Chapter 20
Non-parasitic, Terrestrial and Aquatic Nematodes

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20.1 Introduction

Conventionally, all nematodes that are not animal parasites are called non-parasitic, including the herbivores or plant-parasitic nematodes (Poinar 1983). However, in this chapter the term non-parasitic will be used in a more restricted sense to refer only to non-plant-parasitic, terrestrial, freshwater and, to a certain extent, estuarine nematodes (see Chap. 24). As plant-parasitic nematodes (see Chap. 3) constitute an important feeding group in the soil, their contribution to ecological processes will briefly be discussed under non-parasitic, terrestrial nematodes (see Sect. 20.2).

For a clearer picture of the extent of the work being done on the non-parasitic nematodes of South Africa (SA), this chapter will be divided into five parts, viz. non-parasitic terrestrial nematodes, non-parasitic freshwater nematodes, non-parasitic nematodes from caves and caverns, non-parasitic nematodes from estuaries and a checklist of non-parasitic nematodes described from or found in SA up to 2015. An interesting phenomenon, namely, the discovery of the first multicellular organisms deep under the surface of the earth, that represented non-parasitic nematodes, is discussed in Box 20.1.

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Box 20.1. The Deepest Living, Multicellular Organism Discovered Recently: A Non-parasitic Nematode

The subterranean biosphere extends more than 3 km below the surface of the Earth and presents near inhospitable conditions (extreme temperature, limited space and lack of oxygen) for life. Although prokaryotic organisms have been known to survive at these depths, it was only in 2011 that an international team of scientists provided evidence on the existence of multicellular organisms as deep as 3.6 km below the surface (Borgonie et al. 2011). These organisms were nematodes, sampled from ancient (2,900–12,100 years old) borehole water associated with mineshafts in South Africa. While deoxyribonucleic acid (DNA) evidence of a monhysterid species was found at the latter depth (with a recorded temperature of 48 °C), a new species, namely, *Halicephalobus mephisto* Borgonie, Garcia-Moyano, Litthauer, Bert, Bester, Van Heerden, Möller, Erasmus and Onstott 2011, was discovered 1.3 km below the surface. Temperatures at this depth were recorded at 37 °C. Two other species (*Plectus aquatilis* Andrássy, 1985) and a monhysterid sp. were also collected from borehole water in another mine at a depth of nearly 1 km below the surface. Evidence was provided by Borgonie et al. (2011) that these nematodes fed on a mixture of aerobic and anaerobic bacteria associated with the paleometeoric water. The discovery that multicellular life, in this case nematodes, can survive in extreme conditions deep below the surface of the Earth renewed hopes for finding life on Mars.

20.2 Non-parasitic, Terrestrial Nematodes

Non-parasitic nematodes are common in natural veld with some species being particularly prevalent within SA in cultivated fields (Heyns 1971). These include members of the orders Araeolaimida, Cephalobida, Dorylaimida, Enoplida, Mononchida, Panagrolaimida, Rhabditida, Triplonchida and Tylenchida. Although many taxonomical studies have been conducted, only three ecological works focusing on non-parasitic nematodes discovered locally have thus far been published (Durand et al. 2012; Du Preez et al. 2013, 2015b). However, quite a few dissertations and theses on this topic are in the process of being concluded. Furthermore, presentations with nematode ecology as the topic have also been presented at various nematology congresses/symposia (Du Preez et al. 2013, 2014, 2015a; Marais et al. 2009, 2010; Swart et al. 2014).

Scientists within SA have become increasingly concerned about the health of agricultural soils and are using nematodes as biological indicators. For this purpose, an automated web-based tool known as the Nematode Indicator Joint Analysis (NINJA) (available at http://spark.rstudio.com/bsierieb/ninja) is very useful for the calculation of several ecological indices (Sieriebriennikov et al. 2014). Nematodes may well be the most suitable organisms for environmental diagnosis, especially as more information exists on their taxonomy and feeding roles (Gupta and Yeates 1997) than that exists about other mesofauna. For the producer, soil-inhabiting nematodes are of

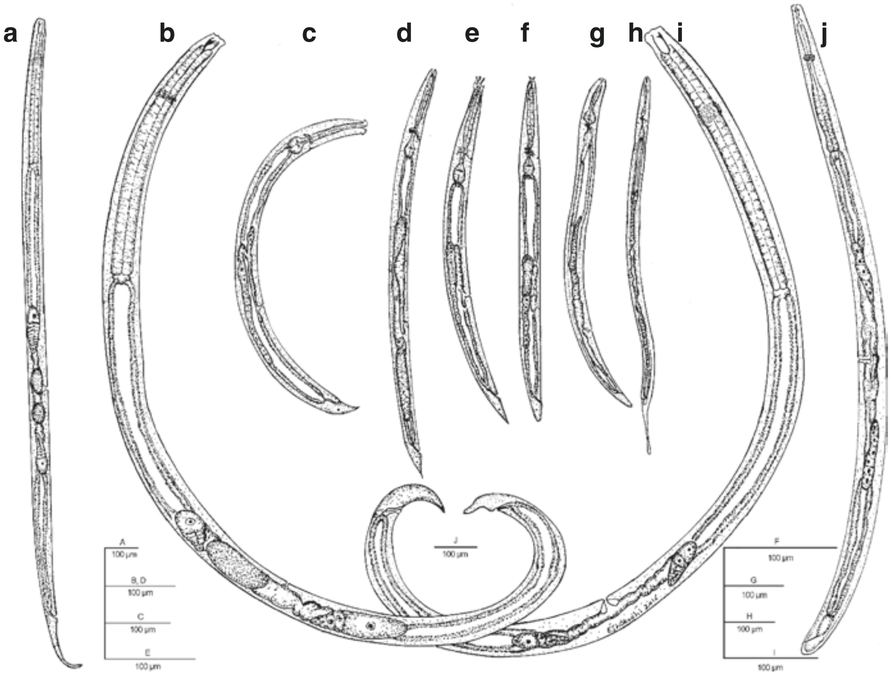

Fig. 20.1 *Mononchus truncatus* Bastian, 1865 (**a** predator), *Mylonchulus sigmaturus* Cobb, 1917 (**b** predator), *Elaphonema* sp. (**c** bacterivore), *Panagrolaimus rigidus* (Schneider, 1866) Thorne, 1937 (**d** bacterivore), *Acrobeles iranicus* Shokoohi, Abolafia and Zad, 2007 (**e** bacterivore), *Acrobeloides nanus* (de Man, 1880) Anderson, 1968 (**f** bacterivore), *Aphelenchus avenae* Bastian, 1965 (**g** fungivore), *Psilenchus aestuarius* Andrássy, 1962 (**h** fungivore), *Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970 (**i** predator), *Labronema vulvapapillatum* (Meyl, 1954) Loof and Grootaert, 1981((**j** predator) (Ebrahim Shokoohi, North West University, Potchefstroom, South Africa)

particular interest. They are small, generally between 0.3 and 5.0 mm long and can be abundant (in their millions) but also diverse (commonly more than 30 taxa) in all soils (Yeates 1979). Although the body form of soil nematodes is similar in all life stages, their greatest apparent morphological diversity can be seen in the head and mouth structures, which are closely related to their feeding habits (Fig. 20.1). Some important and useful terms referred to in the literature are listed and defined in Box 20.2.

Box 20.2. Glossary

Trophic groups of nematodes.

cp (coloniser-persister) scale: assignment of soil and freshwater nematode taxa to a 1–5 linear scale according to their *r* and *K* characteristics (Ferris et al. 2001):

- cp-1: Short generation time, small eggs, high fecundity, mainly bacterivores, feed continuously in enriched media, form dauer juveniles as microbial blooms subside

- cp-2: Longer generation time and lower fecundity than the cp-1 group, very tolerant of adverse conditions and may become cryptobiotic. Feed more deliberately and continue feeding as resources decline. Mainly, bacteri- and fungivores
- cp-3: Longer generation time, greater sensitivity to adverse conditions. Fungi-, bacteri- and carnivores
- cp-4: Longer generation time, lower fecundity, greater sensitivity to disturbance. Besides the other trophic roles, smaller omnivore species
- cp-5: Longest generation time, largest body sizes, lowest fecundity, greatest sensitivity to disturbance. Predominantly carni- and omnivores

r strategists: relatively small nematodes with short life cycles and potentially higher reproductive rates (e.g. non-parasitic nematodes with cp-values of 1 and 2, parasitic nematodes such as *Meloidogyne* spp. and *Ditylenchus africanus* Wendt, Swart, Vrain and Webster, 1995 (previously reported as *D. destructor* Thorne, 1945) (see Sect. 9.3, Chap. 9). Some grow large and have long life cycles with low rates of population increase.

K strategists: relatively large nematodes with long life cycles and low reproduction rates (e.g. non-parasitic nematodes with cp-values >3, parasitic nematodes such as *Longidorus* spp.).

