MOTUs, Morphology, and Biodiversity Estimation: A Case Study Using Nematodes of the Suborder Criconematina and a Conserved 18S DNA Barcode

THOMAS POWERS, TIMOTHY HARRIS, REBECCA HIGGINS, PETER MULLIN, LISA SUTTON, KIRSTEN POWERS

Abstract: DNA barcodes are increasingly used to provide an estimate of biodiversity for small, cryptic organisms like nematodes. Nucleotide sequences generated by the barcoding process are often grouped, based on similarity, into molecular operational taxonomic units (MOTUs). In order to get a better understanding of the taxonomic resolution of a 3' 592-bp 18S rDNA barcode, we have analyzed 100 MOTUs generated from 214 specimens in the nematode suborder Criconematina. Previous research has demonstrated that the primer set for this barcode reliably amplifies all nematodes in the Phylum Nematoda. Included among the Criconematina specimens were 25 morphologically described species representing 12 genera. Using the most stringent definition of MOTU membership, where a single nucleotide difference is sufficient for the creation of a new MOTU, it was found that an MOTU can represent a subgroup of a species (e.g. *Discocriconemella limitanea*), a single species (*Bakernema inaequale*), or a species complex (MOTU 76). A maximum likelihood phylogenetic analysis of the MOTU dataset generated four major clades that were further analyzed by character-based barcode analysis. Fourteen of the 25 morphologically identified species had at least one putative diagnostic nucleotide identified by this character-based approach. These diagnostic nucleotides could be useful in biodiversity assessments when ambiguous results are encountered in database searches that use a distance-based metric for nucleotide sequence comparisons. Information and images regarding specimens examined during this study are available online.

Key words: Criconematidae, DNA taxonomy, phylogeny, barcode analysis, plant parasitic nematodes, nematode diversity.

The estimation of nematode biodiversity exemplifies the challenges in exploring a taxon with a major percentage of its diversity undescribed. In the phylum Nematoda, it is probably an overestimate to suggest that the approximately 27,000 described species represent 5-10% of the existing nematode taxa on the planet (Hugot et al., 2001; Creer et al., 2010; Fonseca et al., 2010). This "well-acknowledged biodiversity identification gap", the ratio of known species (described) to unknown species (not yet described), has been attributed to the small size of nematodes, their simple morphology, intraspecific variation, and the lack of nematode taxonomists (Creer et al., 2010). One study of nematode diversity in a tropical forest in Cameroon estimated that 6,000 scientist-hours of labor were required to sort and catalogue 431 morphologically identified nematode species, for a survey in which over 90% of the specimens could not be assigned to known species (Bloemers et al., 1997). It is no wonder that molecular approaches that can possibly expedite the process of species discovery and description have been actively pursued (Blaxter, 2004; Markmann and Tautz, 2005; Bhadury et al., 2006; Donn et al., 2008; Porazinska et al., 2009, 2010a, 2010b; Powers et al., 2009; Da Silva et al., 2010; Abebe et al., 2011).

Ironically, this identification gap will likely widen as molecular approaches increase in their application. With the advent of high throughput, next generation sequencing, an entire community of nematodes can be rapidly reduced to a single set of sequences (Creer et al. 2010; Porazinska et al., 2010b). These sequences, if they are derived from a common gene following PCR of pooled DNA from the nematode community, may be considered as a set of MOTUs (molecular operational taxonomic units) (Floyd et al., 2002; Blaxter et al., 2005; Caron et al., 2009; Creer et al. 2010; Jones et al. 2011). An MOTU can be defined as a cluster of sequences that fall within a designated cutoff value of sequence identity, the cutoff value being established by the author (Caron et al., 2009). The cutoff value could require 100% sequence identity, in which case each unique sequence is considered a separate MOTU. The taxonomic significance of a given MOTU depends on a number of factors such as the genetic region under analysis, the rate of evolution of that region, experimental error, and the congruence of gene trees and species trees. Since these factors are seldom completely understood, it is not a trivial question to ask, "What does an MOTU represent?"

In this study we explore the performance of a 3' 592 bp 18S barcode as a tool to generate MOTUs and assess nematode diversity. The term barcode in this case refers to the specific region of the 18S gene amplified by the 18S1.2a/18Sr2b PCR primer set, and the nucleotide sequence between them, but not including the primer sequence itself. The barcode was selected due to its evolutionarily conserved nature, exhibiting a balance between phylogenetic breadth and taxonomic resolution. It has previously been used in a phylum-wide molecular survey of nematode communities within a lowland Costa Rican rain forest (Powers et al., 2009), a metagenetic analysis of artificially constructed nematode communities (Porazinska et al., 2009) and a multi-phyla metagenetic survey replicating the aforementioned Costa Rican rain forest study (Porazinska et al., 2010a). MOTUs derived from 18S have the advantage of comparison to the 18S-based Nematode Tree of Life which in its most current published form includes 1215 taxa (van Megen et al., 2009). We assume that MOTUs that

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link with morphologically and taxonomically characterized entities are a richer source of systematic information and maximize information content from studies employing MOTUs unlinked from taxonomically characterized entities. Therefore, a second purpose of this study is to enlarge the reference database in order to facilitate future systematic studies.

To address the question of MOTU representation, we apply the 3' 592 bp 18S barcode to an analysis of a single, globally distributed suborder of plant-parasitic nematodes. The suborder Criconematina Siddiqi, 1980 ranges from the humid tropics to arctic and alpine habitats. There are an estimated 750 described species in the suborder (Subbotin et al., 2005). They are found on a wide range of hosts feeding on plants as diverse as hardwoods, conifers, bromeliads, grasses and moss. They are believed to have a high level of endemicity and are some of the most abundant soil-dwelling plant parasites in tropical forests (Wouts, 2006). Their high endemicity, poor dispersal capabilities, and apparent lack of specialized survival stages make them a potential subject for biogeographic analysis (Bernard and Schmitt, 2005; Wouts, 2006). They are potential indicators for soil disturbance (Bernard, 1992). While a few species appear to be adapted to disturbances associated with agricultural production, the vast majority are confined to native habitats with a relatively stable soil structure (Hoffman and Norton, 1976; Bernard, 1982; Peneva et al., 2000) and tend to disappear when these habitats are disrupted. It is widely believed that Criconematina constitutes a monophyletic group, although the relationships and composition of sub-groups are generally considered to be "taxonomically opaque" and in a perpetual state of taxonomic turmoil (Siddiqi, 2000; Subbotin et al., 2005, 2006; Bert et al., 2008; Hunt, 2008). Monophyly of the suborder has been supported by both molecular and morphological analysis (Holterman et al., 2006; Subbotin et al., 2006; Bert et al., 2008; van Megen et al., 2009).

The nematodes in this study have been obtained through a series of collections spanning the years 1999 to 2010 (Table 1). Nematodes were individually isolated from soil samples, many digitally photographed (most often while alive), measured, processed for PCR, amplified and sequenced for the 18S barcode. Collection localities included non-cultivated as well as cultivated soils, with approximately one-third of the specimens recovered from Costa Rica and the remaining specimens from the United States, Mexico, and Europe. An additional 21 sequences from GenBank were added to the analysis.

The specific objective of this study is to apply a phylogenetic and a character-based barcode analysis to a 100-MOTU dataset of Criconematina specimens. This dataset includes 25 *a priori* identified species, recognized by traditional morphological analysis. The dataset also includes specimens that could not be identified *a priori* to species with confidence. The unknown specimens may represent new species or specimens that do not provide sufficient information for an accurate identification. We attempt to determine if there exists any nucleotide sequence support for the morphologically identified taxa. This analysis should provide insight into the taxonomic resolution of the 18S barcode, which in turn should enhance studies of nematode biodiversity.

MATERIALS AND METHODS

Nematode collections: The earliest collected specimens in this study, those collected between 1999 and 2005, tend to have less associated morphological data, as methods were being developed to obtain both molecular and morphological information from an individual specimen. Two biodiversity surveys contributed a significant number of specimens to this study; a 1999 nematode survey of Konza Prairie, a designated Long Term Ecological Reserve, and a 2005 survey of La Selva Biological Research Station operated by the Organization of Tropical Studies (NSF DEB 0640807) (NSF DEB 9806439). The geographic coverage in this study includes specimens from Atlantic and Pacific coasts, and Central Valley of Costa Rica. North American specimens were collected from 21 U.S. states and a single state in Mexico. Twenty one GenBank accessions were added to the analysis, all of which represent European collections. Four sampling sites represent type localities from which the targeted species was obtained.

Nematode morphological identification: Nematodes were observed by differential interference microscopy on a Leica DMLB microscope, images recorded by a Leica DC300 video camera, and measurements obtained using an eyepiece micrometer at 1000x magnification. Observations were made on living nematodes whenever possible. In some cases such as Bakernema specimens, the elaborate cuticular ornamentation is more visible in living than dead or fixed specimens. After nematode measurement, the slide was carefully dismantled by removing the cover slip, the nematode recovered using a fine insect pin pick, added to an 18ul drop of sterile water, and then smashed on a cover slip with a clear, sterile micropipette tip. Nematode residue was stored in PCR reaction tubes in a -20°C freezer until PCR amplification.

