anthelmintic treatment (Donoghue *et al*., 2015; Fabiani, Lyons, and Nielsen, 2016). Because of this effective immunity, ascarid infections are commonly observed in sucklings, weanlings, and yearlings, but are seen only occasionally in horses older than approximately 18 months of age (Fabiani, Lyons, and Nielsen, 2016).

Recent investigations in populations of untreated foals have identified a biphasic occurrence of *Parascaris* spp. (Donoghue *et al*., 2015; Fabiani, Lyons, and Nielsen, 2016). Adult ascarid burdens reach their peak at 4–5 months of age, as reflected by high ascarid egg counts. After this peak, the adult burdens are eliminated, but a smaller, second wave of infection can be observed at 8–10 months of age. This second infection appears to be short-lived and the adult worms are soon eliminated.

In recent years, many practitioners have observed patent ascarid infections in mature horses, and some individual adult horses resume egg-shedding repeatedly after apparently effective anthelmintic treatments. At present, it is unknown whether these recurrent infections are associated with unique immune deficiencies or with isolates of *Parascaris* that do not elicit a typical immune response, or if they merely reflect increased use of fecal egg counts to monitor horse populations.

Oxyuroidea

The Oxyuroidea, or pinworms, comprise a superfamily of nematodes that reside in a unique niche, the posterior alimentary tract. In addition to equids, other host species for pinworms include humans, rodents, primates, and sheep. The oxyuroids exhibit a unique biological adaptation in that the females do not shed eggs into the feces. Rather, they protrude from the anus and deposit eggs in a sticky film in the perineal area (Figure 1.7). The warm, moist conditions in this microhabitat likely assist in larval development. Ultimately, the dried, proteinaceous film flakes off and eggs are dropped randomly into the environment, where they may persist for several months.

Another curious piece of trivia about pinworm parasites is that their mode of reproduction is unique among nematodes. Males are derived from unfertilized

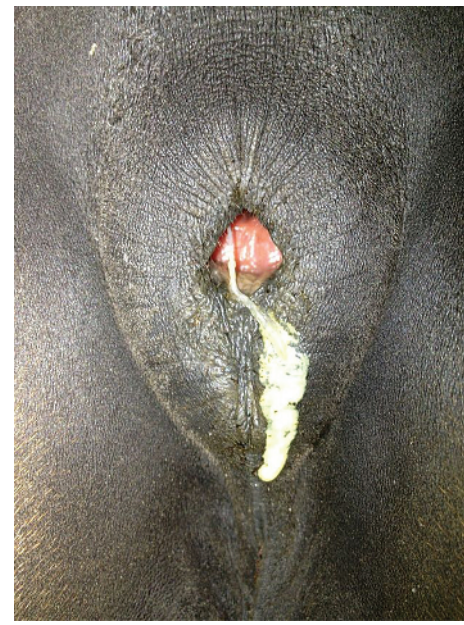

Figure 1.7 Female *Oxyuris equi* laying eggs in the perianal area. (*Source*: Reprinted from Equine Veterinary Education, 28, M.K. Nielsen, Equine tapeworm infections: Disease, diagnosis and control, pp. 388–395, Copyright (2016) with permission from EVJ Ltd, Wiley).

eggs and are thus haploid, whereas females derive from fertilized eggs and are diploid. This mode of reproduction has been termed haplodiploidy (Adamson, 1994). It is believed that this is a strategy for parasite propagation. In the absence of males, new males will automatically arise from unfertilized eggs.

Oxyuris equi

Oxyuris is the common pinworm of horses. Adult females are white, moderate in size (5–8 cm × 5 mm), and have a sharply pointed tail – thus providing the common name for this group. Males are fewer in number and only approximately one-third the size of the adult females. Adult pinworms reside in the dorsal colon, and only females can be observed commuting through the rectum to the maternity ward (Reinemeyer and Nielsen, 2014).