Functional guild: defined as a matrix of the feeding habits of nematodes as well as incorporating their biological, ecological and life history characteristics (which are all incorporated in the cp classification) (Neher et al. 2004).

Faunal profile/simplified food web: an indicator of the state of a given food web where soils are categorised into four quadrants according to the presence, abundance and diversity of non-parasitic, soil-inhabiting nematodes as affected by stressor disturbance(s) (Ferris et al. 2001; Neher et al. 2004).

Enrichment index: a measure of opportunistic bacteri- and fungivore nematodes (cp 1 and 2 values) present in a given soil substrate (Ferris et al. 2001; Neher et al. 2004).

Structure index: using non-parasitic nematodes with higher cp-values (three and more) as an indicator of soil health (Ferris et al. 2001; Neher et al. 2004).

Channel index (CI): an indicator of predominant decomposition pathways (bacterial or fungal) that occur in soil food webs where nematodes are used as indicators of soil health (Ferris et al. 2001; Neher et al. 2004).

20.2.1 Trophic Groups

According to Yeates et al. (1993), the following nematode-feeding/trophic groups are recognised.

20.2.1.1 Herbivores or Plant-Feeders (Plant-Parasitic Nematodes)

These nematode pests feed on vascular plants. To accomplish this, a stomatostylet (Tylenchida and some Aphelenchida) or an onchio- (Triplonchida) or odontostylet (Dorylaimida) is always present in such individuals.

20.2.1.2 Fungivores or Hyphal Feeders

These nematodes penetrate fungal hyphae by using a small and delicate stomato- or odontostylet. In addition to obligate hyphal feeders, this group includes the alternative life cycle of some invertebrate parasites (e.g. *Deladenus* spp.).

20.2.1.3 Bacterivores or Bacterial Feeders

Such nematodes feed on any prokaryotic food source present in the soil substrate. These organisms ingest their food through either a narrow (e.g. *Rhabditis* spp., *Alaimus* spp.) or broad (e.g. *Diplogaster* spp.) mouth.

20.2.1.4 Substrate Feeders

Ingestion by substrate feeders may be incidental to bacterivores, predator and unicellular, eukaryotic-feeding nematodes because more than one food source is ingested by such nematode individuals. The mouth form ranges from being short and broad to long and narrow. Also, teeth may be present in the mouth, which suggests a more predatory lifestyle. The expression ‘nonselective, deposit feeding’ used in reference to aquatic nematodes refers to ingestion of more than one food source.

20.2.1.5 Predators or Animal Feeders

Nematodes referred to under this category ingest invertebrates such as protozoa, nematodes and rotifers either as ‘ingesters’ (e.g. *Diplogaster* spp., *Mononchus* spp., *Nygolaimus* spp.) or as ‘piercers’ (e.g. *Seinura* spp., *Labronema* spp., *Laimaphelenchus* spp.), sucking body fluids through a narrow stylet.

20.2.1.6 Feeders on Eukaryotes

A wide range of nematodes feed on diatoms or other algae, as well as fungal spores and yeast cells. Examples of this trophic group are *Achromadora* spp., *Diplogaster* spp. and *Fictor* spp.

20.2.1.7 Dispersal or Infective Stages of Animal Parasites

Stages of animal-parasitic nematodes occur in the soil as invertebrate (e.g. *Deladenus* spp., *Heterorhabditis* spp.) or vertebrate (e.g. *Strongyloides* spp.) parasites. When these stages feed and contribute to soil processes, they should be included in other appropriate categories, such as fungi- or bacterivores. Furthermore, when they die in the soil they contribute to the nutrient pool. Individuals from, for example, Rhabditida and Diplogasteridae that use animals as phoretic (transport) hosts are, however, not included in this group.

20.2.1.8 Omnivores

Some nematode species appear normally to feed on a wide range of foods (particularly combining feeding types two to six referred to above). These species are restricted to a few members of the Dorylaimida. Examples include *Actinolaimus*, *Aporcelaimellus* and *Kochinema* spp.

Given this range of feeding types, the soil nematode fauna interacts with many other groups of soil organisms. As the soil biota play critical roles in controlling the mineralisation of nutrients for plant growth, studies were conducted on various functional groups of soil organisms in an effort to understand soil processes. According to Magdorf (2001), soil health is a term used by farmers to refer to the condition of their agricultural soil as it relates to growing viable crops. He stated that high-quality soil has the following characteristics:

(i) Sufficient, but not too high in supply of nutrients
(ii) Good structure or tilth
(iii) Sufficient depth for rooting and drainage
(iv) Good internal drainage
(v) Low populations of plant disease and parasitic organisms
(vi) High populations of organisms that promote plant health
(vii) Low weed pressure
(viii) No chemicals harmful to plants
(ix) Resistance to being degraded
(x) Resilience following an episode of degradation

Only a few studies, aimed at studying non-parasitic nematode assemblages, have been conducted in SA. From 2006 to 2008, a nematode survey was conducted in mixed agricultural gardens in three rural villages (Vhembe, Limpopo Province) by the Nematology Unit of the Agricultural Research Council–Plant Protection Research (ARC-PPR, Roodeplaat, Pretoria). The survey was part of a project titled ‘Legumes and protein for resource-poor farmers in Limpopo Province’. The focus of the nematology part of the project rested mainly on the influence of plant-parasitic nematodes on the yield of the different crops, such as bambara groundnut (*Vigna subterranea*), bean (*Phaseolus* sp.), cabbage (*Brassica oleracea*), groundnut (*Arachis hypogaea*), maize (*Zea mays*), okra (*Abelmoschus esculentus*), onion (*Allium cepa*), pumpkin (*Cucurbita pepo*), spinach (*Spinacia oleracea*), sweet potato (*Ipomoea batatas*) and tomato (*Solanum lycopersicum*), while also monitoring the incidence of non-parasitic nematodes. Probably as a result of the lack of agrochemical usage, the abundance and incidence of non-parasitic nematodes was high in the gardens of all three communities. During the drought of 2007, the numbers of all nematodes were reduced, but of great interest was the high population numbers of especially endoparasitic lesion nematodes (*Pratylenchus* spp.) in the roots of plants.

Berry and Rhodes (2006) and Engelbrecht (2012) conducted studies aimed at, amongst others, determining the effects of different green manure cover crops on nematode populations in soils where sugarcane and potato were grown. These authors chose green manure crops as they are known to improve soil health and, when chosen correctly, reduce pest and disease problems. The main benefits of green manure crops are their ability to:

(i) Produce a large amount of biomass, which can be returned to the soil as sufficient organic matter
(ii) Allow crops to develop a large and deep root system to alleviate the effects of soil compaction
(iii) Provide good ground cover so that weed problems are alleviated

As a result of this study, no significant changes in population levels of plant-parasitic (both in roots and soil samples) and non-parasitic nematodes for the summer and winter crops in the sugarcane production system were recorded.

Results from the sugarcane study, however, showed that none of the green manure cover crops resulted in a significant increase in non-parasitic nematode numbers. By contrast, results from the potato study showed pronounced shifts in non-parasitic nematode assemblages in plots where four Brassicaceae cvs, viz. Nemat (*Brassica juncea*), Calienté (*Eruca sativa*), Doublet and Terranova (*Raphanus sativus*), were planted and their aerial parts subsequently incorporated into the soil, compared to nematode assemblages in control plots. Such soils were regarded as ‘stress depleted’ (degraded) and/or ‘stressed enriched’ (disturbed) before incorporation of the green manure crops, but as ‘stable enrich’ (maturing) afterwards and demonstrated the positive effect of these crops in terms of soil health.

A study by Jansen (2014) furthermore showed that no differences in non-parasitic nematode assemblages were recorded from soils in which conventional soybean (*Glycine max*) cvs were grown (with no application of glyphosate for 5 years prior to the study) compared with those where Roundup® Ready cvs were cultivated. Moreover, non-parasitic nematode assemblages from these two systems also did not differ from those collected from adjacent natural veld sites.

