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Reassignment of *Lamanema* from Nematodirinae to Molineinae (Nematoda: Trichostrongyloidea)

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ABSTRACT: The monospecific *Lamanema* historically has been assigned to the Nematodirinae within the Molineidae. Inconsistencies in morphological characters, within a phylogenetic context for Nematodirinae, led to a re-evaluation of the putative relationships and taxonomic placement of *Lamanema*. Among 7 putative synapomorphies for Nematodirinae, *Lamanema* possesses only 1, large eggs. Large eggs, sporadically present in phylogenetically disparate taxa of trichostrongyles, are equivocal with respect to placement of *Lamanema*; it is considered that possession of this single homoplasious character alone is insufficient justification to retain the genus in Nematodirinae. Affinities with the Trichostrongylidae (Cooperiinae or Haemonchinae) have also been proposed; however, *Lamanema* possess neither of 2 synapomorphies that diagnose monophyly of the family. *Lamanema* is retained in the Molineidae and transferred to the Molineinae as it possesses all characters of the family as currently defined. The origin of *Lamanema* represents a secondary colonization of ruminants by molineids and provides no context for elucidating the history of the Nematodirinae and *Nematodirus*.

Lamanema chavez Becklund, 1963, a distinctive trichostrongyloid nematode parasitizing alpacas (*Lama pacos* (L.)) and vicuña (*Vicugna vicugna* (Molina)) in Peru (Becklund, 1963), is the only member of the genus *Lamanema*. Subsequent to the original description, a unique enterohepatic migration by parasitic third- and fourth-stage larvae was recognized and considered to be the cause of significant pathology associated with infections of the parasite (Chavez et al., 1967; Guerrero et al., 1981). This nematode has been considered a characteristic helminth of South American camelids (Guerrero et al., 1981) and has yet to be reported outside of the Neotropical region (see Rickard and Bishop, 1991). *Lamanema chavez* has also been identified in the chinchillid rodent, *Lagidium viscacia* (Molina), in Argentina, the only known noncamelid host (Sutton and Durette-Desset, 1985).

The placement of *L. chavezii* has been problematic. Becklund (1963) assigned this nematode to the Trichostrongylidae, noting that the prominent dorsal tooth and 2 small lateral teeth in the buccal cavity placed *Lamanema* in either the Nematodirinae or the Haemonchinae, but was distinct based on the presence of an accessory bursal membrane. Durette-Desset and Chabaud (1977) raised the Molineinae Skrjabin and Schultz, 1937 (within the Trichostrongylidae) to family status, transferred the Nematodirinae from the Trichostrongylidae to the Molineidae, and placed *Nematodirus* Ransom, 1907, *Lamanema* Becklund, 1963, *Murielus* Dikmans, 1939, *Nematodirella* Yorke and Maplestone, 1926, and *Nematodiroides* Bernard, 1967 within the Nematodirinae. Further evaluation of the synlophe of *Lamanema* led Durette-Desset (1978) to conclude that the perpendicular orientation of the ridges was consistent with either the Trichostrongylidae or Molineidae. Although the structure of the synlophe, the presence of a cephalic vesicle, and the similarity in bursal type may have indicated affinities with the subfamily Cooperiinae within the Trichostrongylidae, it was placed within the Molineidae based on a short ray 4 and the structure of the spicules. Within the Molineidae, Durette-Desset (1978) observed that the presence of an esophageal tooth (neodont of Durette-Desset [1983, 1985]) placed *Lamanema* within the Nematodirinae, stating that this genus represented a transitional form between the Nematodirinae and the Molineinae. In providing the first description of the female of *L. chavezii*, Sutton and Durette-Desset (1985) specified that the perpendicular orientation of the synlophe coupled with the absence of a corona radiata, a structure typical of the Nematodirinae, supported the earlier contention of Durette-Desset (1978) that *Lamanema* was the most primitive member of the Nematodirinae. With the exception of the inclusion of *Rauschia* Durette-Desset, 1979, for some nematode parasites of lagomorphs previously assigned to *Nematodirus* (Durette-Desset, 1979), the composition of the Nematodirinae has remained unchanged (Durette-Desset, 1983, 1985). Concepts concerning the evolution of this subfamily, and those for host-parasite coevolution and biogeography of its constituent taxa have rested, in part, on the retention of *Lamanema* within the Nematodirinae (see Rossi, 1983; Durette-Desset, 1985; Hoberg et al., 1989; Rickard and Hoberg, 1990; Durette-Desset et al., 1994). During preliminary phylogenetic studies of the Nematodirinae (E. Hoberg and L. Rickard, unpubl. obs.), inconsistencies observed in morphological characters with respect to *Lamanema* led us to initiate a reevaluation of the putative relationships and taxonomic placement of this genus.