Female pinworms may be seen protruding from the anus, but are also observed in fresh feces or adhering to a palpation sleeve following a rectal examination. It is believed that female worms die quickly after depositing their eggs.

The larvated eggs are deposited in sheets of a sticky film, which is similar in composition to dried egg albumin. Eggs are ingested from the environment, in much the same fashion as those of *Parascaris* spp. Third stage larvae emerge from eggs in the small intestine and reportedly develop within the mucosa of the cecum and colon. As pinworms approach adulthood, they relocate to the dorsal colon. Adults do not attach to the gut wall and have negligible pathogenicity.

Probstmayria vivipara

Probstmayria is a lesser-known and extremely small pinworm that is occasionally recovered from horses. These worms are nearly invisible to the naked eye, but might be observed during microscopic examination of fresh colonic contents. This pinworm is not known to cause any distinct clinical signs. *Probstmayria*'s reproductive behavior is rare among parasitic nematodes; it is viviparous and can complete its entire life cycle without leaving the host. For this reason, infections often comprise massive numbers of worms, but, again, they have no known clinical impact.

Rhabditoidea

The rhabditoid nematodes are all fairly primitive and exhibit unique life cycle adaptations such as free-living generations and an apparent absence of parasitic males.

Strongyloides westeri

Strongyloides westeri is a small nematode (6–9 mm) that parasitizes the small intestine of suckling foals. Females (parasitic males are unknown) are embedded within the mucosa at the base of the villi (Figure 1.8) and produce small (50 µm × 40 µm), thin-shelled, round to slightly elliptical eggs already containing a larva (Figure 1.9). Patent infections are

Figure 1.8 Female *Strongyloides westeri* from the small intestinal mucosa. Only females are parasitic. (*Source*: Photograph courtesy of Faith Miller).

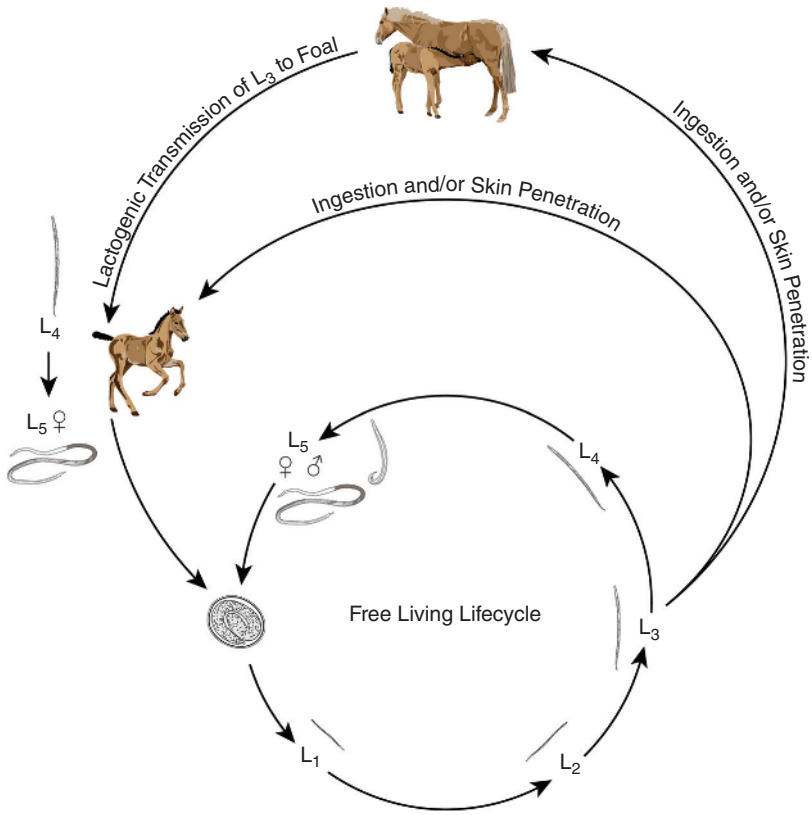

Figure 1.9 The life cycle of *Strongyloides westeri*. This parasite is capable of completing the entire cycle in the environment without entering a host. Horses can get infected by three different routes of transmission; oral ingestion of L_3 larvae, skin penetration by L_3 larvae, or lactogenic transmission of L_3s from mares to foals. Note that only the female parasites are parasitic. (*Source*: Graphics courtesy of Jamie K. Norris).