DNA amplicon characteristics, terminology and assumptions: The 18S1.2a/18Sr2b primer set typically amplifies a 635-bp region of the 18S ribosomal gene, with the 3'most primer located 180-bp from the first internal transcribed spacer (ITS1). The primer set, 18S1.2a: 5'-CGATCAGATACCGCCCTAG-3' (forward) and 18Sr2b: 5'-TACAAAGGGCAGGGACGTAAT-3' (reverse) will amplify nematodes throughout the phylum and will amplify some non-nematode taxa. The term barcode in this study applies to that specific region of the 18S gene bounded by those primers. This barcode is distinct and does not overlap with the 5'-18S barcode region analyzed

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M9 214072 Cricomena sp. F Braulio Carillo National Park, Costa Rica HMI15998 M10 199013 Cricomena sp. Braulio Carillo National Park, Costa Rica F[489376 M11 214061 Cricomena sp. Braulio Carillo National Park, Costa Rica HMI15999 M11 214062 Cricomena sp. F Las Cruces Biological Station, Costa Rica HMI15995 M12 214071 Cricomena sp. F Las Cruces Biological Station, Costa Rica HMI15997 M14 Cricomena sp. Gentlank Aj966480 M15 290 Cricomena splagai F Governor Dodge State Park, WI JE72463 M15 291 Cricomena splagai F Archuleta County, CO JE72465 M16 599 Cricomenoides annulatus F Archuleta County, CO JE72465 M17 124097 Cricomenoide informis Perkins County, NE F[489332 M18 119007 Cricomenoide insuitatus F Paramel Woods, Story County, IA F[489521 M18 119009 Cricomenoide sp. F Natlatco, Mexico F[489352 M18 119007 Cricomenoide sp. F Natlatco, Mexico F[489532 M18 119009	M9	199017	Criconema sp.		Braulio Carillo National Park, Costa Rica	FJ489579
M9214073Cricomena sp.FBruulio Carillo National Park, Costa RicaHMI15999M10199013Cricomena sp.Bruulio Carillo National Park, Costa RicaF[489576M11214061Cricomena sp.JLas Cruces Biological Station, Costa RicaHMI1599M12214062Cricomena sp.FLas Cruces Biological Station, Costa RicaHMI15997M13214071Cricomena sp.FBraulio Carillo National Park, Costa RicaHMI15997M14Cricomena sp.FGenBankState Park, WIJ[972463M15290Cricomena sphagaiJGovernor Dodge State Park, WIJ[972463M16603Cricomena sphagaiFGovernor Dodge State Park, WIJ[972463M17124095Cricomenoide annulatusFArchuleta County, COJ[972466M18119007Cricomenoide informisPerkins County, NEF[489532M18119007Cricomenoide insustatusFParmuel Woods, Story County, IAF[489524M18119007Cricomenoide insustatusFParmuel Woods, Story County, IAF[489525M18119007Cricomenoides insustatusFPartice County, COHMI16399M20214076Cricomenoides insustatusFPartice County, COHMI16392M21132010Discoricomenula limitaneaJLa Selva Biological Station, Costa RicaEU879991M22133011Discoricomenula limitaneaJLa Selva Biological Station, Costa Rica	M9	214072	Criconema sp.	F	Braulio Carillo National Park, Costa Rica	HM115998
M10199013Cricomena sp.Braulio Carillo National Park, Costa RicaF J489575M11214061Cricomena sp.JLas Cruces Biological Station, Costa RicaHM115994M12214062Cricomena sp.FBraulio Carillo National Park, Costa RicaHM115997M13214071Cricomena sp.FBraulio Carillo National Park, Costa RicaHM115997M14Cricomena sp.FBraulio Carillo National Park, Costa RicaHM115997M15290Cricomena sp.FGovernor Dodge State Park, WIJP372463M15291Cricomena splogniFGovernor Dodge State Park, WIJP372463M16599Cricomena splogniFArchuleta County, COJP72465M17124095Cricomenoides annulatusFArchuleta County, COJP372465M17124097Cricomenoides insolutusFParkins County, NEF J489532M18119009Cricomenoides insolutusFParmmel Woods, Story County, IAF J489525M18119009Cricomenoides insolutusFParmmel Woods, Story County, IAF J489526M18119012Cricomenoides sp.FKallalaco, MexicoF J489579M20214076Cricomenoides sp.FKallalaco, MexicoF J489579M21132010Discorricomenoli ImitaneaJLa Selva Biological Station, Costa RicaEU879991M22138012Discorricomenoli ImitaneaJLa Selva Biological Station, Costa RicaEU880	M9	214073	Criconema sp.	F	Braulio Carillo National Park, Costa Rica	HM115999
M10199015Criconema sp.Braulio Carillo National Park, Costa Rica[#]489578M11214061Criconema sp.JLas Cruces Biological Station, Costa RicaHM115994M12214062Criconema sp.FLas Cruces Biological Station, Costa RicaHM115997M13214071Criconema sp.FBraulio Carillo National Park, Costa RicaHM115997M14CCriconema splagniJGovernor Dodge State Park, WIJP972463M15290Criconema splagniJGovernor Dodge State Park, WIJP972463M16599Criconemides annulatusFArchuleta County, COJP972465M16603Criconemides inponisPerkins County, NEFJ489532M17124095Criconemides insidutusFParkine Woods, Story County, IAFJ489532M18119007Criconemides insidutusFPammel Woods, Story County, IAFJ489521M18119007Criconemides insidutusFNatificato, MexicoFJ489521M18119007Criconemides insidutusFNatificato, MexicoFJ489521M18119007Criconemides insidutusJKent County, DEFJ489521M18119007Criconemides insidutusJLa Schwa Biological Station, Costa RicaEUX79992M18119007Criconemides insidutusJLa Schwa Biological Station, Costa RicaEUX95991M20214076Criconemides insidutusJLa Schwa Biological Station, Costa Rica <td< td=""><td>M10</td><td>199013</td><td>Criconema sp.</td><td></td><td>Braulio Carillo National Park, Costa Rica</td><td>FJ489576</td></td<>	M10	199013	Criconema sp.		Braulio Carillo National Park, Costa Rica	FJ489576
M11214061Criconema sp.JLas Cruces Biological Station, Costa RicaHMI15995M13214071Criconema sp.FBraulio Carillo National Park, Costa RicaHMI15997M14Criconema sp.FBraulio Carillo National Park, Costa RicaHMI15997M15289Criconema sphagniFGovernor Dodge State Park, WIJP972462M15290Criconema sphagniFGovernor Dodge State Park, WIJP972463M15291Criconema sphagniFGovernor Dodge State Park, WIJP972464M16599Criconemoids annulatusFArchuleta County, COJP972466M17124095Criconemoids insulatusFArchuleta County, COJP972465M17124097Criconemoids insulatusFParkins County, NEFJ489523M18119009Criconemoides insulatusFPanmel Woods, Story County, IAFJ489521M18119012Criconemoides insulatusJKent County, DEFJ489522M1930Criconemoides sp.FXalatlaco, MexicoFJ489521M20214076Criconemoides sp.FXalatlaco, MexicoFJ489521M21132010Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879091M22138013Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU89007M24138013Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEJ489553 </td <td>M10</td> <td>199015</td> <td>Criconema sp.</td> <td></td> <td>Braulio Carillo National Park, Costa Rica</td> <td>FJ489578</td>	M10	199015	Criconema sp.		Braulio Carillo National Park, Costa Rica	FJ489578
	M11	214061	Criconema sp.	J	Las Cruces Biological Station, Costa Rica	HM115994
M13 2140/1 Creation asp. F Braulio Carillo National Park, Costa Rica HM I1599/ M15 289 Cricomena sphagni F Governor Dodge State Park, WI JP372463 M15 290 Cricomena sphagni F Governor Dodge State Park, WI JP372463 M16 599 Cricomena sphagni F Governor Dodge State Park, WI JP372463 M16 603 Cricomenoides annulatus F Archuleta County, CO JP372463 M17 124095 Cricomenoides informis Perkins County, NE EJ489533 M18 119007 Cricomenoides informis Perkins County, NE EJ489523 M18 119009 Cricomenoides invisitatus F Panmel Woods, Story County, IA EJ489523 M19 30 Cricomenoides invisitatus J Kent County, OC HM116300 M20 214076 Cricomenoides sp. F Xalataco, Mexico EJ489521 M21 132010 Discorricomenella limitanea J La Seba Biological Station, Costa Rica EU870991 M22 132011 Discorricomenella limitanea J La Seba Biological Station, Costa Rica EU880007 M23 138013 Discorricomenella limitanea J La S	M12	214062	Criconema sp.	F	Las Cruces Biological Station, Costa Rica	HM115995
M14Critomena sphagniFGernsankAprobasioM15289Critomena sphagniFGovernor Dodge State Park, WIJP372462M15291Critomena sphagniFGovernor Dodge State Park, WIJP372463M16603Critomena sphagniFGovernor Dodge State Park, WIJP372463M16603Critomenado sinfomisFArchuleta County, COJP372463M17124095Critomenados infomisPerkins County, NEEJ489521M18119007Critomenados infomisPerkins County, NEEJ489521M18119007Critomenados inusitatusFPanmel Woods, Story County, IAEJ489525M18119007Critomenados sp.FLatimer County, DEEJ489525M18119012Critomenados sp.FXalataco, MexicoEJ489525M1930Critomenados sp.FXalataco, MexicoEJ489529M20214076Critomenados sp.FXalataco, MexicoEJ489592M21132010Discorricomendla limitaneaJLa Selva Biological Station, Costa RicaEU879992M23138012Discorricomendla limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discorricomendla limitaneaJLa Selva Biological Station, Costa RicaEJ489539M25158040Discorricomendla limitaneaFLa Selva Biological Station, Costa RicaEJ489539M25158030Discorricomendla limitanea	M13	214071	Criconema sp.	F	Braulio Carillo National Park, Costa Rica	HM115997
M15289Creanema splagniFGovernor Dodge State Park, W1 $JP72462$ M15291Criconema splagniFGovernor Dodge State Park, W1 $JP72463$ M16599Criconema splagniFArchuleta County, CO $JP72465$ M16603Criconemoides annulatusFArchuleta County, CO $JP72466$ M17124095Criconemoides informisPerkins County, NE $FJ89532$ M18119007Criconemoides insustatusFParmel Woods, Story County, IA $FJ89522$ M18119009Criconemoides insustatusFParmel Woods, Story County, IA $FJ89522$ M18119009Criconemoides insustatusJKent County, DE $FJ89522$ M1930Criconemoides pp.FLarimer County, COHM110630M20214076Criconemoides pp.FXalataco, Mexico $FJ89592$ M21132010Discoriconemola phaneJLa Selva Biological Station, Costa RicaEU879991M22138012Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138003Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25158030Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ89553M27151059Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ89553M28184097Discoriconemella limitaneaFLa Selva Biolog	M14	000	Criconema sp.	Б	GenBank	AJ966480
M15290Chronema splagniJGovernor Dodge State Park, W1J P724403M15291Criconemaids annulatusFArchuleta County, COJ P724453M16603Criconemaids annulatusFArchuleta County, COJ P724453M17124095Criconemaids informisPerkins County, NEF J489532M17124097Criconemaids insuitatusFParmel Woods, Story County, IAF J489532M18119007Criconemaids insuitatusFParmel Woods, Story County, IAF J489522M18119002Criconemaids insuitatusFParmel Woods, Story County, IAF J489522M1930Criconemaids sp.FLarimer County, COHM116030M20214076Criconemaids sp.FXalataco, MexicoF J489591M21132011Discorcironemalla limitaneaJLa Selva Biological Station, Costa RicaEU879992M23138012Discorcironemalla limitaneaJLa Selva Biological Station, Costa RicaEU880006M24138030Discorcironemalla limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138030Discorcironemalla limitaneaFLa Selva Biological Station, Costa RicaF J489535M30184027Discorcironemalla limitaneaFLa Selva Biological Station, Costa RicaF J489549M24138030Discorcironemalla limitaneaFLa Selva Biological Station, Costa RicaF J489553M30184027Discorciro	M15 M15	289	Criconema sphagni Criconema shkami	r T	Governor Dodge State Park, WI	JF972462 JE079462
M16DescriptionFActual actionDescriptionM16603Griconemides annulatusFArchuleta County, COJF972466M17124095Griconemides informisPerkins County, COJF972465M17124097Griconemides informisPerkins County, NEFJ489532M18119007Griconemides insuitatusFPanmel Woods, Story County, IAFJ489521M18119009Griconemides insuitatusFPanmel Woods, Story County, IAFJ489525M18119012Griconemides sp.FLarimer County, COHM116030M20214076Griconemides sp.FXalatlaco, MexicoFJ489521M21132010Discorriconemide limitaneaJLa Selva Biological Station, Costa RicaEU879991M22132011Discorriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discorriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25138030Discorriconemella limitaneaFLa Selva Biological Station, Costa RicaEU880008M25138030Discorriconemella limitaneaFLa Selva Biological Station, Costa RicaEU880007M26151041Discorriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489553M27151059Discorriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ4895549M30184027Discorriconemella limitaneaF<	M15 M15	290	Criconema sphagni Criconema sthagni	J F	Governor Dodge State Park, WI	JF972405 JF079464
AltoDiscortionedia annulativeFArchuleta County, COJP72466M17124095Criconemoides informisPerkins County, NEFJ489533M18119007Criconemoides informisPerkins County, NEFJ489533M18119007Criconemoides inusitatusFPammel Woods, Story County, IAFJ489521M18119009Criconemoides inusitatusFPammel Woods, Story County, IAFJ489525M18119012Criconemoides inusitatusFPammel Woods, Story County, IAFJ489525M1930Criconemoides sp.FLarimer County, COHM116030M20214076Criconemoides sp.FXalatlaco, MexicoFJ489521M21132010Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M23138012Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880021M25138030Discoriconemella limitaneaHLa Selva Biological Station, Costa RicaFJ489539M26151041Discoriconemella limitaneaHLa Selva Biological Station, Costa RicaFJ489539M26154041Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489539M27151059Discoriconemella limitaneaFLa Sclva Biological Station, Costa RicaFJ489539M30184030Discoriconemell	M16	599	Criconemoides annulatus	F	Archuleta County CO	JF972404 JF979465
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M18119007Criconemoides inusitatusFPammel Woods, Story County, IA \vec{F} [489521M18119009Criconemoides inusitatusFPammel Woods, Story County, IA \vec{F} [489525M18119012Criconemoides inusitatusJKent County, DE \vec{F} [489525M1930Criconemoides sp.FLarimer County, COHM116030M20214076Criconemoides sp.FXalataco, Mexico \vec{F} [489592M21132010Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22132011Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880012M25138030Discocriconemella limitaneaFLa Selva Biological Station, Costa RicaEU880021M26151041Discocriconemella limitaneaFLa Selva Biological Station, Costa RicaF J489539M28183097Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF J489549M29184026Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF J489559M30184030Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF J489554M31184030Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF J489559M32154100Hemicalosia sp.J<	M17	124097	Criconemoides informis		Perkins County, NE	FJ489533
M18119009Criconemoides inusitatusFParmel Woods, Story County, IAF [489522M18119012Criconemoides inusitatusJKent County, DEF [489525M1930Criconemoides sp.FLarimer County, COHIM116030M20214076Criconemoides sp.FXalatlaco, MexicoF [489591M20214077Criconemoides sp.FXalatlaco, MexicoF [489592M21132010Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22132011Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138012Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25138030Discocriconemella limitaneaFLa Selva Biological Station, Costa RicaEU880012M26151041Discocriconemella limitaneaMLa Selva Biological Station, Costa RicaF [489553M28183097Discocriconemella limitaneaFLas Chuces Biological Station, Costa RicaF [489554M30184027Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF [489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M33B40030Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF [489554M30184030Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaF [M18	119007	Criconemoides inusitatus	F	Pammel Woods, Story County, IA	FJ489521