In order to establish the comparative context for *Lamanema*, nematodes representing a number of genera and species of trichostrongyloids were examined from the U.S. National Parasite Collection (USNPC), USDA, Beltsville, Maryland (Table I). Specimens were studied as temporary wholemounts. Nematodes were cleared in either phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) or in glycerine-alcohol (90 parts 70% ethanol and 10 parts glycerine) and examined with differential interference contrast light microscopy.

Further comparative evaluations for *Nematodirella*, *Rauschia*, *Nematodiroides*, and *Murielus* were dependant upon the original descriptions or redescriptions of Bernard (1965, 1967), Dikmans (1939), and Durette-Desset (1974, 1979). Systematics for the Trichostrongyloidea is consistent, in part, with that pro-

posed by Durette-Desset (1983, 1985) with modifications related to the Trichostrongylidae based on Hoberg and Lichtenfels (1992, 1994); this disregards a proposal to elevate these and other related strongyles to the rank of suborder (Durette-Desset and Chabaud, 1993; Durette-Desset et al., 1994).

Presence of a well developed synlophe is consistent with placement of *Lamanema* in the Trichostrongyloidea and a simple perpendicular orientation is typical of Molineidae and Trichostrongylidae (Durette-Desset, 1985). *Lamanema* can be excluded from the Trichostrongylidae based on the presence of a tail spine in the female and a short ray 4 in the male bursa, the contrasting condition for these attributes representing synapomorphies for the family (Hoberg and Lichtenfels, 1994). Consequently the contention of Becklund (1963) for a relationship with either Haemonchinae or Cooperiinae is not supported. Based on morphological characters diagnosing the Molineidae, retention of *Lamanema* within this family appears justified. Durette-Desset and Chabaud (1977), characterized the molineids as follows: (1) synlophe generally present with ridges oriented perpendicularly to the body wall or having a ventrodorsal orientation; (2) buccal capsule absent; (3) cephalic vesicle present (with 1 exception); (4) didelphic or monodelphic; and (5) caudal spine always present in the female. These characters are typical of *Lamanema*, although some attributes are clearly plesiomorphic relative to the Trichostrongylidae (Hoberg and Lichtenfels, 1994).

The subfamilies of the Molineidae do not currently have an unequivocal phylogenetic basis, and synapomorphies for the Nematodirinae, Molineinae, Anoplostrongylinae, or the Ollulaninae are not clearly defined. Based on taxonomic outgroup comparisons to other Molineidae and the Trichostrongylidae (Hoberg and Lichtenfels, 1994), however, putative synapomorphies for the Nematodirinae include: (1) presence of corona radiata (with absence in *Murielus*); (2) very long, filiform spicules; (3) fusion of spicule tips; (4) symmetrical membrane enveloping spicule tips; (5) dorsal ray divided and separated at base; (6) gubernaculum absent; and (7) large eggs. Of these characters, presence of a corona radiata, long, filiform spicules, absence of a gubernaculum, and large eggs are homoplasious relative to restricted groups within the Strongylida and Trichostrongyloidea. Conversely, the fusion of the spicule tips, the presence of a symmetrical membrane, and the dorsal ray divided at the base are unequivocal synapomorphies for the Nematodirinae. *Lamanema* possesses only 1 of the 7 putative synapomorphies, i.e., large eggs, and additional structural characters that phylogenetically diagnose the Nematodirinae are absent. Thus, inclusion of *Lamanema* in the Nematodirinae appears to be refuted based on phylogenetically informative characters.

Exclusion of the genus from the Nematodirinae necessitates assigning it to 1 of the 3 remaining subfamilies: Molineinae, Anoplostrongylinae, or Ollulaninae. The latter subfamily contains only *Ollulanus* Leuckart, 1865, which is characterized by monodelphy, bursal type 2-1-2, and lack of a synlophe (Durette-Desset, 1985); examination of specimens in the present study, however, indicates that *O. tricuspis* possess cuticular ridges (L. Rickard, unpubl. obs.). In contrast, the Anoplostrongylinae is frequently didelphic, has bursal type 2-1-2, and a ventrodorsal axis of orientation for the synlophe. The Molineinae is didelphic, has bursal type 2-1-2 tending to type 3-2, and synlophe with ridges oriented perpendicular to the body

TABLE I. Specimens examined to establish context for placement of *Lamanema*.