Of great interest to local nematologists studying the role of nematodes in soil are the findings of Moens et al. (2004). They commented that feeding-type classification of nematodes, which usually relies strongly on buccal morphology, may create problems especially as there are many unresolved questions on nematode food sources and feeding rates. For instance, the food sources of the delicately speared Tylenchidae and Psilenchidae remain largely unknown. Although these nematode groups often occur in high population densities in the rhizosphere of plants, direct feeding on plant roots has not been documented. Furthermore, no apparent negative effects on plants are evident. They have been classified as fungal feeders, root hair

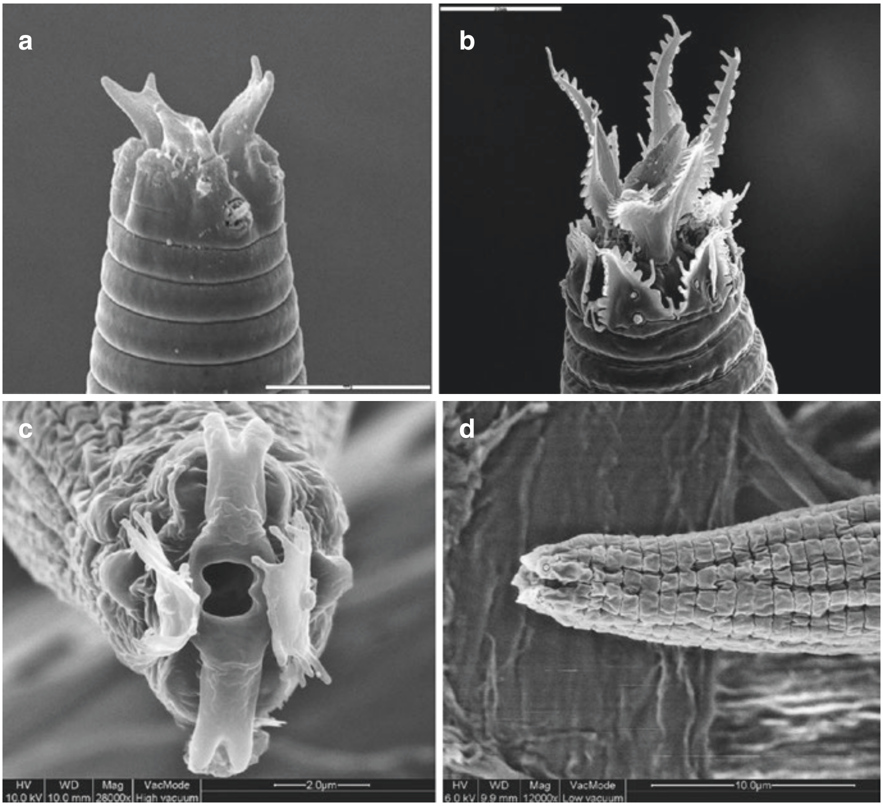

Fig. 20.2 (**a**–**d**) Bacterivore nematodes *Chiloplacus* (**a**), *Acrobeles* (**b**), *Diploscapter* (**c**), *Panagrolaimus* (**d**) (**a** and **b** Ebrahim Shokoohi and **c** and **d** Louwrens Tiedt, North-West University, South Africa)

feeders and plant-associated nematodes (Yeates et al. 1993; Yeates and Bongers 1999). Also, soil bacterial feeders may ingest whole bacterial cells, but the range of differently sized and shaped buccal cavities, lips and appendages exhibited by bacterivores suggests various strategies for obtaining this resource. This phenomenon is illustrated by Fig. 20.2a–d that represents bacterivores that have been recorded from the Bakwena Cave, Gauteng Province, SA, by Durand et al. (2012). Likewise, Venette and Ferris (1998) demonstrated that not all bacteria are suitable food for bacterivores and linked this, amongst other things, to cell size. Moens et al. (1999) showed that four coexisting species of Monhysteridae all respond differently to the presence of different bacteria. Such response differences relate not only to the bacterial strains offered, but also to density, age, growth conditions and activity of the bacteria. Also of great interest is the work by Mikola and Setälä (1998), who demonstrated that bacterial-feeding nematodes perform species-specific rather than guild-specific functions in the soil food web (Fig. 20.3). These studies have far-reaching implications, e.g. the effectiveness of the enrichment of soil by adding bacteria and fungi.

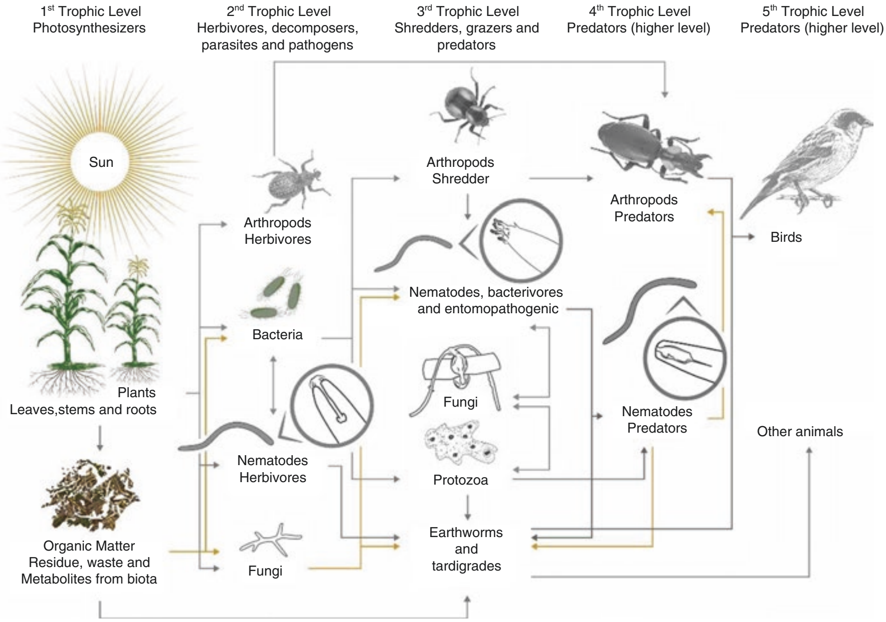

Fig. 20.3 A food web with special reference to nematode individuals from various trophic groups that form an intrinsic part of this process in soils (Hannes Visagie, North West University, Potchefstroom)

Nematodes normally face two options during their journey in soils, namely, (i) maximising energy gains either by moving to a better feeding location or (ii) foraging within a given patch.

The choice between these options will depend on the nematode's functional response to a given type of food and on the presence, suitability and detectability of alternative food sources. Current work suggests that the relative abundance of fungi- and bacterivores is sensitive to management activities and may thus be a good indicator of underlying changes in the composition of the nematode faunal structure. The decrease in diversity of nematode fauna with increasing level of management reflects not only physical disturbance and change in quality of organic matter being returned to the soil but also possible increases in specific herbivores associated with crops (Yeates and Bongers 1999). Generally, soils with annual arable crops contain fewer nematode species, whereas up to 154 species have been recorded in grasslands (Hodda and Wanless 1994). Should permanent grassland be regarded as sustainable, it may provide a baseline for the composition/diversity of the nematode fauna in a given soil.

20.3 Non-parasitic, Freshwater Nematodes

Nematodes usually encountered in freshwater habitats (e.g. dams, karst systems, lakes and streams) are all microscopic in size, ranging from about 0.25 to 10 mm in length. Although some of these are several mm long, they are seldom more than

30–40 µm in diameter. Thus, they are normally not visible to the human eye (Heyns 2002). Most studies on freshwater nematodes in SA, including a preliminary survey by Heyns (1976), were done from 1976 to 1984 (Heyns and Kruger 1983). An interesting observation from this work was that the number of genera per sample was perceptibly lower in polluted streams in the Witwatersrand than in less polluted streams elsewhere (Heyns 1982). Groups particularly affected in this way were the Actinolaimoidea, Belondiroidea, Chromadorida, Dorylaimoidea, *Ironus* spp., Mononchida and *Plectus* spp. Conversely, the abundance of the genera *Monhystera* and *Tobrilus* was higher in polluted samples. Heyns (1982) stated that the observed variation in abundance could be attributed either to a direct toxic effect of the pollutants on the nematodes or to a disruption of their food source. Heyns and Coomans (1980, 1983) discussed and illustrated crystalloids in the body wall of *Chronogaster* spp. and *Chronogaster rotundicauda* Heyns and Coomans, 1984. Nuss (1984) described refractive crystalloids in the body of *Tobrilus gracilis* (Bastian, 1865) Andrássy, 1959, that, once analysed, revealed high sulphur content. Hence, Nuss (1984) considered the crystalloids as part of a detoxification system for sulphide ions that are expressed by the sulphide tolerance of the species and might explain their presence in sulphidic habitats. Poinar (1983) stated that in rivers, members of the Diplogasteroidea appear to be most abundant in waters with medium to heavy pollution, while the Rhabditoidea are especially common in extremely polluted water.

Relatively little taxonomic work has been done on terrestrial non-parasitic nematodes and even less on freshwater nematodes. However, a series of papers on the nematodes from the rivers of the Kruger National Park were published between 1991 and 1993 (Botha and Heyns 1990, 1991, 1992a, b, c, 1993a, b) and included a compendium of the *Mesodorylaimus* spp. and a checklist of the 31 nematode species of the orders Araeolaimida, Chromadorida, Dorylaimida, Enoplida, Monhysterida, Mononchida and Tylenchida from SA. These nematodes were extracted from sediments collected from several rivers in the park. Although aquatic nematodes were found, several species that are usually found in terrestrial habitats were also collected from these rivers. This is not unusual since terrestrial nematodes are commonly found in rivers and other freshwater bodies after having been washed into them with runoff from irrigation and/or torrential rains.