primarily seen in foals because strong immunity to *Strongyloides* develops fairly quickly, but older horses are occasionally found infected as well. Larvated eggs appearing in the feces of a yearling or older horse invariably are those of strongyles rather than *Strongyloides*. Eggs pass in the feces and L_1 larvae which emerge in the environment can follow various patterns of development (Figure 1.9). Some larvae become free-living males or females. The larvae of veterinary concern, however, are those that halt their free-living development as third stage larvae, and are restricted to a parasitic existence.

Foals can be infected with *Strongyloides* by one of three possible routes: skin penetration by third stage larvae, ingestion of third stage larvae from a contaminated environment, or lactogenic transmission from the mare. The latter route is possible because *Strongyloides* larvae do not become established in the alimentary tract of immune, adult horses. Rather, they are distributed to various somatic tissues, where they may reside for years. In mares, the hormones of pregnancy and lactation presumably stimulate the somatic larvae to resume migration and travel to the mammary glands. From this location, they are present in mare's

milk from the fourth day post-partum and are ingested by suckling foals (Lyons, Drudge, and Tolliver, 1973). Numbers of larvae in the milk peak at about 10–12 days post-partum, but larvae have been recovered from milk samples up to 47 days after birth. The highest concentrations of larvae have been recovered from samples collected in the morning (Lyons, Drudge, and Tolliver, 1973).

The extent to which these lactogenic larvae undergo pulmonary migration once they reach the foal remains unclear. Available evidence suggests that lactogenically acquired larvae are quicker to develop into patent infections in foals compared with infective larvae ingested orally from the environment (Lyons, Drudge, and Tolliver, 1973). One possible explanation is that lactogenic larvae do not have a tissue migration stage within the foals. Larvae acquired via the transcutaneous route, however, do migrate through the lungs before establishing in the small intestine.

Most *S. westeri* infections in foals are asymptomatic, but symptomatic infections will be described in Chapter 2.

Halicephalobus deletrix

Halicephalobus (syn: *Micronema*) is a free-living rhabditoid nematode that occasionally takes up residence within living tissues. It usually gains entry to the mammalian body through grossly contaminated lacerations or possibly through mucous membranes. *Halicephalobus* causes granulomatous lesions and is locally or systemically invasive. Spontaneous infections are seen occasionally in horses and generally involve cephalic tissues (gingiva and underlying bone, sinuses, brain) or well-vascularized organs such as the kidney (Ferguson *et al.*, 2011). Recent observations have provided evidence of a hematogenous spread of this parasite to these distant sites (Henneke *et al.*, 2014). Human infections have been reported, but generally are subsequent to severe tissue damage and gross contamination with manure or soil.

Atypically for most parasitic nematodes, adult *Halicephalobus* reproduce within the host, resulting in superinfections with adults and larvae in all stages of development.

Spiruroidea

All spiruroid nematodes require an arthropod intermediate host for transmission to a vertebrate vector. The spiruroids affecting horses occur either as adults in stereotypic locations or as larvae in a variety of aberrant tissues.

Habronema muscae

Habronema muscae are approximately 1 to 2.5 cm in length and occur in the stomach of equids. They produce very tiny (16 µm × 45 µm), thin-shelled, larvated eggs that are passed in the feces. In the environment, larvae emerge and are ingested by adult dipterans (*e.g.*, *Musca domestica*) or are swallowed by feeding maggots. Infection is completed via ingestion of dead flies in feed stuffs or water. Alternatively, infective *Habronema* larvae may travel to the mouth parts of living flies and be deposited in wounds or at mucocutaneous junctions during feeding activities.