M18119012Criconemoides inusitatusJKent County, DEFFM1930Criconemoides sp.FLarimer County, COHIM16030M20214076Criconemoides sp.FXalataco, MexicoFJ489591M20214077Criconemoides sp.FXalataco, MexicoFJ489592M21132010Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22138012Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879992M23138013Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880081M26151041Discoriconemella limitaneaMLa Selva Biological Station, Costa RicaFJ489535M27151059Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489549M29184026Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489552M30184027Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankA7284624M34Hemicriconemoides pseud	M18	119009	Criconemoides inusitatus	F	Pammel Woods, Story County, IA	FJ489522
M1930Criconemides sp.FLarimer County, COHM116030M20214076Criconemides sp.FXalatlaco, MexicoFJ48959M20214077Criconemides sp.FXalatlaco, MexicoFJ48959M21132010Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22132011Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879992M23138012Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880121M26151041Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaEJ89539M28183097Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489539M28184027Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489539M30184027Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489539M30184030Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489539M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489539M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021 <t< td=""><td>M18</td><td>119012</td><td>Criconemoides inusitatus</td><td>J</td><td>Kent County, DE</td><td>FJ489525</td></t<>	M18	119012	Criconemoides inusitatus	J	Kent County, DE	FJ489525
M20214076Criconemoides sp.FXalatlaco, MexicoF[489591M20214077Criconemoides sp.FXalatlaco, MexicoF[489592M21132010Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22138012Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879992M23138012Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discocriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25138030Discocriconemella limitaneaFLa Selva Biological Station, Costa RicaEU880121M26151041Discocriconemella limitaneaMLa Selva Biological Station, Costa RicaEJ489539M28183097Discocriconemella limitaneaFLas Clava Biological Station, Costa RicaEJ489539M28184026Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaEJ489554M30184027Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaEJ489554M31184031Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaEJ489554M32154004Hemicaloosia sp.JCurtis Prairie, WIHM116020M33Hemicriconemoides pseudobrachyurusGenBankAY284623M34Hemicriconemoides pseudobrachyurusGenBankAY284624M3626	M19	30	Criconemoides sp.	F	Larimer County, CO	HM116030
M20214077Criconemoides sp.FXalatlaco, MexicoF[489592M21132010Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22138012Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880017M25154041Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaEU880121M26151041Discoriconemella limitaneaMLa Selva Biological Station, Costa RicaF[489539M28183097Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaF[489539M28184027Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF[489554M30184030Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF[489554M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF[489554M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M34Hemicriconemoides pseudobrachyurusGenBankAY284622M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266H	M20	214076	Criconemoides sp.	F	Xalatlaco, Mexico	FJ489591
M21132010Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU879991M22132011Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU870992M23138012Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138030Discoriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25138030Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaEU8800121M26151041Discoriconemella limitaneaMLa Selva Biological Station, Costa RicaFJ489535M27151059Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489549M28183097Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489552M30184026Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M33Iemicriconemoides pseudobrachyurusGenBankAY284623M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284623M36266Hemicriconemoides wessoniFArcholod Biological Station, FLHM116034M38585H	M20	214077	Criconemoides sp.	F	Xalatlaco, Mexico	FJ489592
M22132011Discoriconenella limitaneaJLa Selva Biological Station, Costa RicaEU8/0907M23138012Discoriconenella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discoriconenella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25138030Discoriconenella limitaneaFLa Selva Biological Station, Costa RicaEU880121M26151041Discoriconenella limitaneaMLa Selva Biological Station, Costa RicaFJ489539M27151059Discoriconenella limitaneaKLa Selva Biological Station, Costa RicaFJ489539M28183097Discoriconenella limitaneaFLa Selva Biological Station, Costa RicaFJ489559M29184026Discoriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M30184030Discoriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discoriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M33Hemicriconenoides pseudobrachyurusGenBankAV284623M34Hemicriconenoides pseudobrachyurusGenBankAV284623M35Hemicriconenoides pseudobrachyurusGenBankAV284623M36266Hemicriconenoides wessoniJIchetucknee River, Columbia County, FLJF972467M38585 </td <td>M21</td> <td>132010</td> <td>Discocriconemella limitanea</td> <td>J</td> <td>La Selva Biological Station, Costa Rica</td> <td>EU879991</td>	M21	132010	Discocriconemella limitanea	J	La Selva Biological Station, Costa Rica	EU879991
M23138012Discorriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880007M24138013Discorriconemella limitaneaJLa Selva Biological Station, Costa RicaEU880008M25138030Discorriconemella limitaneaFLa Selva Biological Station, Costa RicaEJ8805121M26151041Discorriconemella limitaneaMLa Selva Biological Station, Costa RicaFJ489539M28183097Discorriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489552M30184026Discorriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M30184027Discorriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M30184030Discorriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M31184031Discorriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM1160201M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArcholod Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniFIchetucknee River, Columbia County, FL <t< td=""><td>M22</td><td>132011</td><td>Discocriconemella limitanea</td><td>J</td><td>La Selva Biological Station, Costa Rica</td><td>EU879992</td></t<>	M22	132011	Discocriconemella limitanea	J	La Selva Biological Station, Costa Rica	EU879992
M24138013Distortionendia timitaneajLa Selva Biological Station, Costa RicaEU 880000M25138030Discocriconenella limitaneaFLa Selva Biological Station, Costa RicaEU 880121M26151041Discocriconenella limitaneaMLa Selva Biological Station, Costa RicaFJ489535M27151059Discocriconenella limitaneaFLa Selva Biological Station, Costa RicaFJ489539M28183097Discocriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489549M29184026Discocriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M30184027Discocriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discocriconenella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116020M33Hemicriconenoides pseudobrachyurusGenBankAY284622M34Hemicriconenoides pseudobrachyurusGenBankAY284624M36266Hemicriconenoides wessoniJArchbold Biological Station, FLHM116035M38585Hemicriconenoides wessoniJIchetuknee River, Columbia County, FLJF972467M38586Hemicriconenoides wessoniJIchetuknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankAJ966471M41571Hemicycliophor	M23 M94	138012	Discocriconemeula limitanea	J	La Selva Biological Station, Costa Rica	EU880007
M25Distortioneneilal limitaneaFLa Serva Biological Station, Costa RicaFJ489535M27151059Discoriconemella limitaneaLa Selva Biological Station, Costa RicaFJ489535M28183097Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaFJ489535M29184026Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489552M30184027Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M30184030Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972468M39Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972469M40Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972469M40Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972469M41571Hemicriconemoides pp. <td< td=""><td>M24 M95</td><td>138013</td><td>Discocriconemetta timitanea Discocriconemetta limitanea</td><td>J F</td><td>La Selva Biological Station, Costa Rica</td><td>EU880191</td></td<>	M24 M95	138013	Discocriconemetta timitanea Discocriconemetta limitanea	J F	La Selva Biological Station, Costa Rica	EU880191
M201910 IIDiscorticontended limitationMLa Selva Biological Station, Costa RicaF [489539M27151059Discorticonemella limitaneaFLa Selva Biological Station, Costa RicaF [489539M29184026Discorticonemella limitaneaFLa Selva Biological Station, Costa RicaF [489539M30184027Discorticonemella limitaneaFLas Cruces Biological Station, Costa RicaF [489553M30184030Discorticonemella limitaneaFLas Cruces Biological Station, Costa RicaF [489553M31184031Discorticonemella limitaneaFLas Cruces Biological Station, Costa RicaF [489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHMI16020M32164097Hemicaloosia sp.JCurtis Prairie, WIHMI16021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides pseudobrachyurusGenBankAY284624M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972468M39Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972468M39Hemicriconemoides wessoniFIchet	M25 M26	151041	Discocriconemella limitanea	M	La Selva Biological Station, Costa Rica	FI489535
M28183097Discoriconemella limitaneaFLa Selva Biological Station, Costa RicaF/489549M29184026Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF/489552M30184027Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF/489553M30184030Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF/489554M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaF/489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116020M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankElementAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470	M20 M27	151059	Discocriconemella limitanea	141	La Selva Biological Station, Costa Rica	FI489539
M29184026Discoriconemella limitanaFLas Cruces Biological Station, Costa RicaFJ489552M30184027Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M30184030Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniFArchbold Biological Station, FLHM116034M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470	M28	183097	Discocriconemella limitanea	F	La Selva Biological Station, Costa Rica	FI489549
M30184027Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489553M30184030Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discocriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38585Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FGrundy State Forest, TNJF972469M43575Hemicycliophora sp.FGrundy State Park, FLJF972471	M29	184026	Discocriconemella limitanea	F	Las Cruces Biological Station. Costa Rica	FI489552
M30184030Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489554M31184031Discoriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankEU669914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M30	184027	Discocriconemella limitanea	F	Las Cruces Biological Station, Costa Rica	FJ489553
M31184031Discorriconemella limitaneaFLas Cruces Biological Station, Costa RicaFJ489555M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankEU669914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470	M30	184030	Discocriconemella limitanea	F	Las Cruces Biological Station, Costa Rica	FJ489554
M32154100Hemicaloosia sp.JCurtis Prairie, WIHM116020M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankEU669914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470	M31	184031	Discocriconemella limitanea	F	Las Cruces Biological Station, Costa Rica	FJ489555
M32164097Hemicaloosia sp.JCurtis Prairie, WIHM116021M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972467M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M32	154100	Hemicaloosia sp.	J	Curtis Prairie, WI	HM116020
M33Hemicriconemoides pseudobrachyurusGenBankAY284622M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M32	164097	Hemicaloosia sp.	J	Curtis Prairie, WI	HM116021
M34Hemicriconemoides pseudobrachyurusGenBankAY284623M35Hemicriconemoides pseudobrachyurusGenBankAY284624M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M33		Hemicriconemoides pseudobrachyurus		GenBank	AY284622
M35Hemicriconemoides pseudobrachyurusGenBankAY284024M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M34		Hemicriconemoides pseudobrachyurus		GenBank	AY284623
M36266Hemicriconemoides wessoniJArchbold Biological Station, FLHM116034M37267Hemicriconemoides wessoniFArchbold Biological Station, FLHM116035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FIonathan Dickinson State Park, FLJF972470	M35	0.00	Hemicriconemoides pseudobrachyurus	-	GenBank	AY284624
M301Z01Hemicriconemoiaes wessoniFArchoold Biological Station, FLHM110035M38585Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF972467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora conidaGenBankEU669914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FIonathan Dickinson State Park, FLJF972470	M36 M27	266	Hemicriconemoides wessoni	J	Archbold Biological Station, FL	HM116034
M36565Hemicriconemoides wessoniFIchetucknee River, Columbia County, FLJF9/2467M38586Hemicriconemoides wessoniJIchetucknee River, Columbia County, FLJF972468M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora conidaGenBankEU669914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470	M37 M29	267	Hemicriconemoides wessoni	F F	Archbold Biological Station, FL Johotuskass Biver Columbia County FL	HM116035
M39Hemicycliophora conidaJIcheutecknee Kiver, continuita county, FLJF972408M39Hemicycliophora conidaGenBankAJ966471M40Hemicycliophora conidaGenBankEU66914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470	M38	280 586	riemicriconemoides wessoni Hemicriconemoides suessoni	r T	Ichetucknee River, Columbia County, FL	JF972407 IF079468
M40Hemicycliophora conidaGenBankFUG0914M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M30	560	Hemicocliophora conida	J	GenBank	J1972400 AJ066771
M41571Hemicycliophora sp.FGrundy State Forest, TNJF972469M42574Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972470M43575Hemicycliophora sp.FJonathan Dickinson State Park, FLJF972471	M40		Hemicycliophora conida		GenBank	EU660014
M42 574 Hemicycliophora sp. F Jonathan Dickinson State Park, FL JF972470 M43 575 Hemicricanemoidee sp. F Jonathan Dickinson State Park, FL JF972470	M41	571	Hemicycliophora sp	F	Grundy State Forest, TN	IF979469
M43 575 Hemicricanemoide sp. F. Lonathan Dickinson State Park FI. IF979471	M42	574	Hemicycliophora sp.	F	Jonathan Dickinson State Park. FL	JF972470
1 Johanna Deckinson State Fark, TE J157211	M43	575	Hemicriconemoides sp.	F	Jonathan Dickinson State Park, FL	JF972471