These studies indicate the complexity of the freshwater habitat and also that a good understanding of the benthic nematode community remains of great importance for determining pollution and other types of aquatic disturbances. Heyns (2002) gave valuable information on the extraction of nematodes from aquatic sediments, their morphology and biology as well as keys designed specifically for the identification of freshwater nematodes. He also constructed a key to the orders of the Nematoda that may occur in the freshwaters of southern Africa and stated that the process was essentially complicated by two factors: Firstly, the lack of information since little research has been done on freshwater nematodes in this region and, secondly, the fact that not all nematodes collected from the mud or sand at the bottom of a dam or stream can arbitrarily be regarded as aquatic organisms. Terrestrial nematodes, both non-parasitic and plant-parasitic, sourced from other water bodies are frequently found in large numbers in the bottom sediment where they can survive for long periods. Moreover, many nematode families and even genera contain both terrestrial and aquatic species. Thus, when such a species is found in a water sample, it is particularly difficult to discern whether or not it is truly an aquatic form. *Chronogaster* appears to exhibit an exceptional amount of genetic plasticity regarding habitat selection and adaptation. In fact, *Chronogaster africana* Heyns and Coomans 1980 is cited as occurring in multiple aquatic and terrestrial habitats (Heyns and Coomans 1980).

Of special interest is the report by Hugo and Malan (2010) on nematodes found during a survey of irrigation water in SA. Plant-parasitic nematodes were targeted, and although the nematode numbers seemed to be relatively low, more research is needed to establish the presence and extent of nematodes in local freshwater systems.

20.4 Nematodes from Caves and Caverns

Karst system research has only recently started in southern Africa, and therefore relatively little is known about the unique ecology characterising these systems (Durand et al. 2012). Delicate ecosystems are housed in karst environments containing unique and complex faunal assemblages, some of which are endemic (Culver and Pipan 2010). Furthermore, solution cavities, conduits, fissures and aquifers are predominant features of such landscapes resulting in complex, dynamic and sometimes highly interconnected networks (Williams 2008). This may lead to the formation of an interface between the surface and groundwater. However, as a result of its interconnectivity, these subterranean environments are extremely vulnerable to pollution and degradation by humans (Bonacci et al. 2009). Polluted aquifers pose a severe risk to human and livestock health as abstracted groundwater is commonly used for agricultural and domestic use. Dropping groundwater levels may also lead to sinkhole formation, which has claimed many lives in the past. South Africa is famous for its old and extensive karst system, which is dominated by dolomite deposits covering a large area stretching from the North-West Province, through Gauteng, into Mpumalanga and Limpopo Province (Durand 2008; Du Preez 2014).

When karst systems are damaged by pollutants, including sewage and agrochemicals, to such a degree that their ability to sustain life is compromised, it is very likely that many species of organisms will disappear before they have been studied and documented. For documentation of a karst system, the Bakwena Cave near Irene (Gauteng) has been studied by the SA Karst Ecology Study Group (SAKES) from May 2008 to May 2010. Durand et al. (2012) stated that this cave system is inhabited by bats, fungi, bacteria, nematodes and several arthropod groups in a complex, intricate and interdependent food web. Six localities from the cave were sampled, viz. (i) under ferns and mosses against the walls of the entrance in the daylight zone, (ii) the floor of the main chamber in the twilight zone, (iii) dry bat guano from the floor of the main chamber in the twilight zone, (iv) fresh guano from a side chamber in total darkness, (v) the sediment from a groundwater pool approximately 30 m below the surface and in total darkness and (vi) the floor of the side chamber in total darkness (Durand et al. 2012). Results from this study showed that nematodes were the most common and widely diffused organisms in the Bakwena Cave. In total they represented 11 orders, 23 families and 27 genera. Two localities, viz. the entrance of the cave and underground pool, represented subterranean sampling areas where the most nematode species were recorded.

Another study by Du Preez et al. (2013) reported five nematode genera, namely, *Aphelenchoides*, *Criconema*, *Helicotylenchus*, *Panagrolaimus* and *Rhabditis*, from Knocking Shop and Gatkop, two caves located near Krugersdorp (Gauteng Province) and Thabazimbi (Northern Province), respectively. More recently, Du Preez et al. (2015b) reported a total of 53 nematode genera from sediment, soil and guano samples collected from the Wonderfontein Cave (Gauteng Province). This cave system developed in the dolomitic river banks of the Wonderfontein Spruit (Witwatersrand Basin) and is subjected to the influx of water from the same water body. Of the 53 identified nematode genera, which represented most trophic groups, 22 have never before been reported from a cave environment. Du Preez et al. (2015b) also provided an updated list of cavernicolous nematodes from southern Africa (Table 20.1).

Although a number of nematode taxa have been reported from local subterranean environments, especially in cave ecosystems, information on the functioning of,

Table 20.1 Cavernicolous nematodes from southern Africa

Genus	Trophic group (cp-value)	Habitat	Country	Reference
Achromadora	Eu (3)	Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Acrobeles	Ba (2)	Soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Acrobeloides	Ba (2)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Alaimus	Ba (4)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Anaplectus	Ba (2)	Soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Aphelenchoides	Fu/Her	Soil (daylight zone)	SA , BS	Jansen Van Rensburg (2010); Durand et al. (2012); Du Preez et al. (2013)
Aphelenchus	Fu (2); Her	Soil (twilight zone), Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Aporcelaimus	Om (5)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Boleodorus	Her	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Cephalobus	Ba (2)	Soil	BS	Du Preez et al. (2013)
Chiloplectus	Ba (2)	Soil (total darkness)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Criconema	Her	Soil	BS	Du Preez et al. (2013)
Cylindrolaimus	Ba (3)	Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)

Table 20.1 (continued)

Genus	Trophic group (cp-value)	Habitat	Country	Reference
Diplogasteroides	Ba (1)	Fresh guano (total darkness)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Diploscapter	Ba (1)	Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Discolaimus	Ca (5)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Ditylenchus	Fu/Her (2)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Eumonhysterida	Ba (1)	Soil (total darkness)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Helicotylenchus	Her	Cave pool, soil	SA, BS	Jansen Van Rensburg (2010); Durand et al. (2012); Du Preez et al. (2013)
Meloidogyne	Her	Soil	BS	Du Preez et al. (2013)
Mesorhabditis	Ba (1)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010), Durand et al. (2012)
Monhystrella	Ba (1)	Cave pool, dry guano (twilight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Mononchus	Ca (4)	Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Mylonchulus	Ca (4)	Cave pool, soil (twilight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Neoactinolaimus	Om (4)	Soil	BS	Du Preez et al. (2013)
Panagrolaimus	Ba (1)	Cave pool, dry guano (twilight zone), fresh guano (total darkness)	SA, BS	Jansen Van Rensburg (2010); Durand et al. (2012); Du Preez et al. (2013)
Paracrobeles	Ba (2)	Soil	BS	Du Preez et al. (2013)
Plectus	Ba (2)	Cave pool, soil (daylight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Pratylenchus	Her	Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Prismatolaimus	Ba (3)	Cave pool, soil	SA, BS	Jansen Van Rensburg (2010); Durand et al. (2012); Du Preez et al. (2013)
Rhabditis	Ba (1)	Soil	BS	Du Preez et al. (2013)
Trichodorus	Her	Cave pool	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Tylenchorhynchus	Her	Cave pool, soil (twilight zone)	SA	Jansen Van Rensburg (2010); Durand et al. (2012)
Xiphinema	Her	Soil	BS	Du Preez et al. (2013)
Zeldia	Ba (2)	Soil	BS	Du Preez et al. (2013)

SA = South Africa, *BS* = Botswana
Du Preez et al. (2015b)

services provided by and trophic interactions of such nematode assemblages remains extremely limited. Furthermore, Hodda et al. (2006) stated that true cavernicolous (cave-dwelling) (Box 20.3) nematodes seem to consist of only a few species restricted to such or very similar habitats, together with accidental occupants and species with wide environmental tolerances. However, in order to understand fully the functioning and structure of nematodes occurring in cave environments, further research efforts should be undertaken.

Box 20.3. How Nematodes Survive in Caves: A World View

Similar to the deep-subsurface nematodes found in South Africa, caves also present unique challenges for the survival of life. The lack of sunlight and thus autotrophic production (Hodda et al. 2006), as well as the desolate nature of some cave environments, sometimes only allow the survival of highly adapted species (Romero 2009; Culver and Pipan 2010). Nonetheless, energy is still required to sustain subterranean ecosystems. This is mostly available in the form of organic matter that enters the subterranean environment via percolating and flowing water (dissolved and/or suspended), wind, gravity, animal movement and roots (Culver and Pipan 2010). Once energy becomes available to the subterranean environment, it forms part of the associated ecosystem, which may include various vertebrate (e.g. bats, rodents, fish and salamanders) and invertebrate (e.g. nematodes, insects, arachnids and crustaceans) species (Romero 2009). Biodiversity hotspots may also be found in caves and include bat guano heaps, freshwater bodies and areas subject to substantial energy flow from the surface.