Within the stomach, the parasites become adults in about eight weeks. Adult *Habronema* are found in close contact with the gastric mucosa, but they cause no clinical problems. The larvae deposited in wounds or at mucocutaneous junctions, however, can result in proliferative, ulcerated lesions that tend to increase in size throughout the fly season (see Chapter 2).

Habronema microstoma

Habronema microstoma is a less common species in this superfamily that uses stable flies (*Stomoxys calcitrans*) as intermediate hosts. There are no major differences in the biology or pathogenicity of the two *Habronema* species.

Draschia megastoma

The life cycle of *Draschia megastoma* is virtually identical to that of the *Habronema* spp. and the house fly (*Musca domestica*) is the preferred intermediate host. The major biological difference is that adult specimens of *Draschia* are found in large (5 cm × 5 cm), tumor-like, fibrous masses that are usually located near the *margo plicatus* of the stomach. The *margo* is the junction of the glandular and non-glandular gastric epithelium of equids. *Draschia* adults and associated lesions were observed in 22 of 55 horses necropsied in 1984 (Reinemeyer *et al.*, 1984). However, *D. megastoma* apparently has become quite rare because none of the authors has seen a single gastric lesion in hundreds of horses necropsied since ~1985.

Thelazia lacrymalis

Horses are the definitive hosts of one species of *Thelazia,* or eye worms. As adults, *Thelazia* are found within the conjunctival *cul de sac* or beneath the nictitating membrane. Adult females produce larvae, which are present in the tear film of an infected eye. The usual intermediate host is the house fly, *Musca domestica*, or face fly, *Musca autumnalis*. Apparently, flies feeding on ocular discharges ingest larvae, which then develop to the infective stage within the body of the fly. Another horse is infected when the vector fly returns to feed on its lacrimal secretions. Infective stages leave the mouth parts of the fly, enter the conjunctival sac of the horse, and initiate a new infection.

Eye worms are thought to be relatively innocuous.

Filarioidea

The filarioidea comprise a superfamily of long, thin nematodes that often reside in organs with no direct connection to the external environment. Therefore, these worms are challenged with disseminating their reproductive products away from the host so they can undergo the development necessary to infect a new generation of hosts. Filarioids accomplish this goal by producing small, motile, reproductive stages known as microfilariae. Microfilariae circulate in the blood or lymph, or migrate to the skin. From these locations, they are ingested by arthropod intermediate hosts which feed on the tissues or secretions of live horses.

Onchocerca

Onchocerca cervicalis and *O. gutturosa* adults are sometimes referred to as "neck threadworms" because they are found deep in the connective tissues of the nuchal ligament. Adults of *O. reticulata* reside in connective tissues in the distal limbs. Microfilariae are produced by female worms, and they enter the circulatory system and travel to the dermis and epidermis. Here, they are ingested by feeding *Culicoides* (midges) or *Simulium* (black flies). Microfilariae develop within the tissues of the fly, migrate to the dipteran mouth parts as infective L_3s, and reinfect another equid during subsequent feeding episodes. In the new host, infective stages migrate to the target connective tissues and begin reproducing ~6 months after inoculation. Adult worms are capable of remaining alive for several years. The prevalence of *Onchocerca* spp. is generally unknown in managed horses, but one survey in central Kentucky found that 24% of examined horses harbored adult worms (Lyons *et al.*, 2000).

Setaria equina

Setaria equina is a filarioid nematode that resides free within the abdominal cavity of equids. Although not pathogenic, it is a very prominent finding at necropsy, which is hard to disavow in the presence of lay witnesses. Microfilariae are produced within the peritoneal cavity, but enter the circulation and can be found in peripheral blood. From here, they are ingested by feeding mosquitos, and

transmission is similar to that described earlier for the genus *Onchocerca*.