TABLE 1. MOTUs and individual specimens used in this study.

MOTU	NID No.	Species ID	Stage ^a	Locality	Accession No.
M44	597	Hemicycliophora sp.	F	Archuleta County, CO	JF972472
M44	598	Hemicycliophora sp.	F	Archuleta County, CO	JF972473
M44	118058	Hemicycliophora gracilis	J	Barta Bros. Ranch, NE	HM115993
M45	5091	Hemicycliophora sp.	J	Niobrara River, Cherry County, NE	HM116018
M45	5092	Hemicycliophora sp.	J	Niobrara River, Cherry County, NE	HM116019
M46	135032	Hemicycliophora sp.	F	La Selva Biological Station, Costa Rica	EU880119
M46	183098	Hemicycliophora sp.	J	La Selva Biological Station, Costa Rica	FJ489550
M47	214069	Hemicycliophora sp.	F	Las Cruces Biological Station, Costa Rica	FJ489588
M47 M49	214070	Hemicycliophora sp.	F	Las Cruces Biological Station, Costa Rica	FJ489589 FJ1206241
M40	440	Hemicycliophora thienemanni Hemicycliophora tybica	F	Genbalik	E0300341 IE079474
M49	450	Hemicycliophora typica Hemicycliophora typica	F	Greece	JF972474 JF979475
M50	577	Lohocriconema sp	F	Ichetucknee River, Columbia County FL	JF972476
M51	1	Lobocriconema thornei	F	Cass County, NE	FI489593
M51	2	Lobocriconema thornei	I	Cass County, NE	FJ489594
M51	226063	Lobocriconema thornei	F	Homestead Natl. Mon., NE	AY911948
M51	226069	Lobocriconema thornei	F	Nine-Mile Prairie, NE	AY911950
M51	226070	Lobocriconema thornei	F	Homestead Natl. Mon., NE	AY911949
M52		Loofia thienemanni		GenBank	AY284629
M53		Loofia thienemanni		GenBank	AY284628
M54	5	Mesocriconema curvatum	F	Kalsow Prairie State Preserve, IA	FJ489595
M54	18	Mesocriconema curvatum	F	Chase County, NE	HM116006
M54	19	Mesocriconema curvatum	F	Williams Prairie State Preserve, IA	HM116007
M54	23	Mesocriconema curvatum	F	Nance County, NE	HM116023
M54 M54	24	Mesocriconema curvatum	F	Nance County, NE Broching County SD	HM116024
M54 M54	25	Mesocriconema curvatum	F F	Brookings County, SD Brookings County SD	HM116025
M54	119006	Mesocriconema curvatum	I I	Sheeder Proirie State Preserve IA	FI480590
M54	124088	Mesocriconema curvatum	J	Polk County NE	FI489526
M54	124089	Mesocriconema curvatum		Polk County, NE	FI489527
M54	155077	Mesocriconema curvatum	F	Konza Prairie. KS	AY919186
M54	223086	Mesocriconema curvatum	F	Lancaster County, NE	AY919190
M54	223087	Mesocriconema curvatum	F	Nine-Mile Prairie, NE	AY919191
M55	223083	Mesocriconema sp.	J	Nine-Mile Prairie, NE	AY919187
M55	223084	Mesocriconema sp.	F	Nine-Mile Prairie, NE	FJ489517
M56	223088	Mesocriconema curvatum	J	Nine-Mile Prairie, NE	FJ489518
M57	431	Mesocriconema discus	F	Brookings County, SD	HM116047
M57	433	Mesocriconema discus	F	Brookings County, SD	HM116048
M57	443	Mesocriconema discus	J	Brookings County, SD	HM116049
M57 ME9	444	Mesocriconema aiscus	F	Brookings County, SD	HM110050
M58	183090	Mesocriconema ornatum Mesocriconema sp	F	Heredia Province Costa Rica	JF972477 FI480548
M59	124090	Mesocriconema sp. Mesocriconema rusticum	J F	Waldo County ME	FI489598
M59	124091	Mesocriconema rusticum	1	Waldo County, ME	FI489529
M59	199022	Mesocriconema rusticum	F	Lamoille County, VT	FI489580
M59	199026	Mesocriconema rusticum	F	Rich County, UT	FJ489582
M59	223085	Mesocriconema rusticum	F	Lancaster County, NE	AY919188
M59	228021	Mesocriconema rusticum		UNL East Campus, Lancaster County, NE	JF972478
M60	155078	Mesocriconema rusticum	F	Konza Prairie, KS	AY919189
M61	135026	Mesocriconema sp.	J	La Selva Biological Station, Costa Rica	EU880076
M62	151051	Mesocriconema sp.	J	La Selva Biological Station, Costa Rica	FJ489537
M62	184010	Mesocriconema sp.	F	La Selva Biological Station, Costa Rica	FJ489566
M62	184016	Mesocriconema sp.	F	La Selva Biological Station, Costa Rica	FJ489568
M62	184020	Mesocriconema sp.	F	La Selva Biological Station, Costa Rica	FJ489569
M03 M62	4	Mesocriconema xenoplax	F	Cass County, NE Kalaan Drainia Stata Draama IA	HM116002
M63	0 7	Discocriconementa inarata	r F	Kalsow Prairie State Preserve, IA	HM116005 Ll40ADA0
M63	0	Discocriconemella in arata	F	Kalsow Prairie State Preserve, IA	FI480507
M63	9 11	Discocriconemella inarata	r F	Kalsow Prairie State Preserve IA	HM116011
M63	125097	Discocriconemella inarata	T.	Kalsow Prairie State Preserve IA	FI489558
M63	125028	Discocriconemella inarata		Kalsow Prairie State Preserve. IA	FJ489559
M63	125029	Discocriconemella inarata		Kalsow Prairie State Preserve. IA	FI489560
M63	150022	Discocriconemella inarata	I	Kalsow Prairie State Preserve, IA	FJ489561
M63	150023	Discocriconemella inarata	F	Kalsow Prairie State Preserve, IA	FJ489562
M63	150032	Discocriconemella inarata	F	Kalsow Prairie State Preserve, IA	FJ489563