However, some cave ecosystems, such as that associated with Movile Cave (Romania), are chemoautotrophically based (Poinar and Sarbu 1994). Within the latter system, the presence of hydrogen sulphide-rich thermal water facilitates the growth of floating fungal mats, which ultimately sustain an ecosystem of 33 endemic species (Sarbu et al. 1996). Nematodes also form part of this extreme, isolated cave ecosystem and include five highly adapted bacterivores, namely, *Poikilolaimus* sp., *Monhystrella* sp., *Panagrolaimus c.f. thienemanni*, *Udonchus tenuicaudatus* Cobb, 1913 and *Chronogaster troglodytes* Poinar and Sarbu 1994 (Poinar and Sarbu 1994; Muschiol and Traunspurger 2007; Muschiol et al. 2015). The latter species was described as the first true cavernicolous (cave-dwelling) nematode.

Although some nematode species clearly play an intricate role in the functioning of subterranean ecosystems, it is hypothesised that most cavernicolous nematodes are only accidental inhabitants (temporary residents). Such nematodes likely enter the subterranean environment via similar pathways to that of organic matter and other invertebrates (Hodda et al. 2006; Du Preez et al. 2015b). Ultimately, the role that nematodes play in the functioning of subterranean ecosystems is poorly understood and requires further study.

20.5 Non-parasitic Nematodes from Estuaries

Estuaries and estuarine sediments are commonly defined as having more than 1 % salinity (Hodda et al. 2006). Furstenberg and De Wet (1983) recorded two plant-parasitic nematode species, *Helicotylenchus californicus* Sher, 1966, and an unknown *Tylenchus* sp., as being predominant at all sites of salt marsh vegetation sampled at the Swartkops Estuary, Port Elizabeth (Eastern Cape Province). Whether the sediment was also sampled is not clear from their report. According to Hodda et al. (2006), some freshwater nematodes in estuaries are indeed plant-feeders associated with vascular plants (e.g. *Tylenchus* spp., *Helicotylenchus* spp., *Meloidogyne* spp., *Heterodera* spp. and *Hirschmanniella* spp.).

Since 2012, the Nematology Unit of the ARC–PPR has been involved in a study of the nematodes from the Isipingo Estuary near Durban Harbour, KwaZulu-Natal Province. The sediment from the rhizosphere of mangroves (*Rhizophora mucronata*) was sampled as part of a PhD study of Krishni Naidoo at the University of KwaZulu-Natal. The nematode genera found during this survey are listed according to their trophic levels in Table 20.2. This is an ongoing study and other research initiatives on the nematodes are underway. For a more in depth description of the nematodes in estuaries, see Chap. 24.

20.6 Checklist of Non-parasitic Nematodes in South Africa

This list (Table 20.3) contains the non-parasitic nematodes identified in SA from aquatic and terrestrial ecosystems. Classification is according to Andrássy (2005, 2007, 2009), except for the Mononchida, which was classified according to Ahmad and Jairajpuri (2010).

Table 20.2 Nematodes identified from the Isipingo Mangrove Estuary (A. Swart, Agricultural Research Council–Plant Protection Research Institute, Pretoria, 2016, personal communication)

Bacterivore	Predator	Bacterivore/predator	Herbivore (plant parasite)
Areaolaimida, *Camacolaimus* sp., *Deontolaimus* sp., *Desmodora* sp., *Ethmolaimus* sp., *Monhystera* sp., *Monhystrella* sp., *Panagrolaimus* sp., *Plectus* sp., *Prodesmodora* sp., *Rhabditis* sp., *Theristus* sp.	*Tobrilus* sp.	*Koerneria* sp., *Fictor* sp.	*Hemicycliophora ripa* Van den Berg, 1981, *Hemicycliophora typica* de Man, 1921, *Rotylenchus* sp.

Table 20.3 The classification of non-parasitic nematodes that were identified from aquatic (A) and terrestrial (T) habitats in arboreal areas (Ar), caves (C) and estuaries (E) according to Andrássy (2005, 2009), except for the Mononchida, which was classified according to Ahmad and Jairajpuri (2010)

Class Secernentea von Linstow, 1905
Order Rhabditida Chitwood, 1933
Suborder Teratocephalina Andrássy, 1974
Family Teratocephalidae Andrássy, 1958
Genus *Teratocephalus* de Man, 1876
Teratocephalus diversiannulatus Swart and Heyns, 1989 (T)
Teratocephalus lirellus Anderson, 1969 (T)
Suborder Cephalobina Andrássy, 1974
Superfamily Cephaloboidea Filipjev, 1934
Family Cephalobidae Filipjev, 1934
Subfamily Acrobelinae Thorne, 1937
Genus *Acrobeles* von Linstow, 1877
Acrobeles annulatus Heyns and Hogewind, 1969 (T)
Acrobeles bushmanicus Heyns, 1969 (T)
Acrobeles farzanae Heyns, 1995 (T)
Acrobeles sheasbyi Heyns and Hogewind, 1969 (T)
Acrobeles singulus Heyns, 1969 (T)
Acrobeles sparsus Heyns, 1969 (T)
Acrobeles thornei Heyns, 1962 (T)
Genus *Acrobeloides* Cobb, 1924
Acrobeloides butschlii (de Man, 1884) Thorne, 1925 (T)
Genus *Acrobelophis* Andrássy, 1984
Acrobelophis lentus (Maupas, 1900) Vinciguerra and Clausi, 1996 (T)
Genus *Paracrobeles* Heyns, 1968
Paracrobeles laterellus Heyns, 1968 (T)
Genus *Penjatinema* Heyns and Swart, 1998
Penjatinema natalense Heyns and Swart, 1998 (T)
Genus *Seleborca* Andrássy, 1985
Seleborca complexa (Thorne, 1925) Andrássy, 1985 (T)
Seleborca dimorpha (Heyns and Hogewind, 1969) Andrássy, 1958 (T)
Seleborca mariannae (Andrássy, 1968) Andrássy, 1985 (T)
Seleborca recurva (Heyns, 1969) Andrássy, 1985 (T)
Genus *Stegelleta* Thorne, 1983
Stegelleta incasa (Thorne, 1937) Thorne, 1938 (T)
Genus *Zeldia* Thorne, 1937
Zeldia punctata (Thorne, 1925) Thorne, 1937 (T)
Subfamily Cephalobinae Filipjev, 1934
Genus *Cephalobus* Bastian, 1865
Cephalobus persegnis Bastian, 1865 (T)
Genus *Eucephalobus* Steiner, 1936

Table 20.3 (continued)

Eucephalobus oxyuroides (de Man, 1876) Steiner, 1936
Eucephalobus tribei Swart and Heyns, 1997 (Ar, insect galleries, dead pine tree)
Family Elaphonematidae Heyns, 1962
Subfamily Elaphonematinae Heyns, 1962
Genus *Elaphonema* Heyns, 1962
Elaphonema mirabile Heyns, 1962
Elaphonema messinae Van den Berg, Swart and Heyns, 1984 (T)
Family Osstellidae Heyns, 1962
Subfamily Osstellinae Heyns, 1962
Genus *Osstella* Heyns, 1962
Osstella hamata Heyns, 1962
Family Panagrolaimidae Thorne, 1937
Subfamily Panagrolaiminae Thorne, 1937
Genus *Panagrolaimus* Fuchs, 1930
Panagrolaimus magnivulvatus Boström, 1995 (T, nesting material, Antarctica)
Subfamily Tricephalobinae Andrássy, 1976
Genus *Halicephalobus* Timm, 1956
Halicephalobus mephisto Borgonie, García-Moyano, Litthauer, Bert, Bester, Van Heerden, Möller, Erasmus and Onstott, 2011 (A)
Subfamily Turbatricinae Goodey, 1943
Genus *Turbatrix* Peters, 1927
Turbatrix aceti (Mueller, 1783) Peters, 1927 (A)
Superfamily Chambersielloidea Thorne, 1937
Family Chambersiellidae Thorne, 1937
Subfamily Macrolaiminae Sanwal, 1971
Genus *Macrolaimus* Maupas, 1900
Macrolaimus richteri Swart and Heyns, 1992 (T)
Suborder Rhabditina Chitwood, 1933
Superfamily Rhabditoidea Örley, 1880
Family Mesorhabditidae Andrássy, 1976
Subfamily Mesorhabditinae Andrássy, 1976
Genus *Mesorhabditis* Osche, 1952
Mesorhabditis spiculigera (Steiner, 1936) Dougherty, 1953 (T)
Mesorhabditis striatica Dassonville and Heyns, 1984 (A)
Subfamily Parasitorhabditinae Lazarevskaya, 1965
Genus *Parasitorhabditis* Fuchs, 1937
Parasitorhabditis obtusa (Fuchs, 1915) Chitwood and Chitwood, 1950 (Ar, insect galleries, dead pine tree)
Family Diploscapteridae Micoletzky, 1922
Genus *Diploscapter* Cobb, 1913
Diploscapter coronatus (Cobb, 1893) Cobb, 1913 (C, bat guano)
Suborder Diplogastrina Micoletzky, 1922