Parafilaria multipapillosa

Adult *Parafilaria* occur in subcutaneous and intermuscular connective tissue of horses. Nodules form in the overlying skin, and the nodules may rupture and bleed or leak tissue fluids. First stage larvae are present in the exudate from bleeding lesions and are ingested by feeding horn flies (*Hematobia irritans*). Larvae develop to the infective third stage within the fly and are transferred to horses when flies feed on lachrymal secretions or skin wounds. The larvae then migrate in the subcutaneous tissues and develop to the adult stage within a year. Eggs and microfilariae can readily be identified in smears taken from lesion exudates.

Trichostrongyloidea

Trichostrongyloids are fairly small nematodes that reside within the stomach or abomasum and small intestine of grazing animals. Most trichostrongyloids are parasites of ruminants. The free-living portions of the life cycle are virtually identical to those of the strongyloid nematodes discussed earlier.

Trichostrongylus axei

Trichostrongylus axei is the only gastrointestinal nematode that horses share with other domestic animals. This parasite occurs in the abomasum of sheep, cattle, and goats, and there is some possibility of cross-infection among the various host species.

T. axei females reside in the stomach, and produce eggs which are deposited in feces. They are fairly similar to those of the strongyloid group, but tend to be slightly smaller, more delicate, and one end of the egg is somewhat pointed. *Trichostrongylus* infection can be diagnosed readily by differential coproculture (see Chapter 9). Horses are infected by accidental ingestion of larvae during grazing. Incoming larvae invade gastric glands and develop to the adult stage, whereupon they emerge into the lumen and begin to lay eggs 3 to 4 weeks after infection.

In ruminants, *T. axei* infection is susceptible to anthelmintics of the benzimidazole and macrocyclic lactone classes; similar efficacy is likely in horses. However, a specific label claim does not exist for any equine products, due to the difficulty of demonstrating efficacy against infections of such low prevalence.

Dictyocaulus arnfieldi

Dictyocaulus arnfieldi is the lungworm of equids. Adults live in the terminal bronchioles and can be found in the major airways. Gravid females deposit eggs in bronchial secretions, which are carried proximally by the ciliary apparatus or spontaneous coughing. From the pharynx, the larvae are swallowed and then passed in the feces. Diagnosis involves using the Baermann technique to demonstrate larvae in the feces.

D. arnfieldi is considered a normal parasite of donkeys, because it reproduces readily and induces little pathogenicity. Horses, however, will rarely support an infection to the adult stage because they are not suitable definitive hosts. Infected horses usually have a history of sharing common pasture with donkeys.

Cestodes

Anoplocephalinae

Equids harbor three species of cestodes, but only one of those can be considered common. All are members of a closely related family and, like nearly all other cestodes, require an intermediate host for transmission. Unlike nematodes, equine cestodes apparently do not release individual eggs on a regular basis. Rather, terminal (gravid) proglottids probably detach and disintegrate during transit to the external environment (Figure 1.10).

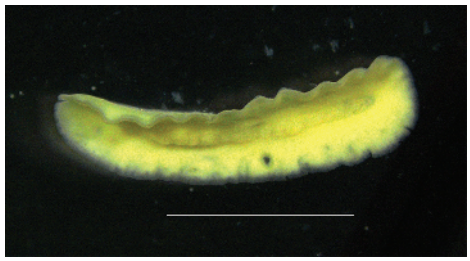

Figure 1.10 Gravid proglottid (tapeworm segment) of *Anoplocephala perfoliata*. Size bar = 1 cm. (*Source*: Photograph courtesy of Jamie K. Norris).

This results in a rather patchy distribution of cestode eggs within the fecal output of infected horses, with obvious diagnostic implications (see Chapter 9).

In the environment, cestode eggs within feces are ingested by free-living mites of the family Oribatidae, which are endemic in soils world-wide. After ingestion, an oncosphere (essentially the scolex of a future adult worm) is digested from the egg within the alimentary tract of the mite. The oncosphere migrates into the hemocoel (body cavity) of the mite and develops into an infective stage known as a cysticercoid (Figure 1.11). Cysticercoids probably remain infective for the lifespan of the mite host and it is likely that infected mites can persist in the environment for longer than a single season.