TABLE 1. Continued

MOTU	NID No.	Species ID	Stage ^a	Locality	Accession No.
M63	150033	Discocriconemella inarata	F	Kalsow Prairie State Preserve, IA	FJ489564
M63	150034	Discocriconemella inarata	F	Kalsow Prairie State Preserve, IA	FJ489565
M63	199025	Mesocriconema sp.	F	Reichelt Prairie, IA	FJ489581
M63	223080	Mesocriconema xenoplax	F	Konza Prairie, KS	AY919194
M63	223081	Mesocriconema xenoplax	F	Konza Prairie, KS	AY919193
M63	223082	Mesocriconema xenoplax	F	Fresno County, Fresno, CA	AY146454
M63	223089	Mesocriconema xenoplax	F	UC-Davis collection	AY919192
M64	17	Mesocriconema sp.	F	Williams Prairie State Preserve, IA	HM116005
M65		Mesocriconema xenoplax		GenBank	AY284625
M66		Mesocriconema xenoplax		GenBank	AY284626
M07 M68	928	Nielohorriconema semopiax	F	Douglas County NE	A1264027 HM116021
M68	194093	Neolobocriconema serratum	Г	Boone County MO	FI489530
M68	124094	Neolobocriconema serratum		Boone County, MO	FI489531
M68	150018	Neolobocriconema serratum	F	Boone County, MO	FI489534
M69	151049	Nothocriconemoides sp.	F	La Selva Biological Station, Costa Rica	FI489536
M69	151052	Nothocriconemoides sp.	F	La Selva Biological Station, Costa Rica	FJ489538
M70	155085	Ogma decalineatum	F	Konza Prairie, KS	AY919222
M70	226065	Ogma decalineatum	F	Nine-Mile Prairie, NE	AY919221
M70	226068	Ogma decalineatum	F	Nine-Mile Prairie, NE	AY919220
M71	226064	Ogma fimbriatum	F	Niobrara River, Cherry County, NE	AY911952
M72	720	Ogma menzeli	F	Great Smoky Mntns. Natl. Park, TN	JF972479
M72	721	Ogma menzeli	F	Great Smoky Mntns. Natl. Park, TN	JF972480
M72	722	Ogma menzeli	J	Great Smoky Mntns. Natl. Park, TN	JF972481
M73	07	Ogma menzeli	F	GenBank	EU669919
M74	27	Ogma octangulare	F	Mt. Philo State Park, VT	HM116027
M74 M74	28	Ogma octangulare	F T	Mt. Philo State Park, VI Mt. Philo State Park, VI	HM116028
M74 M75	29	Ogma octangulare Ogma sovmouri	J F	Mt. Philo State Park, VI Pachaug State Forest CT	HM116041
M75 M76	308 90	Ogma seymouri Ogma sp	r I	Marion County OR	HM116099
M76	20	Ogma sp.	J	Butts County, GA	HM116032
M76	291 987	Ogma sp.	J F	Sauk County WI	HM116032
M76	314	Ogma fimbriatum	F	Baltimore County, MD	HM116045
M76	347	Ogma fimbriatum	I	Baltimore County, MD	HM116046
M76	83051	Ogma sp.	Ĵ	Manitoba, Canada	HM116008
M76	83052	Ogma sp.	J	Manitoba, Canada	HM116009
M76	83064	<i>Ogma</i> sp.	J	Lava Mountain, ID	HM116010
M76	214066	<i>Ogma</i> sp.	F	Braulio Carillo National Park, Costa Rica	FJ489585
M76	214067	Ogma sp.	F	Braulio Carillo National Park, Costa Rica	FJ489586
M76	214068	Ogma sp.	F	Braulio Carillo National Park, Costa Rica	FJ489587
M76	214078	Criconema sp.	F	UW Arboretum, Seattle, WA	HM116001
M76	055	Ogma cobbi	Ŧ	GenBank	EU669918
M77 M79	257	Ogma sp.	J	Jasper County, SC	HM116033
M70	100000	Ogma sp.	IVI T	La Selva Biological Station, Costa Rica	EU800101
M78	184015	Ogma sp.	J F	La Selva Biological Station, Costa Rica	FJ489507 FI480588
M78	214004 214065	Ogma sp.	F	La Selva Biological Station, Costa Rica	FI489583
M79	184021	Ogma sp.	F	Las Cruces Biological Station, Costa Rica	FI489570
M79	184022	Ogma sp.	F	Las Cruces Biological Station, Costa Rica	FI489571
M79	184023	Ogma sp.	F	Las Cruces Biological Station, Costa Rica	FI489572
M79	214063	Ogma sp.	Ī	Las Cruces Biological Station, Costa Rica	HM115996
M80	214074	Ogma sp.	F	Las Cruces Biological Station, Costa Rica	FJ489590
M80	214075	Ogma sp.	J	Las Cruces Biological Station, Costa Rica	HM116000
M81		Paratylenchus dianthus	-	GenBank	AJ966496
M82	155069	Paratylenchus latescens	F	Konza Prairie, KS	AY912039
M83		Paratylenchus microdorus		GenBank	AY284632
M84		Paratylenchus microdorus		GenBank	AY284633
M85		Paratylenchus cf. neoamblicephalus		GenBank	AY284634
M86	141021	Paratylenchus sp.	J	La Selva Biological Station, Costa Rica	EU880081
M87		Paratylenchus straeleni		GenBank	AY284630
M88	000005	Paratylenchus straeleni		GenBank	AY284631
M89 M00	226067	Paratylenchus variatus	F	Konza Prairie, KS	AY919230
M90 M00	101004	Trophotylenchulus sp.	Г т	La Selva Biological Station, Costa Rica	F1489540
M90 M91	184002	Trophotylenchulus sp. Trophotylenchulus sp.	J	La Selva Biological Station, Costa Rica	FJ489541

TABLE 1. Continued.

MOTU	NID No.	Species ID	Stage ^a	Locality	Accession No.
M92	183051	Trophotylenchulus sp.	I	La Selva Biological Station, Costa Rica	FJ489547
M93	226066	Trophotylenchulus sp.	Ĵ	Konza Prairie, KS	DQ080539
M93	226071	Trophotylenchulus sp.	Ĩ	Konza Prairie, KS	AY146455
M94	140015	Tylenchocriconema alleni	Ĵ	La Selva Biological Station, Costa Rica	EU880060
M95	183017	Tylenchocriconema alleni	F	La Selva Biological Station, Costa Rica	FJ489542
M96	183026	Tylenchocriconema alleni	F	La Selva Biological Station, Costa Rica	FJ489544
M97		Tylenchulus semipenetrans		GenBank	AJ966511
M98	14	Xenocriconemella macrodora	F	Minneapolis, MN	FJ489598
M98	15	Xenocriconemella macrodora	F	Minneapolis, MN	FJ489599
M98	16	Xenocriconemella macrodora	F	Minneapolis, MN	HM116004
M98	107	Xenocriconemella macrodora	F	Butler County, NE	JF972482
M98	164093	Xenocriconemella macrodora	I	Montgomery County, MD	HM116012
M98	201090	Xenocriconemella macrodora	F	Blue Mounds State Park, WI	HM116016
M99	193072	Xenocriconemella macrodora	F	CERA Woods, Grinnell, IA	FJ489556
M99	193073	Xenocriconemella macrodora	F	CERA Woods, Grinnell, IA	FJ489557
M99	201087	Xenocriconemella macrodora	F	CERA Woods, Grinnell, IA	HM116013
M99	201088	Xenocriconemella macrodora	F	Blue Mounds State Park, WI	HM116014
M99	201089	Xenocriconemella macrodora	F	Blue Mounds State Park, WI	HM116015
M100	201091	Xenocriconemella macrodora	F	Blue Mounds State Park, WI	HM116017

by Floyd et al., (2002). In this study, a single nucleotide difference is sufficient to designate a new MOTU. Both strands of the amplified product were sequenced in these analyses by direct sequencing at the University of Arkansas Medical Center Sequencing Facility.

We assume that each individual specimen is represented by a single 3'-18S barcode sequence. We know this is not the case among all nematodes species, as in the polyploid species of *Meloidogyne* and other select species (Abad et al., 2008; Lunt, 2008). Several specimens in this study produced nucleotide sequences that indicated heterogeneity within the barcode of that individual. Those specimens are noted in Tables 2 and 3. All sequences used in this study have been added to GenBank (Table 1).

Each specimen is supplied with a voucher identification number or Nematode ID (NID) number. These numbers have been applied sequentially and chronologically. In some cases NID numbers were applied retroactively. When multiple amplifications are made from a single specimen, a unique amplification number is associated with the NID number. MOTU designations were applied following the pooling of redundant sequences by the Redundant Taxa tool in Maclade.