(continued)

Table 20.3 (continued)

Superfamily Diplogastroidea Micoletzky, 1922
Family Diplogastridae Filipjev and Schuurmans Stekhoven, 1941
Genus *Acrostichus* Rahm, 1928
Acrostichus secundus (Bovien, 1837) Andrássy, 2005 (A)
Genus *Diplogasteritus* Paramonov, 1952
Diplogasteritus nudicapitatus (Steiner, 1914) Paramonov, 1952 (A)
Genus *Paroigolaimella* Paramonov, 1952
Paroigolaimella bernensis (Steiner, 1914) Andrássy, 1958 (A)
Family Neodiplogastridae Paramonov, 1952
Subfamily Neodiplogastrinae Paramonov, 1952
Genus *Mononchoides* Rahm, 1928
Mononchoides gracilis Dassonville and Heyns, 1984 (A)
Genus *Mononchoides* Rahm, 1928
Mononchoides gracilis Dassonville and Heyns, 1984 (A)
Order Aphelenchida Siddiqi, 1980
Suborder Aphelenchina Geraert, 1966
Superfamily Aphelenchoidea Fuchs, 1937
Family Aphelenchidae Fuchs, 1937
Genus *Aphelenchus* Bastian, 1865
Aphelenchus avenae Bastian, 1865 (T)
Family Paraphelenchidae Goodey, 1951
Genus *Paraphelenchus* Micoletzky, 1922
Paraphelenchus pseudoparietinus (Micoletzky, 1922) Micoletzky, 1925 (T)
Paraphelenchus amblyurus Steiner, 1934 (T)
Superfamily Aphelenchoidoidea Skarbilovich, 1947
Family Aphelenchoididae Skarbilovich, 1947
Genus *Laimaphelenchus* Fuchs, 1938
Laimaphelenchus patulus Swart, 1997 (Ar)
Genus *Aphelenchoides* Fischer, 1894
Aphelenchoides africanus Dassonville and Heyns, 1984 (A)
Aphelenchoides chamelocephalus (Steiner, 1926) Filipjev, 1934 (T)
Aphelenchoides composticola Franklin, 1957 (T)
Aphelenchoides haguei Maslen, 1979 (Ar)
Aphelenchoides helicus Heyns, 1964 (T)
Order Tylenchida Thorne, 1949
Suborder Tylenchina Chitwood in Chitwood and Chitwood, 1950
Superfamily Tylenchoidea Örley, 1880
Family Anguinidae Nicoll, 1935
Genus *Ditylenchus* Filipjev, 1936
Ditylenchus equalis Heyns, 1964 (T)
Class Penetrantia Andrássy, 1974
Subclass Enoplia Pearse, 1942
Order Enoplida Filipjev, 1929

Table 20.3 (continued)

Suborder Oncholaimina De Coninck, 1965
Superfamily Oncholaimoidea Filipjev, 1916
Family Oncholaimidae Filipjev, 1916
Genus *Oncholaimus* Dujardin, 1845
Oncholaimus deconincki Heyns and Coomans, 1977 (A)
Oncholaimus jessicae Coomans and Heyns, 1986 (A)
Suborder Ironina Siddiqi, 1983
Superfamily Ironoidea de Man, 1876
Family Ironidae de Man, 1876
Genus *Ironus* Bastian, 1865
Ironus ignavus Bastian, 1865 (A)
Ironus crassatus Argo and Heyns, 1972 (A)
Ironus dentifurcatus Argo and Heyns, 1972 (A)
Ironus ernsti Argo and Heyns, 1972 (A)
Ironus lautus Argo and Heyns, 1972 (A)
Ironus longicaudatus de Man, 1884 (A)
Ironus tenuicaudatus de Man, 1876 (A)
Suborder Tripylina Andrássy, 1974
Superfamily Prismatolaimoidea Micoletzky, 1922
Family Prismatolaimidae Micoletzky, 1922
Genus *Prismatolaimus* de Man, 1880
Prismatolaimus parvus Milne, 1963 (A)
Family Onchulidae Andrássy, 1964
Genus *Limonchulus* Andrássy, 1963
Limonchulus heynsi Swart and Furstenberg, 1993 (A)
Superfamily Tripyloidea de Man, 1876
Family Tobrilidae De Coninck, 1965
Subfamily Tobrilinae De Coninck, 1965
Genus *Neotobrilus* Tsalolikhin, 1981
Neotobrilus longus (Leidy, 1852) Tsalolikhin, 1981 (A)
Genus *Eutobrilus* Tsalolikhin, 1981
Eutobrilus ampiei Joubert and Heyns, 1979 (A)
Eutobrilus annetteae Joubert and Heyns, 1979 (A)
Eutobrilus diversipapillatus (Daday, 1905) Andrássy, 1959 (A)
Eutobrilus floridensis Joubert and Heyns, 1979 (A)
Eutobrilus heptapapillatus (Joubert and Heyns, 1979) Swart and Heyns, 1988 (A)
Genus *Epitobrilus* Tsalolikhin, 1981
Epitobrilus stefanskii (Micoletzky, 1925) Andrássy 2007 (A)
Genus *Macrotobrilus* Tsalolikhin, 1981
Macrotobrilus elephas (Andrássy, 1964) Tsalolikhin, 1981 (A)
Subfamily Tobriloidinae Tsalolikhin, 1976
Genus *Tobriloides* Loof, 1973

(continued)

Table 20.3 (continued)

Tobriloides loofi Swart and Heyns, 1990 (T)
Family Tripylidae de Man, 1876
Genus *Trischistoma* Cobb, 1913
Trischistoma ursulae Argo and Heyns, 1973 (A)
Subclass Dorylaimia Inglis, 1983
Order Alaimida Siddiqi, 1983
Suborder Alaimina Clark, 1961
Superfamily Alaimoidea Micoletzky, 1922
Family Amphidelidae Andrássy, 2002
Genus *Paramphidelus* Andrássy, 1977
Paramphidelus monohystera (Heyns, 1962) Andrássy, 1977
Paramphidelus trichurus (Siddiqi and Brown, 1965) Andrássy, 1977
Order Mononchida Jairajpuri, 1969
Suborder Mononchina Kirjanova and Krall, 1969
Superfamily Mononchoidea Filipjev, 1934
Family Mononchidae Filipjev, 1934
Subfamily Mononchinae
Genus *Mononchus* Bastian, 1865
Mononchus truncatus Bastian, 1865 (T)
Mononchus aquaticus Coetzee, 1968 (A, T)
Mononchus tunbridgensis (T)
Genus *Prionchulus* Cobb, 1916
Prionchulus muscorum (Dujardin, 1845) Wu and Hoeppli, 1929 (T)
Genus *Clarkus* Jairajpuri, 1970a
Clarkus papillatus (Bastian, 1865) Jairajpuri, 1970 (T)
Clarkus sheri (Mulvey, 1967) Jairajpuri, 1970 (T)
Genus *Coomansus* Jairajpuri and Khan, 1977
Coomansus parvus (de Man, 1880) Jairajpuri and Khan, 1977 (T)
Family Mylonchulidae Jairajpuri, 1969
Subfamily Mylonchulinae Jairajpuri, 1969
Genus *Mylonchulus* Cobb, 1916
Mylonchulus minor (Cobb, 1893) Cobb, 1916 (A, T)
Mylonchulus brachyuris (Bütschli, 1873) Cobb, 1917 (T)
Mylonchulus brevicaudatus (Cobb, 1917) Altherr, 1954 (T)
Mylonchulus hawaiiensis (Cassidy, 1931) Andrássy, 1958 (T)
Mylonchulus incurvus (Cobb, 1917) Andrássy, 1958 (T)
Mylonchulus lacustris (Cobb N.A. in Cobb, M.V., 1915) Andrássy, 1958 (T)
Mylonchulus sigmaturus (Cobb, 1917) Altherr, 1953 (T)
Mylonchulus striatus (Thorne, 1924) Andrássy, 1958 (T)
Subfamily Sporonchulinae Jairajpuri, 1969
Genus *Granonchulus* Andrássy, 1958
Granonchulus decurrens (Cobb, 1917) Andrássy, 1958 (T)

Table 20.3 (continued)