Horses are infected via inadvertent ingestion of vector mites while grazing. The cysticercoids are digested free of the mite's tissue in the horse's gastrointestinal tract and primitive scolices attach to the lining of the preferred region of gut. Adult cestodes are able to regenerate an entire organism (known as a strobila) from the attached scolex.

Anoplocephala perfoliata

Anoplocephala perfoliata is the most common cestode of equids world-wide, and has been reported from every continent except Antarctica. It is a moderately sized worm, ranging from 1 to 8 cm in length and 1 to 2 cm in width and can be identified by the presence of lappets beneath each of the four suckers on the scolex (Figure 1.12). Proglottids are very small (10–20 mm by 5 mm, but <1 mm thick) and have a yellow-grayish appearance (Figure 1.10). Unlike the cestodes of other mammalian species, it is rare to observe proglottids in the feces of horses, at least of those infected with *A. perfoliata*. *Anoplocephala* infection can be diagnosed by fecal examination, but this technique has fairly low sensitivity in horses, as discussed elsewhere (see Chapter 9).

A. perfoliata is a rare exception to the rule that all adult cestodes reside within the small intestine of their vertebrate host. Adult and developing *A. perfoliata* are mostly found attached to the lining of the cecum and the majority tend to cluster around the cecal side of the ileocecal valve. Additional masses of cestodes are sometimes observed at various locations in the cecum and individual specimens may be attached to the mucosa of the ventral colon or ileum. The longevity of individual specimens of *A. perfoliata* is unknown, but tapeworms mature and remain within the gut through the winter, to be replaced by a new burden during the grazing season.

Several studies have demonstrated a clear, seasonal pattern in the prevalence and abundance of *A. perfoliata*. In temperate climates, most patent infections are observed in the second half of the year, reflecting infections that were acquired and established over the preceding grazing season (Meana *et al.*, 2005).

Anoplocephala magna

True to its name, *A. magna* is the largest cestode occurring in equids and may achieve 80 cm in length. *A. magna* normally attaches to the mucosa in the distal small intestine and can be differentiated from *A. perfoliata* by its relative size and preferred location in the host. For definitive identification of individual specimens