DNA preparation, sequence alignment, phylogenetic and character-based analysis: DNA was amplified and sequenced as previously described (Powers et al., 2010). 18S sequences were edited and assembled using CodonCode Aligner (CodonCode Corp, Dedham, Massachusetts), DNA aligned by MUSCLE 3.7 (Edgar, 2004) and maximum likelihood analysis generated by PHYML 3.0 using approximate likelihood-ratio tests for the estimation of branch support (Anisimova et al., 2006). The FASTA file for the MOTU dataset is available in Dryad (DOI-pending).

Character-based barcode analysis of nucleotide sequences is an alternative approach to species diagnosis using DNA barcodes (DeSalle et al., 2005; Sarkar et al., 2008). It differs from the more traditional method of barcode analysis in that it is not a distance-based approach, but rather treats the nucleotide sites in a DNA sequence as characters and the different character states, A,T,C,G, are referred to as character attributes (CA) (Sarkar et al., 2002) or nucleotide diagnostics (ND) (Wong et al., 2009). A nucleotide diagnostic can be designated simple and pure when a particular nucleotide is fixed for a particular species, and found in all members of that species and no others. Compound nucleotide diagnostics consist of several nucleotide sites where the combination of nucleotides at those sites is only found in one species. In this study only pure, simple nucleotide diagnostics are analyzed. In large datasets, the first step in character-based barcode analysis is the generation of a phylogenetically derived guide tree which is subsequently examined node by node for the presence of diagnostic nucleotides. The computer program CAOS (Characteristic Attributes Organization System) is an automated method for the discovery of nucleotide diagnostics (Sarkar et al., 2008). The 100-MOTU 3'-18S barcode dataset was simple enough to conduct a manual analysis of nucleotide diagnostics using the maximum likelihood tree and its major clades as a guide tree.

Online access: Images and measurements of terminal taxa from the barcode tree are available online (http://nematode.unl.edu/CriconematidProject_Trees.htm). Individual specimens are listed by their NID numbers in Table 1.

RESULTS

Barcode characteristics: This dataset is comprised of 100 18S barcode MOTUs derived from 214 sequences from nematodes in the suborder Criconematina (Table 1). The ClustalW alignment is 602 nucleotides in length

 2 Criconema permistum (1) 3 Criconema sp. (2) 5 Criconema sp. (1) 1 Criconema sp. (5) 0 Criconema sp. (2) 	0000	42 43 T T T T T T T T T T T T T T T T T T T T	TTC C 46	F T T T T T T T T T T		A A A A A A A A A A A A A A A A A A A	T T T T T	A A A A			0000 0 33	0 34! 0 0 0 34!	0000 C	T T T C T	T T C C	TTT T 152		C T T T 361		363 2363 25						CCCC C ² ⁴	A A A A	A A A A G C	CAGG A		TTT C		A A A A		0000 U	0000 0 223 26 ⁵	523 564 56 6 6 6 A 6 6 6 A 6 6 6 A 6 6 6 A 7 6 6 A 6 6 6 A	523 564 568 55 G G G A C G G G A C G G G A C G G G A C G G G A C G G G A C G G G A C G G G A C G G G A C G G A C C
 Criconema sp. (1) Criconema sp. (1) Criconema sp. (1) Criconema sp. (1) Criconema sphagni (3) Hemicriconemoides 	0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	T T T T T T T T T T T T T T T T T T T	J J F J J F			~ ~ ~ ~ ~ ~	*****	* * * * * *	004000	0000000	0000000	0000000	0000000	0000000	000000			нннонн	000000						0000000	HOCCCC	A A A A A	C A C A A	0000 0		υυυυυυ	1111111 111111111111111111111111111111	00707 007 07 07 07 07 07 07 07 07 07 07	C T G A C	C T G A G C T G A G C T G A A/C C T G A G C T G A G C T G A G C T G A G	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	C T G A G G A C T G A G G A C T G A A/G G A C T A A G G A C T G A G G A	C T G A G G A C T G A A G A C C T G A A G A C C A C T G A G G A C </td
pseudobrachyurus GB (1) Hemicriconemoides pseudobrachyurus CD (1)	C G	ТС	H	A (U U	A	Т	A	C	C	Ċ	Ċ	Ċ	C	F	F	C	F	Ŀ	I		F,	F	F	C	C	¥	Ċ	Ċ		C	C	C C	с Т G А	СТ СА С	СТСАСС	стсаса	стсассас
 35 Hemicriconemoides pseudobrachyurus GB (1) 	C G	T C	T	V	0 0	A	A	¥	C	C	Ċ	Ċ	Ċ	U	F	F	C	F	ت	1		E ,	L	F	C	C	¥	Ċ	Ċ		U	с С	C T C	СТ G А	ст ба G	стсас	стсаст	стбАССТС
 36 Hemicriconemoides wessoni (1) 37 Hemicriconemoides 	G T G T	T C T C	L L	E E	L C	A A	T T	A A	C C	υü	T T	G A	U U	υü	υυ	нн	υυ	υυ	E E						υυ	υυ	A A	A A	U U	0 0	73 73	E E	C C L	T G A	CTGAG	CTGAGG	C T G A G G A C T G A G G A	T G A G G A C T G A G G A C
wessoni (1) 38 Hemicriconemoides wessoni (2)	G T	T C	Т	Ľ	LC	Y	Т	¥	C	U	Ċ	Ċ	Ċ	U	U	F	C	F	E				F	H	U	U	V	A	Ċ	0		Т	Т Т	T G A	TGAG	TGAGG	TGAGGA	TGAGGAC
43 Hemicriconemoides sp. (1)	U U	T C	E (ΕI	L C	A I	E I	A .	U U	U U	U U	5	5	U U	U U	ΕI	υ	E I	ບໍ	' 	- I			E 1	U U	U U	A .	A (Ċ U	U U		ΕI	U H	T G	T G A G	T G A G	T G A G G A	T G A G G A C
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 73 Ogma menzeli GB (1) 74 Ogma octangulare (3) 75 Ogma octangulare (3) 	יט ט ט ט ט		υυ		J E C			A A ·	o o c	o o c	000	00	000	U U U	U F (H E I	י ט ט						000	o o o	• ۹ د	000	00				ט ט - ר ו	A A A	U C C V V V C C V C C V C V C V C			
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 79 Ogma sp. (4) 30 Ogma sp. (2) 	A T G C	T T T	υυ	E E	00	Q A	ΕĿ	Q A	υυ	υυ	ი ი	3 3	ი ი	υυ	υυ	нг	ບບ	нн	 აა			0 F	0 F	H H	ΗÜ	υυ	4 4	4 4	30	ΡU	r	E E	C C T T	A G T T T T	TGGG		T G G G G A C A	T G G G G A C T G A G G A C
38 Xenocriconemella	C C	ТС	Н	A A	℃	Ċ	L	Ċ	C	U	Ċ	Ċ	A	C	U	Ċ	C	J	Ċ	-	–	F	F	F	C	C	A	Ċ	Ċ	0		L	T G	TGA	TGAG	TGAGG	TGAGGA	TGAGGAC
macrodora (6) 99 Xenocriconemella	G T	ТС	F	A 4	C A	Ċ	F	Ċ	U	U	Ċ	Ċ	V	U	U	Ċ	<u> </u>	Ū	ت ت	1		F	F	E	U	U	V	Ċ	G	C		Г	T C	T G A	TGAG	TGAGG	TGAGGA	TGAGGAC
macrodora (5) 100 Xenocriconemella 110 macrodora (1)	G C/J	T C	Т	A 4	o ⊿	Ċ	Г	C	U	U	G	Ċ	¥	C	U	Ċ	U	U	ت ن	L	L D	L,	L	E	U	C	V	Ċ	G	C		Г	T G	T G A	TGAG	TGAGG	TGAGGA	TGAGGAC

Clade A polymorphic and diagnostic nucleotide positions with diagnostic characters. Diagnostic nucleotides are those shared by all individuals of a species and not found in any other diamnestic nucleotide characters are shaded without a bold outline. Numbers after taxon labels refer to the number of TABLE 2.

TABLE 3. Clade B polymorphic and diagnostic nucleotide positions with diagnostic characters. Diagnostic nucleotides are those shared by all individuals of a species and not found in any other species. The diagnostic nucleotide characters are shaded with a bold outline. Numbers after taxon labels refer to the number of specimens examined. GB refers to sequences obtained from GenBank. Numbering of the nucleotide position starts with 1 which is the first nucleotide following primer 18S1.2a.

													Pe	ositio	n										
MOTU	Taxa	38	43	44 45	6 46	53	212	333	349	350	351	353	361	363	364	367	400	476	488	489	491	500	502	503	512
M4	Mesocriconema crenatum (1)	Т	А		- T	С	G	С	G	С	Т	С	Т	С	Т	А	С	А	G	А	А	Т	С	С	С
M21	Discocriconemella limitanea (1)	Т	G		<u> </u>	Т	G	С	G	Т	С	С	С	Т	С	A	С	G	Т	G	G	С	Т	С	C
M22	Discocriconemella limitanea (1)	C	С	Т А	С	С	G	А	G	С	С	Т	С	Т	—	Α	С	G	Т	G	G	С	Т	G	Α
M23	Discocriconemella limitanea (1)	C	С	Т А	С	С	G	А	G	С	Т	С	С	Т	—	А	С	G	Т	G	G	С	Т	G	А
M24	Discocriconemella limitanea (1)	C	С	Т А	С	С	G	А	G	С	\mathbf{C}	С	С	Т	—	A/G	С	G	Т	G	G	С	Т	G	А
M25	Discocriconemella limitanea (1)	C	G		- C	С	Α	С	G	Т	\mathbf{C}	С	С	Т	С	А	С	G	Т	G	G	Т	С	G	С
M26	Discocriconemella limitanea (1)	C	С	Т А	С	С	G	А	G	С	\mathbf{C}	C/T	С	Т	—	А	С	G	Т	G	G	С	Т	G	А
M27	Discocriconemella limitanea (1)	Т	G		- C	С	G	С	G	Т	\mathbf{C}	C/T	С	Т	С	А	С	G	Т	G	G	С	Т	C/G	C
M28	Discocriconemella limitanea (1)	C	С	Т А	С	С	G	А	G	С	\mathbf{C}	С	С	Т	—	А	С	G	Т	G	G	С	Т	G	А
M29	Discocriconemella limitanea (1)	С	G		- C	Т	G	С	С	Т	\mathbf{C}	С	С	Т	С	А	А	G	Т	G	G	С	Т	С	С
M30	Discocriconemella limitanea (2)	C	G		C	Т	G	С	G	Т	\mathbf{C}	С	С	Т	С	A	С	G	Т	G	G	С	С	С	_C_
M31	Discocriconemella limitanea (1)	С	С	ТТ	С	С	G	А	G	С	С	Т	С	Т	_	А	С	G	Т	G	G	С	Т	G	А

which includes 10 hypothesized sites of nucleotide insertion or deletion (indels). There are 470 (78%) invariant and 132 polymorphic nucleotide sites in the dataset. Among the polymorphic nucleotide sites, 56 (42%) are singletons, positions where a single MOTU has a nucleotide not shared by any others in the dataset.