Granonchulus subdecurrens Coetzee, 1966 (T)
Family Cobbonchidae Jairajpuri, 1969
Genus *Cobbonchus* Andrássy, 1958
Cobbonchus artemisiae Coetzee, 1968 (T)
Cobbonchus charlesi Coetzee, 1966 (T)
Cobbonchus diannae Coetzee, 1965 (T)
Cobbonchus eurystoma Coetzee, 1965 (T)
Cobbonchus heynsi Coetzee, 1965 (T)
Cobbonchus mauritianus (Williams, 1958) Clark, 1960 (T)
Cobbonchus megalus Coetzee, 1966 (T)
Cobbonchus ockerti Coetzee, 1965 (T)
Cobbonchus rotundicaudatus Coetzee, 1968 (T)
Cobbonchus thesigeri Coetzee, 1968 (T)
Family Iotonchidae Jairajpuri, 1969
Subfamily Iotonchinae Jairajpuri, 1969
Genus *Iotonchus* Cobb, 1916
Iotonchus acutus Heyns and Lagerwey, 1965 (T)
Iotonchus geminus Heyns and Lagerwey, 1965 (T)
Iotonchus litoralis Coetzee, 1967 (T)
Iotonchus loteniae de Bruin and Heyns, 1992 (T)
Iotonchus monhystera (Cobb, 1917) Jairajpuri, 1970 (T)
Iotonchus pauli Heyns and Lagerwey, 1965 (T)
Iotonchus rinae Coetzee, 1967 (T)
Iotonchus risoceiae (Carvalho, 1955) Andrássy, 1858 (T)
Iotonchus spinacaudatus Coetzee, 1967 (T)
Iotonchus transkeiensis Heyns and Lagerwey, 1965 (T)
Genus *Jensenonchus* Jairajpuri and Khan, 1982
Jensenonchus antedontoides (Coetzee, 1967) Andrássy, 1993
Order Dorylaimida Pearse, 1942
Suborder Nygolaimina Ahmad and Jairajpuri, 1979
Superfamily Nygolaimoidea Thorne, 1935
Family Nygolaimidae Thorne, 1935
Subfamily Nygolaiminae Thorne, 1935
Genus *Aquatides* Heyns, 1968
Aquatides thornei (Schneider, 1937) Thorne, 1974 (A)
Genus *Solididens* Heyns, 1968
Solididens bisexualis (Thorne, 1930) Heyns, 1968 (T)
Solididens capensis Heyns, 1967 (T)
Solididens spiralis Loos, 1946 (T)
Solididens vulgaris (Thorne, 1930) Thorne, 1974 (T)
Solididens xosorum Heyns, 1967 (T)
Genus *Nygolaimus* Cobb, 1913
Nygolaimus brachyuris (de Man, 1880) Thorne, 1930 (T)

(continued)

Table 20.3 (continued)

Nygolaimus anneckei Heyns, 1967 (T)
Nygolaimus directus Heyns, 1967 (T)
Nygolaimus dorotheae Heyns, 1967 (T)
Nygolaimus elainnae Botha and Heyns, 1990b (T)
Genus *Laevides* Heyns, 1968
Laevides laevis (Thorne, 1939) Heyns, 1968 (T)
Genus *Paravulvus* Heyns, 1968
Paravulvus andrassyi Heyns, 1967 (T)
Paravulvus hartingii (de Man, 1880) Thorne, 1929 (T)
Family Nygolaimidae Thorne, 1935
Subfamily Nygolaimellinae Clark, 1961
Genus Nygolaimellus Loos, 1949
Nygolaimellus macmacus Heyns, 1967
Nygolaimellus rectalus Heyns, 1967
Suborder Dorylaimina Pearse, 1936
Superfamily Dorylaimoidea de Man, 1876
Family Actinolaimidae Thorne, 1939
Subfamily Actinolaiminae Thorne, 1939
Genus *Actinolaimus* Cobb, 1913
Actinolaimus perplexus Heyns and Argo, 1970
Genus *Neoactinolaimus* Thorne, 1967
Neoactinolaimus crassidens Heyns and Argo, 1970 (T)
Genus Paractinolaimus Meyl, 1957
Paractinolaimus microdentatus (Thorne, 1939) Meyl, 1957 (T)
Paractinolaimus prodenticulatus Heyns and Argo, 1970 (T)
Paractinolaimus vigor Thorne, 1967 (T)
Paractinolaimus xosorum Heyns and Argo, 1970 (T)
Family Crateronematidae Siddiqi, 1969
Subfamily Lordellonematinae Siddiqi, 1969
Genus *Lordellonema* Andrássy, 1959
Lordellonema porosum (Heyns, 1963) Heyns, 1963 (T)
Family Thornenematidae Siddiqi, 1969
Subfamily Thornenematinae Siddiqi, 1969
Genus *Thornenema* Andrássy, 1959
Thornenema baldum (Thorne, 1939) Andrássy, 1959 (A, T)
Thornenema cavalcantii Lordello, 1955 (T)
Family Nordiidae Jairajpuri and Siddiqi, 1964
Subfamily Pungentinae Siddiqi, 1964
Genus *Lenonchium* Siddiqi, 1965
Lenonchium fimbricaudatum Swart and Heyns, 1991 (A)
Genus *Kochinema* Heyns, 1963
Kochinema proamphidum Heyns, 1963 (T)
Subfamily Nordiinae Jairajpuri and Siddiqi, 1964

Table 20.3 (continued)

Genus *Longidorella* Thorne, 1939
Longidorella microdorus (de Man, 1880) Goodey, 1963 (T)
Family Dorylaimidae de Man, 1876
Subfamily Dorylaiminae de Man, 1876
Genus *Laimydorus* Siddiqi, 1969
Laimydorus africanus Botha and Heyns, 1993 (A)
Laimydorus olifanti Botha and Heyns, 1991 (A)
Genus *Dorylaimus* Dujardin, 1845
Dorylaimus asymphydorus Andrássy, 1969 (T)
Subfamily Mesodorylaiminae Andrássy, 1969
Genus *Calcaridorylaimus* Andrássy, 1986
Calcaridorylaimus sirgeli Heyns and Meyer, 1995 (A, T)
Genus *Mesodorylaimus* Andrássy, 1959
Mesodorylaimus mesonyctius (Kreis, 1930) Andrássy, 1959 (T)
Mesodorylaimus aegypticus (Andrássy, 1958) Andrássy, 1959 (A)
Mesodorylaimus arvensis (Cobb in Thorne and Swanger, 1936) Andrássy, 1959 (A, T)
Mesodorylaimus bainsi Basson and Heyns, 1974 (T)
Mesodorylaimus importunes Basson and Heyns, 1974 (A, T)
Mesodorylaimus intermedius Dassonville and Heyns, 1984 (A)
Mesodorylaimus johanni Basson and Heyns, 1974 (T)
Mesodorylaimus kowyni Basson and Heyns, 1974 (T)
Mesodorylaimus margaritus Basson and Heyns, 1974 (T)
Mesodorylaimus mesonyctius (Kreis, 1930) Andrássy, 1959 (A, T)
Mesodorylaimus paralitoralis Basson and Heyns, 1974 (T)
Mesodorylaimus potus Heyns, 1963 (T)
Mesodorylaimus pseudosubtilis Basson and Heyns, 1974 (T)
Mesodorylaimus rotundolabiatus Basson and Heyns, 1974 (T)
Mesodorylaimus sanctus Basson and Heyns, 1974 (T)
Mesodorylaimus transkeiensis Basson and Heyns, 1974 (T)
Mesodorylaimus usitatus Basson and Heyns, 1974 (A)
Mesod*orylaimus vaalensis* Heyns and Kruger, 1983 (A, T)
Genus *Namaquanema* Heyns and Swart, 1993
Namaquanema hanki Heyns and Swart, 1993 (T)
Subfamily Prodorylaiminae Andrássy, 1959
Genus *Prodorylaimus* Andrássy, 1959
Prodorylaimus paralongicaudatus (Micoletzky, 1925) Andrássy, 1959 (T)
Prodorylaimus rionensis (Gerlach, 1954) Andrássy, 1959 (T)
Family Aporcelaimidae Heyns, 1965
Subfamily Aporcelaiminae Heyns, 1965
Genus *Aporcelaimellus* Heyns, 1965
Aporcelaimellus obtusicaudatus (Bastian, 1865) Altherr, 1968 (A)

(continued)

Table 20.3 (continued)