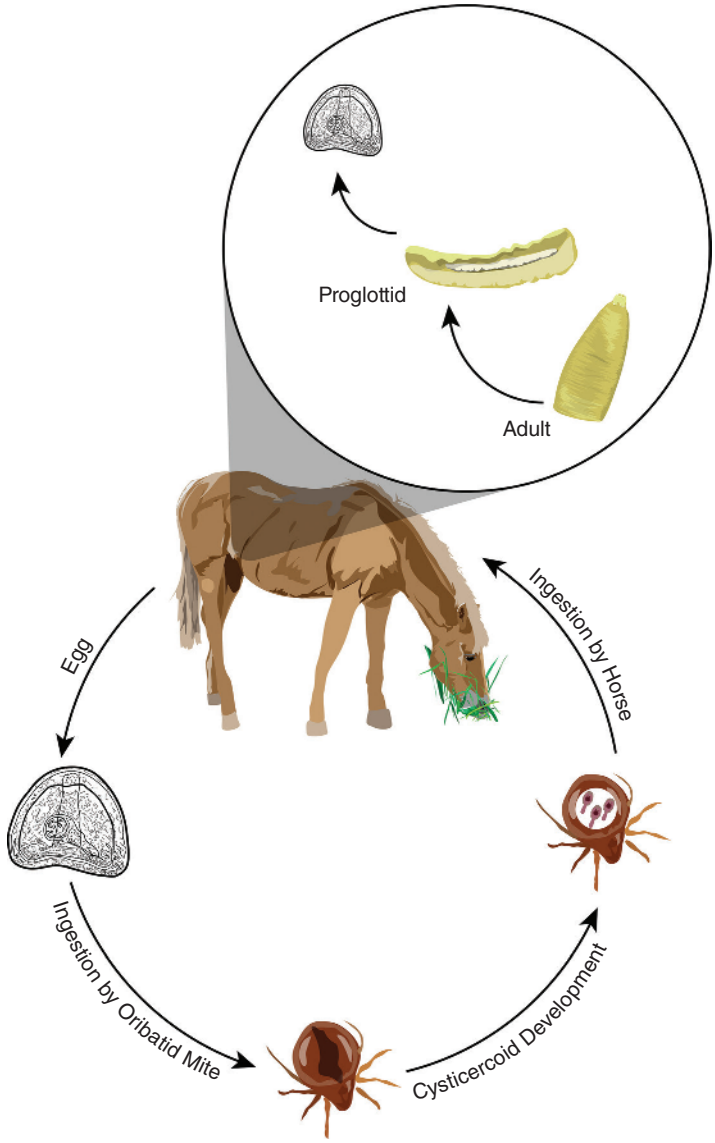

Figure 1.11 Life cycle of *Anoplocephala perfoliata*. Oribatid mites act as intermediate hosts and are ingested by horses while grazing. Proglottids are released from adult tapeworms and are subsequently disintegrated to liberate the eggs inside. (*Source*: Graphics courtesy of Jamie K. Norris).

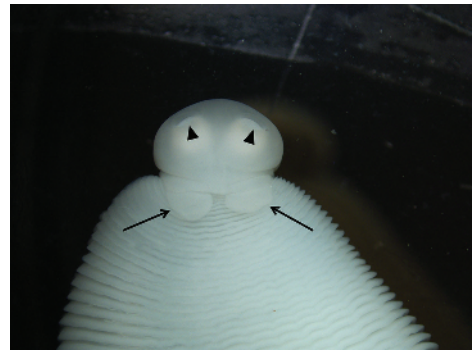

Figure 1.12 Anterior end of an *Anoplocephala perfoliata* specimen obtained from the cecum of a horse at necropsy. This species is characterized by four suckers (arrow heads) with corresponding lappets (arrows) just beneath them. (*Source*: Photograph courtesy of Jamie K. Norris).

A. magna lacks the lappets described for *A. perfoliata* above. Proglottids of *A. magna* are between 2 and 5 cm wide and can sometimes be observed in the feces.

Nearly a century ago, *A. magna* was reportedly far more prevalent than *A. perfoliata*, but the relative ranking of these species has reversed over time. At the present time, *A. magna* is encountered infrequently world-wide.

Anoplocephaloides mamillana (formerly *Paranoplocephala mamillana*)

This is a very uncommon parasite of equids, which normally attaches to the mucosa of the proximal small intestine. It is a very tiny worm, only 6–50 mm long and 4–6 mm wide. Proglottids are similarly small, about 2 by 5 mm, but are sometimes observed motile in the feces. *A. mamillana* is little more than a biological oddity and diagnostic differential; infections are not known to have any clinical impact.

Arthropods

Only one arthropod will be discussed herein, namely members of the genus *Gasterophilus*, known commonly as bot flies.

Horse bot flies are members of a larger family, known as oestrid flies. Although the biological details and the host distributions differ markedly, all oestrid flies employ the same general strategy. Accordingly, oestrid offspring avoid unfavorable environmental conditions by passing their immature stages (termed "instars") within the body of an intended host. The oestrids of large domestic animals deposit eggs or larvae directly onto the intended host. Once the larval stage becomes active (after egg-hatching in some cases), they enter the host by specific routes. Thus, some oestrids (*e.g.*, *Hypoderma* of cattle) hatch from eggs attached to the hair coat, and the larvae penetrate intact skin and undergo sustained systemic migrations. Others (*e.g.*, *Oestrus* of sheep) are deposited as larvae within the nares and migrate only locally and develop within the sinuses. In most cases, the larvae overwinter within the host, emigrate from the host in spring, pupate in the soil, and emerge as adults to complete another generation. Most oestrids are univoltine, meaning they propagate only a single generation per year.