USNPC no.	Parasite species	Host species
<i>Lamanema</i> :		
60136	<i>L. chavezii</i> Becklund, 1965	<i>Lama pacos</i>
58008	<i>L. chavezii</i>	<i>Vicugna vicugna</i>
59946	<i>L. chavezii</i>	"Llama"
804C*	<i>L. chavezii</i>	<i>Lagidium viscacia boxi</i>
<i>Nematodirus</i> :		
58180	<i>N. maculosus</i> Becklund, 1956	<i>Oreamnos americana</i>
66613	<i>N. maculosus</i>	<i>O. americana</i>
61450	<i>N. odocoilei</i> Becklund and Walker, 1967	<i>Odocoileus hemionus</i>
79902	<i>N. odocoilei</i>	<i>Rangifer tarandus</i>
56730	<i>N. archari</i> Sokolova, 1948	<i>Ovis canadensis</i>
86989	<i>N. spathiger</i> (Railliet, 1896)	<i>Ovis aries</i>
69984	<i>N. battus</i> Crofton and Thomas, 1951	<i>O. aries</i>
86988	<i>N. filicollis</i> (Rudolphi, 1802)	<i>O. aries</i>
86990	<i>N. helvetianus</i> May, 1920	<i>Bos taurus</i>
<i>Nematodirella</i> :		
69355	<i>N. antilocaprae</i> (Price, 1927)	<i>Antilocapra americana</i>
67873	<i>N. antilocaprae</i>	<i>A. americana</i>
33099	<i>N. longissimespiculata</i> (Romanovich, 1915)	<i>R. tarandus</i>
<i>Murielus</i> :		
30461	<i>Murielus harpeticulus</i> Dikmans, 1939	<i>Ochotona princeps</i>
<i>Haemonchus</i> :		
70382	<i>H. placei</i> (Place, 1893)	<i>B. taurus</i>
33156	<i>H. contortus</i> (Rudolphi, 1803)	<i>O. aries</i>
<i>Parostertagia</i> :		
30166	<i>P. heterospiculum</i> Schwartz and Alicata, 1933	<i>Tayassu tajacu</i>
<i>Cooperia</i> :		
904†	<i>Cooperia nietzi</i> Mönnig, 1932	<i>Tragelaphus strepsiceros</i>
70083	<i>C. oncophora</i> (Railliet, 1898)	<i>B. taurus</i>
70084	<i>C. punctata</i> (Linstow, 1907)	<i>B. taurus</i>
<i>Ollulanus</i> :		
81891	<i>O. tricuspis</i> Leuckart, 1865	<i>Felis concolor</i>

* Helminthological Collection, Museo de La Plata, Argentina.

† International Institute of Parasitology, St. Albans, U.K.

surface. *Lamanema* has the latter suite of characters and is consistent with the Molineinae; thus, we propose reassignment of *Lamanema* to this subfamily.

It has been assumed that *L. chavezii* is a characteristic nematode in South American camelids (see Guerrero et al., 1981; Sutton and Durette-Desset, 1985). *Lamanema* has been postulated as the most primitive member of the Nematodirinae, and this observation has been used to support the hypothesis that the subfamily arose in the New World from primitive Molineinae. *Lamanema* then constitutes the link between the 2 subfamilies (e.g., Rossi, 1983; Durette-Desset, 1985). Within Nematodirinae, 2 lineages are then linked to *Lamanema*. Following an origin for Nematodirinae during the Oligocene, divergent lineages radiated in lagomorphs and in ruminants (Durette-Desset and Chabaud, 1981; Rossi, 1983; Durette-Desset, 1985; Durette-Desset et al., 1994). Among ruminants, the genus *Nematodirus* originated in the Nearctic among Camelidae and secondarily became distributed in the Neotropics and Palearctic coinciding with dispersal of hosts and parasites following colonization of cervids and cap-

rine bovids. *Lamanema* would then represent a relictual parasite in South American Camelidae. Exclusion of *Lamanema* from the Nematodirinae would refute the foundation for this hypothesis and may be compatible with a Palearctic origin for the subfamily (see Hoberg et al., 1989; Rickard and Hoberg, 1990).

The origin of *Lamanema* may represent a secondary colonization of ruminants by molineids and provides no context for elucidating the history of the Nematodirinae and *Nematodirus*. Due to the severe disease that can be caused by infections of *L. chavezii* in the alpaca, the parasite has been well studied. This focus has led to substantial documentation of the nematode's occurrence in alpacas in Peru. It is possible, however, with continued survey and inventory of the South American fauna that *Lamanema* will be found to be representative of the typical parasite fauna in rodents. Indeed this may be compatible with the report of *L. chavezii* in chinchillid rodents from Argentina (Sutton and Durette-Desset, 1985).

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