Barcode species analysis: The dataset includes 25 nominal species identified by the authors through microscopic examinations of morphological characteristics. A maximum likelihood tree for the 100 MOTUs is presented in Figure 1. Four clusters with moderate support values (0.80-0.93) have been identified and were labeled A-D for character-based barcode analysis.

Within clade A, there are nine morphologically identified nominal species not considering GenBank entries (Fig. 1, Table 2). Included in this clade are species that morphologically fall within the genera Ogma, Xenocriconemella, Criconema, and Hemicriconemoides. Five of the Ogma species possessed morphological characters that permitted assignment to known species. However, neither phylogenetic analysis nor character-based barcode analysis recognized all Ogma MOTUs as collectively comprising a natural group exclusive of the other genera in the clade. Ogma decalineatum and O. octangulare shared a T at nucleotide 67 to the exclusion of all other MOTUs in clade A (Table 2). Another nucleotide character (C) at position 391 provides evidence for relatedness of these two species to O. seymouri. The O. menzeli MOTU from Tennessee (M72) differs by two nucleotides from the European O. menzeli in GenBank (M73). M76 is a broadly distributed MOTU, one of only two MOTUs found in both Costa Rica and the United States. Additionally, it shares 100% identity with GenBank accession EU669918, an O. cobbi reported from Europe. Morphologically, the adult females that represent M76 include a range of phenotypes, particularly in the arrangement of scales on the adult female cuticle.

Xenocriconemella macrodora is represented by 12 specimens and three MOTUs (M98, M99, M100) collected from five U.S. states. There are four diagnostic nucleotide sites, including two insertions, which are observed in every specimen of this species. These are found at nucleotide positions 349, 352, 363, and 364. Hemicriconemoides wessoni was collected at two sites in Florida, one site within 60 miles of the type locality. Three MOTUs were observed for this species, each diagnosable by nucleotides T and G at positions 362 and 365 respectively. Criconema permistum and C. sphagni were represented by one and three specimens respectively, each containing a single, unique fixed nucleotide. Other Criconema species in clade A are not united by shared derived characters, reflecting a lack of phylogenetic support for the genus.

Clade B, with the exception of a single MOTU (M4), is exclusively represented by *Discocriconemella limitanea* from Costa Rica (Table 3). The clade is well-supported phylogenetically. *D. limitanea* is represented by 12 specimens and 11 MOTUs which break into two discrete subgroups. There are six nucleotide sites that separate the two subgroups. Morphologically, however, there are no characters that appear to discriminate between the subgroups, and both subgroups are found in Las Cruces and La Selva Biological Research Stations, geographically distinct rainforest habitats of Costa Rica. MOTU M4 was recovered from cultivated passionfruit in Costa Rica and conforms morphologically to *Mesocriconema crenatum* (Loof, 1964) De Grisse & Loof, 1965.

Clade C includes six nominal species identified by morphology (Table 4). Both phylogenetic analysis and character-based barcode analysis support *Mesocriconema rusticum* and *M. curvatum* as diagnosable species within this clade. Nucleotide sites at 472 and 488 diagnose *M. rusticum*, and an additional two synapomorphic characters at sites 46 and 503 support a sister group relationship with *M. ornatum. Mesocriconema rusticum* was



FIG. 1. Maximum likelihood tree of Criconematina 18S 3' MOTUs. Shaded clades A-D were analyzed separately by character-based barcode analysis. Species binomials followed by GB were sequences added to the analyses from GenBank. Images and measurements of terminal taxa can be seen at http://nematode.unl.edu/CriconematidProject_Trees.htm Approximate likelihood-ratio test support values above 0.80 identify nodes of relatively strong support.

TABLE 4. Clade C polymorphic and diagnostic nucleotide positions with diagnostic characters. Diagnostic nucleotides are those shared by all individuals of a species and not found in any other species. The diagnostic nucleotide characters are shaded with a bold outline. Synapomorphic characters are shaded without a bold outline. Numbers after taxon labels refer to the number of specimens examined. GB refers to sequences obtained from GenBank. Numbering of the nucleotide position starts with 1 which is the first nucleotide following primer 18S1.2a.

		Position
MOT	U Taxa	10 31 34 36 37 38 43 46 47 48 49 53 56 59 75 109 197 212 214 322 341 349 351 353 360 365 367 369 384 398 400 408 472 476 483 487 488 491 496 503 504 544 561 564 574 579 581 582 599 600 601
4 M	Mesocriconema	T C C G G T A C A A G C G G C C G G C T C G A T G G C G G G G T C G T A C G T A G T A T G A G T T
M8	sp. (1) Mesocriconema	T C C G G T A C A A G C G G C C G G C C C G A T G G C C G G C C G T C G T A C A T A G T A T G A G T T
M54	sp. (1) Mesocriconema	TTGGGTACAAGCCACC C A G C A G C C T A T A G T G G A T C G T A C G T A G T A G T G A G T T
M55	curvatum (13) Mesocriconema	тссебтассабсебс с а а с а е с т т т а е т е е е т т е т а е т а е т т е т е
M56	sp. (2) Mesocriconema	TTGGGTACAAGCCACC C A G C A G C C T T A T A G T G G A T C G T A C G A G C G A T C C G T T
M57	curvatum (1) Mesocriconema	тссебтассаесесссссссстсатссстсатссстсатссстасста
M58	discus (4) Mesocriconema	тссеесстасесесс с е с с е с с с е а т е е с е е т с е т а е е т а е т а е т а е т т е а е т т
M59	ornatum (2) Mesocriconema	тссеетсталесеесс с с с с с с с т с с л т с с с д с с т т л с с т т л с с т л с т т л с
M60	rusticum (6) Mesocriconema	сссеетсталесеесс с с с с с с с т с с а т с с с с а с с т т а с с т а с с т а с т т а с
M61	rusticum (1) Mesocriconema	тссебстссаесебсс с а с с а а с с т е а т е е с е е а т с е т а с е т а е т а е т т е а е т т
M62	sp. (1) Mesocriconema	T C C G G T T C C A A C G C C A G T A G C T A T G G C A G G T C G T A C G T A G T A T G A G T T
M63	sp. (4) Mesocriconema venoblav	тссебтассаесессса ссаасстсата стсеттсета сетасета сата са
M64	(18) Mesocriconema	ТСС 6 6 C A C C A G C A G C A G C C T G A T G G C G G A T C G T A C G T A G T A T G A G T T
M65	sp. (1) Mesocriconema	ТСССЕТАССАЕССЕТСА ССАССТТССССССССССССССС
M66	xenoplax GB (1) Mesocriconema	ТССССТАССАССАССТСАССТСАТССТССССССССССС
M67	xenoplax GB (1) Mesocriconema	тссебсаессаа ссалосто стелтся с стелта с сталоворессание и сталови.
M69	xenoplax GB (1) Nothocriconemoid	ST C C A C T C C C C A T G A C G G G G G G G G G G G G G G G G G
	sp. (2)	

represented by 6 specimens and two MOTUs collected from 5 U.S. states. Four nucleotide sites, 31, 34, 56, and 59 diagnose *M. curvatum*. MOTU M63 was represented by 18 specimens and includes two morphologically identifiable species *M. xenoplax* and *Discocriconemella inarata*. A previous paper has addressed the more detailed taxonomy of these two species (Powers et al., 2010). There are no diagnosable characters in this 18S barcode for discrimination between *M. xenoplax* and *D. inarata*. Three additional MOTUs, M65, M66 and M67 from GenBank have been identified as *M. xenoplax* from Europe. *Mesocriconema discus* (M57) was collected at its type locality in South Dakota, however there were no discrete nucleotide characters that could be considered as diagnosable nucleotide sites.

Clade D was largely comprised of Hemicycliophora species, the two related sheath genera Hemicaloosia and Loofia, Lobocriconema, and Criconemoides species (Table 5). Criconemoides annulatus (M16), represented by two specimens from the Rocky Mountains in Colorado, possessed three diagnostic nucleotide sites. Lobocriconema thornei (M51) and a closely related Lobocriconema species (M50) had four synapomorphic sites, and each was diagnosable by a single autapomorphic site. Among the sheath genera, two synapomorphic nucleotide sites at 43 and 47 united all specimens. Hemicycliophora gracilis, represented by a single MOTU collected in Colorado and Nebraska, possessed five autapomorphic diagnostic sites. Hemicycliophora typica and the two species from GenBank in this dataset did not possess diagnosable nucleotides in the 18S barcode.

Five notable, diagnosable species in the 100-MOTU dataset did not fall within clades A-D (Table 6). Bakernema inaequale is a species endemic to North America and immediately recognizable by its irregularly arranged, membranous cuticular scales. Seven specimens from Tennessee and Connecticut shared a single MOTU (M1) and were diagnosable in the full dataset by an A at nucleotide position 63. Criconemoides informis (M17) had two diagnostic nucleotides: an A and T at positions 343 and 357, respectively. Criconemoides inusitatus (M18), collected from the type locality in Ames, IA and from Delaware, had a single diagnostic nucleotide site at position 365. A species morphologically conforming to Neolobocriconema serratum (M68) collected from Missouri and Nebraska, had a single diagnostic site at position 360. Three MOTUs (M94, M95, M96) represented the unusual criconematid nematode Tylenchocriconema alleni, a species known solely from epiphytic bromeliads in the new world tropics (Raski and Siddiqui, 1975). Two nucleotide sites at 347 and 348 were diagnostic for the three MOTUs.