Female flies of the genus *Gasterophilus* attach eggs to individual hairs of equid hosts (Figure 1.13) and larvae gain access to the oral cavity via routes that vary by species. Bot larvae generally overwinter within the equine alimentary tract, pass from the host in the feces during spring or early summer, and pupate in loose soil. Adult flies emerge from the soil one to two months later and emerge to mate and reproduce. Adult oestrids have very brief

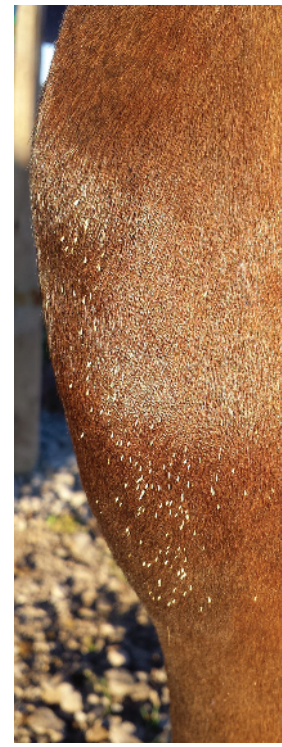

Figure 1.13 *Gasterophilus* spp. eggs attached to the haircoat of the leg.

life spans, due in part to the absence of mouthparts, which renders them incapable of ingesting nutrients.

Gasterophilus intestinalis

Gasterophilus intestinalis is the most prevalent and numerous of the bot species in domesticated horses. Female flies hover and glue individual eggs to hair shafts on the distal forelimbs and occasionally along the neck and mane. Eggs hatch in response to contact with a horse's lips (Bello, 1967), hatch immediately, and attach to the lips and tongue. Eggs that are laid on the mane are probably ingested by herd mates during mutual grooming. First instar larvae burrow into the tongue, creating small airshafts in their wake in the process. First instars are reported to remain within the tongue for up to 21 days (Cogley, Anderson, and Cogley, 1982). They subsequently migrate to the gingival pockets around the molars and premolars, where they molt to the second instar. After about 4 weeks in the oral cavity, they relocate to the stomach, where they attach to the mucosa in the non-glandular portion and develop to the third instar. *G. intestinalis* third instar larvae are about 2 cm long and 5–8 mm wide, dark brownish red in color, and have several rows of spines (Figure 1.14). Burdens of several hundred bots are common in horses, and can be visualized easily and even enumerated gastroscopically.

Gasterophilus nasalis

Female *Gasterophilus nasalis* flies deposit their eggs in the intermandibular area. The eggs hatch spontaneously and larvae crawl independently to the lips, enter the oral cavity, and develop in pockets in the tongue and around the cheek teeth. Ultimately, second instars are swallowed and continue their development in the alimentary tract. Second and third instar *G. nasalis* prefer to attach in the ampulla of the duodenum, just a few centimeters past the pylorus.

Figure 1.14 Third instars of *Gasterophilus intestinalis* (left) and *G. nasalis* (right). Note the characteristic double rows of spines on *G. intestinalis*. (*Source*: Photograph courtesy of Jennifer L. Bellaw).

Other *Gasterophilus* species

Other bot species that apparently do not occur in North America include *Gasterophilus inermis* and *G. hemorrhoidalis*. The latter species attaches in masses in the distal small colon and rectum of donkeys in Africa, and has been documented as a cause of rectal prolapse. Other minor species are distributed around the globe, but none has distinctive pathogenicity.

Trematodes

Trematodes are uncommon parasites of horses in most developed countries. The liver fluke, *Fasciola hepatica*, occasionally infects horses, but is seen only in areas where fascioliasis is endemic in traditional, ruminant hosts. Horses with liver fluke infections inevitably have been pastured where microclimates favor the development of molluscan intermediate hosts. Readers are referred to Nansen, Andersen, and Hesselholt (1975) for a detailed description of the life cycle and clinical features of equine *Fasciola* infection.

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