DISCUSSION

The small number of phylogenetically informative nucleotide sites (76) and the relatively few well-supported clades observed in the maximum likelihood tree indicate that limited phylogenetic inference can be derived from this 3' region of 18S. None of the well-supported clades could be interpreted as support for the existing morphologically-based classification of Criconematina sensu Siddigi (2000). Conversely, there is not strong support for alternative groupings of MOTUs. Simply there are not enough phylogenetically informative sites in this 18S barcode to construct a robust phylogeny. Subbotin et al., (2005, 2006) arrived at a similar conclusion with analysis of the D2/D3 region of 28S rDNA. Those studies included 23 nominal taxa from 11 genera. The 38 samples analyzed exhibited a geographic coverage that included two specimens from North America, 12 from Venezuela, and the remaining specimens from Europe. According to the authors, "none of the phylogenetic analyses of the D2-D3 dataset allowed resolution of the relationships between main lineages."

Lack of phylogenetic resolution does not mean that the 3'-18S barcode does not have value as a measure of biodiversity or as an aid in diagnostics. A major advantage of the primer set is that PCR amplification is consistent and reliable across the entire nematode phylum. That consistency allows for an unbiased comparison of nematode community composition. Within the suborder Criconematina, barcode discrimination is at multiple taxonomic levels. In some cases a single MOTU clearly identified a complex of species. MOTU 76, for example, corresponded to a group of Ogma species that have scales arranged singularly in longitudinal rows along the length of the body, or arranged in rows consisting of clusters of 4-6 scales, or with scales densely packed on the annules forming a continuous elongated fringe. Similarly MOTU 63 consists of geographically wide-spread North American isolates that conform to Mesocriconema xenoplax and Discocriconemella inarata, a grassland species that appears to have secondarily lost the submedian lobes (Powers et al., 2010). In other cases, multiple MOTUs seem to correspond to a morphologically conserved species complex. Discocriconemella limitanea is comprised of multiple MOTUs with no indication of corresponding morphological change. The nucleotide variability within the barcode identifies subgroups that may suggest the existence of cryptic species. Here the barcode analysis has provided initial evidence in the species discovery process and should be followed by a complete taxonomic analysis to resolve the taxonomic status of the subgroups.

The absence of a direct correspondence between MOTUs as defined in this study (1 bp cutoff) and morphologically identified species suggest that the MOTUs generated by the 3'-18S barcode should not be uncritically considered as proxies for species. The relationship between MOTUs and species can be evaluated by character-based DNA barcode analysis, which is a method to discover diagnostic characters in species where the delimitation step has already been established TABLE 5. Clade D polymorphic and diagnostic nucleotide positions with diagnostic characters. Diagnostic nucleotides are those shared by all individuals of a species and not found in any other species. The diagnostic nucleotide characters are shaded with a bold outline. Synapomorphic characters are shaded without a bold outline. Numbers after taxon labels refer to the number of specienes examined. GB refers to sequences obtained from GenBank. Numbering of the nucleotide position starts with 1 which is the first nucleotide following primer 18S1.2a.

	572	C	C	C	C	C	Н	C	C	H	C	C	C	C	C	C	C	C	U
	571	A	Η	Η	H	Η	Г	Η	Н	C	Н	Н	H	Η	Н	H	Η	Н	F
	541	G	A	A	A	A	Α	A	A	A	A	A	A	A	A	Α	A	A	Υ
	519	G	Α	A	A	A	Α	A	A	A	A	A	A	A	Υ	Α	A	Α	Υ
	513	Н	H	H	H	Η	Τ	Η	Н	Η	H	Н	H	Η	Н	C	Η	Η	Н
	507	A	V	A	A	V	A	Α	V	A	A	A	A	V	A	A	A	G	A
	503	C	G	U	C	C	C	C	C	U	C	C	C	C	U	H	H	U	C
	496	G	V	A	V	A	A	A	V	A	A	A	A	V	A	A	A	V	A
	489	Н	H	H	H	Η	Τ	Η	Н	Η	H	Н	H	Η	Н	H	C	Η	Г
	488	G	H	G	Ċ	G	G	G	G	G	G	G	G	G	Ċ	A	A	G	C
	476	A	G	G	Ċ	G	G	G	G	A	G	G	G	G	G	G	Ċ	G	C
	366	C	C	C	U	H	C	C	C	C	C	C	C	C	C	C	U	C	C
	365	G	Н	H	Ċ	Ċ	C	G	Ċ	Ċ	G	Ċ	G	Ċ	Ċ	H	H	G	Ċ
	364	C	Ι	Ι		I	I	Ι		Ι	Ι		Ι	Ι		Ι		I	I
	363	Н	I			I					Ι		Ι	Ι		Ι		I	I
	362	Н	U	G	H	Η	G	Г	Н	Н	H	Н	H	Н	Ċ	C	U	H	F
	361	Н	L	H	A	A	A	Г	V	A	H	A	A	V	A	H	H	A	V
	100 360	U	H	H	H	C	C	Н	U	C	A	U	C	Н	C	C	C	H	F
F	Posit	C	C	C	U	C	C	Н	U	C	C	C	C	C	C	C	C	C	C
	353	C	C	U	U	C	C	C	Н	U	C	H	H	H	C	C	U	H	L
	352	H	H	H	H	H	A	A	V	A	A	A	A	A	\mathbf{V}	H	H	A	A
	351	H	U	U	H	C	L	H	Н	H	H	C	C	Н	H	H	H	H	L
	341	G	IJ	Ċ	Ċ	Ċ	Ċ	G	Ċ	A	Ċ	G	G	G	Ċ	G	Ċ	J	Ċ
	340	A	Ċ	G	H	Ċ	G	A	Ċ	H	Y	G	G	G	C	G	Ċ	Ċ	J
	339	C	F	U	C	C	C	C	C	C	C	C	C	C	C	C	C	U	C
	333	C	V	A	V	A	A	A	V	A	A	A	A	V	A	A	A	V	A
	212	G	A	A	Ċ	Ċ	G	G	Ċ	G	G	V	G	G	C	G	Ċ	Ċ	C
	158	H	G	G	Ċ	G	G	G	G	IJ	G	G	G	G	Ċ	G	Ċ	G	Ċ
	152	H	A	A	V	V	A	A	V	G	A	V	A	V	V	A	A	A	Α
	151	G	Ċ	G	Ċ	Ċ	Ċ	G	Ċ	A	Ċ	G	Ċ	Ċ	Ċ	G	Ċ	G	C
	89	Н	H	H	H	Η	C	Η	Н	H	H	Н	H	Η	Н	Η	Η	Η	Н
	7 48	A	H	A	C	A	A	C	A	T	C	A	A	C	A	L	H	C	C
	46 4	C	ГО	г С	T	C	C	T	C	T	T	C	C	T	T	Ľ	L	T	T
	43	H	H	E	C	C	C	C	C	C	C	C	C	C	C	A	A	C	C
	42	Н	Η	Н	H	H	Г	Н	Н	C	Н	H	H	Н	F	Н	H	H	L
	5 38	L	L	L	E /	C V	L	L	C	L	C	C	C _	L	L	L	T _	L	E
	1 01	A.	4	5)	4	a A	1) a	a > A	a A	<i>a</i>	a A	a 7	a A	a a	a V	4	₹,	A,	0
	Таха	Criconemoides	sp. (1) Criconemoides	annulatus () Sriconemoides	sp. (1) Hemicaloosia	sp. (2) Hemicycliophor	conida GB (Hemicycliophor	conida GB (Hemicycliophor	sp. (1) Hemicycliophor	sp. (1) Hemicycliophor	gracuus (3) Hemicycliophor	sp. (2) Hemicycliophor	sp. (2) Hemicycliophor	sp. (2) Hemicycliophor	tmenemanni GB (1) Hemicycliophor	typica (2) Lobocriconema	sp. (1) Lobocriconema	(c) thorner (c) Loofia	thienemanni GB (1) Loofta thienemanni
	MOTU	M6	M16	M19 (M32	M39	M40	M41	M42	M44	M45	M46	M47	M48	M49	M50	M51	M52	M53

TABLE 6. Diagnostic nucleotide positions for species not included in clades A-D. These species compared against the entire Criconematina data set. Numbers after taxon labels refer to number of specimens examined. Numbering of the nucleotide position starts with 1 which is the first nucleotide following primer 18S1.2a.

MOTU	Taxa	At position	Has	All others have
M1	Bakernema inaequale (7)	63	А	G
M17	Criconemoides informis (2)	343	А	С
	J	357	Т	G
M18	Criconemoides inusitatus (3)	365	А	G/T
M68	Neolobocriconema serratum (4)	360	G	C/T
M94	Tylenchocriconema alleni (1)	347	Т	
		348	С	_
M95	Tylenchocriconema alleni (1)	347	Т	_
		348	С	_
M96	Tylenchocriconema alleni (1)	347	Т	_
		348	С	_

(DeSalle et al., 2005; DeSalle 2006; Kelly et al., 2007; Rach et al., 2008; Wong et al., 2009; Naro-Maciel et al., 2010). As a character-based approach it is compatible with traditional morphological identification systems in its recognition of diagnostic characteristics based on the assumption that members of established taxonomic groups share attributes that are absent from comparable groups (Sarkar et al., 2002; Rach et al. 2008). Bakernema *inaequale*, for example, is diagnosable by the presence of irregularly spaced membranous scales on the cuticle and an A at nucleotide position 63 in the 3'-18S barcode. Xenocriconemella macrodora is diagnosable by an approximately 100 um flexible stylet, an A and G substitution at positions 349 and 352 respectively, plus a TC insertion at position 363-364. In the 100-MOTU Criconematina dataset, 14/25 a priori identified species had at least one diagnostic character. Moreover, in several cases, while no diagnosable nucleotide characters were recognized at the species level, a synapomorphic character was present that indicated grouping at a higher taxonomic level (e.g. Ogma decalineatum, O. octangulare, O. seymouri). Given the evolutionarily conserved nature of the 3' portion of the 18S gene, it is surprising that over 50% of the known species would possess putative diagnostic nucleotides. Alternative explanations for the apparent diagnostic signal could be attributed to sequencing error, insufficient sampling of species and populations, or misidentification of the nominal species. The validation of these results will require increased sampling of species throughout their known range. These caveats notwithstanding, from a biodiversity and biogeographic perspective the application of this barcode to a comparison of nematode communities could hasten the effort to describe the pattern of nematode diversity as it currently exists at the landscape scale. Also the characterization of new MOTUs will identify gaps in the taxonomic knowledge and lead to species discovery. Furthermore, it is important to emphasize that barcode approaches, whether they target individual specimens or an entire community of specimens, are still dependent on reference databases to convey meaningful taxonomic information, with the recognition that sequences alone, apart from their biological context, are limited in their systematic value (Hajibabaei et al., 2007; Stevens et al., 2011).

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