Aporcelaimellus adriani Botha and Heyns, 1990 (T)
Aporcelaimellus amylovorus Thorne and Swanger (1936), Heyns (1965)
Aporcelaimellus glandus Botha and Heyns, 1991 (A, T)
Aporcelaimellus micropunctatus Botha and Heyns, 1990 (A, T)
Aporcelaimellus parapapillatus Botha and Heyns, 1990 (T)
Genus *Aporcelaimus* Thorne and Swanger, 1936
Aporcelaimus pseudospiralis Botha and Heyns, 1990 (T)
Genus *Makatinus* Heyns, 1965
Makatinus punctatus Heyns, 1965 (T)
Makatinus capensis Heyns, 1965 (T)
Makatinus macropunctatus Heyns, 1967 (T)
Genus *Tubixaba* Monteiro and Lordello, 1980
Tubixaba minima Botha and Heyns, 1990 (T)
Subfamily Sectonematinae Siddiqi, 1969
Genus *Sectonema* Thorne, 1930
Sectonema brevicauda Heyns, 1965 (T)
Sectonema probulbum (Heyns, 1965) Siddiqi, 1995 (T)
Sectonema pseudoventrale Heyns, 1965 (T)
Family Qudsianematidae Jairajpuri, 1965
Subfamily Qudsianematinae Jairajpuri, 1965
Genus *Allodorylaimus* Andrássy, 1986
Allodorylaimus diadematus (Cobb in Thorne and Swanger, 1936) Andrássy, 1986 (T)
Genus *Crassolabium* Yeates, 1967
Crassolabium annae Van Reenen and Heyns, 1986 (T)
Crassolabium christiani Van Reenen and Heyns, 1986 (T)
Crassolabium nothus (Thorne and Swanger, 1936) Peňa-Santiago and Ciobanu, 2008 (T)
Crassolabium surikae Van Reenen and Heyns, 1986 (T)
Genus *Skibbenema* Van Reenen and Heyns, 1986
Skibbenema constrictum Van Reenen and Heyns, 1986 (T)
Genus *Talanema* Andrássy, 1991
Talanema mauritiense Williams, 1959 (T)
Genus *Labronema* Thorne, 1939
Labronema pygmaeum Heyns, 1963 (T)
Subfamily Lordellonematinae Siddiqi, 1969
Genus *Lordellonema* Andrássy, 1959
Lordellonema porosum (Heyns, 1963) Heyns, 1963 (T)
Subfamily Discolaiminae Siddiqi, 1969
Genus *Discolaimus* Cobb, 1913
Discolaimus acuticapitus Furstenberg and Heyns, 1965
Discolaimus bicorticus Furstenberg and Heyns, 1965

Table 20.3 (continued)

Discolaimus constrictus Heyns, 2001 (T)
Discolaimus deaconi Botha and Heyns, 1991 (A)
Discolaimus intermedius Heyns and Lagerwey, 1965
Discolaimus krugeri Furstenberg and Heyns, 1965
Discolaimus levinae Furstenberg and Heyns, 1965
Discolaimus major Thorne, 1939 (T)
Discolaimus monoplanes Heyns, 1963 (A, T)
Discolaimus similis Thorne, 1939
Genus *Discolaimium* Thorne, 1939
Discolaimium sublatum Heyns, 1963 (T)
Genus *Eudorylaimus* Andrássy, 1959
Eudorylaimus fransus Heyns, 1963 (T)
Eudorylaimus nudicaudatus Heyns, 1993 (T, Antarctica)
Genus *Microdorylaimus* Andrássy, 1986
Microdorylaimus rapsus (Heyns, 1963) Andrássy, 1986 (T)
Subfamily Carcharolaiminae Thorne, 1967
Genus *Carcharolaimus* Thorne, 1939
Carcharolaimus crassicostatus Heyns and Argo, 1969 (T)
Superfamily Belondiroidea Thorne, 1939
Family Dorylaimellidae Jairajpuri, 1964
Genus *Dorylaimellus* Cobb, 1913
Dorylaimellus aferoides Jordaan and Heyns, 1984 (T)
Dorylaimellus andrassyi Heyns, 1963 (T)
Dorylaimellus imitator Heyns, 1963 (T)
Dorylaimellus jonsoni (Jordaan and Heyns, 1984) Jairajpuri and Ahmad, 1992 (T)
Dorylaimellus meridionalis Jordaan and Heyns, 1984 (T)
Dorylaimellus monticolus Clark, 1963 (T)
Dorylaimellus projectus Heyns, 1962 (T)
Dorylaimellus tenuidens Thorne, 1939 (T)
Dorylaimellus vexator Heyns, 1963 (T)
Genus *Axodorylaimellus* Jairajpuri and Ahmad, 1980
Axodorylaimellus parvulus (Thorne, 1939) Jairajpuri and Ahmad, 1980 (T)
Family Swangeriidae Jairajpuri, 1964
Subfamily Swangeriinae Jairajpuri, 1964
Genus *Oxydirus* Thorne, 1939
Oxydirus gangeticus Siddiqi, 1966 (A, T)
Superfamily Tylencholaimoidea Filipjev, 1934
Family Tylencholaimidae Filipjev, 1934
Subfamily Tylencholaiminae Filipjev, 1934
Genus *Chitwoodius* Jiménez-Guirado and Peña-Santiago, 1992
Chitwoodius transvaalensis Furstenberg and Heyns, 1966 (T)

(continued)

Table 20.3 (continued)

Genus *Tylencholaimus* de Man, 1876
Tylencholaimus gertii Kruger, 1956 (T)
Tylencholaimus obscurus Jairajpuri, 1965 (T)
Tylencholaimus proximus Thorne, 1939 (T)
Family Mydonomidae Thorne, 1964
Subfamily Mydonominae Thorne, 1964
Genus *Dorylaimoides* Thorne and Swanger, 1936
Dorylaimoides dactylurus Heyns, 1963 (T)
Dorylaimoides paraconurus Heyns, 1963 (T)
Dorylaimoides pretoriensis Heyns, 1963 (T)
Dorylaimoides thecolaimus Heyns, 1963 (T)
Subfamily Vanderlindiinae Siddiqi, 1969
Genus *Vanderlindia* Heyns, 1964
Vanderlindia duplopapillata Heyns, 1964 (T)
Family Leptonchidae Thorne, 1935
Subfamily Leptonchinae Thorne, 1935
Genus *Leptonchus* Cobb, 1920
Leptonchus transvaalensis Heyns, 1963 (A, T)
Genus *Proleptonchus* Lordello, 1955
Proleptonchus krugeri Botha and Heyns, 1992 (A)
Subfamily Tyleptinae Jairajpuri, 1964
Genus *Tyleptus* Thorne, 1939
Tyleptus striatus Heyns, 1963 (T)
Subfamily Xiphinemellinae Jairajpuri, 1964
Genus *Xiphinemella* Loos, 1950
Xiphinemella christiae de Bruin and Heyns, 1991 (T)
Xiphinemella eversa (Heyns, 1963) Siddiqi, 1966 (T)
Xiphinemella marindae de Bruin and Heyns, 1991 (T)
Order Mermithida Hyman, 1951
Suborder Isolaimina Inglis, 1983
Superfamily Isolaimoidea Timm, 1969
Family Isolaimidae Timm, 1969
Genus *Isolaimium* Cobb, 1920
Isolaimium africanum (Hogewind and Heyns, 1967) Heyns and Swart, 1988 (T)
Isolaimium incus Hogewind and Heyns, 1967 (T)
Class Torquentia Andrássy, 1974
Order Monhysterida De Coninck and Schuurmans Stekhoven, 1933
Suborder Monhysterina De Coninck and Schuurmans Stekhoven, 1933
Superfamily Monhysteroidea de Man, 1876
Family Monhysteridae de Man, 1876
Subfamily Monhysterinae de Man, 1876
Genus *Monhystera* Bastian, 1965

Table 20.3 (continued)

Monhystera stagnalis Bastian, 1965 (A)
Monhystera gabaza (Joubert and Heyns, 1980) Jacobs and Heyns, 1994 (A)
Monhystera magnacephala (Joubert and Heyns, 1980) Jacobs and Heyns, 1994 (A)
Monhystera somereni Allgén, 1952 (A)
Monhystera wangi Wu and Hoeppli, 1929 (T)
Genus *Geomonhystera* Andrássy, 1981
Geomonhystera pervaga (Argo and Heyns, 1973) Andrássy, 1981 (T)
Family Xyalidae Chitwood, 1951
Order Araeolaimida De Coninck and Schuurmans Stekhoven, 1933
Suborder Leptolaimina Lorenzen, 1979
Superfamily Haliplectoidea Chitwood, 1951
Family Haliplectidae Chitwood, 1951
Genus *Haliplectus* Cobb, 1913
Haliplectus algoensis Swart and Heyns, 1992 (T)
Haliplectus bickneri (Chitwood, 1956) Swart, Heyns and Coomans, 1993 (T)
Family Plectidae Örley, 1880
Subfamily Plectinae Örley, 1880
Genus *Plectus* Bastian, 1865
Plectus parietinus Bastian, 1865 (T)
Plectus antarcticus de Man, 1904 (T, Antarctica)
Plectus aquatilis Andrássy, 1985 (A)
Plectus cirratus Bastian, 1865 (A)
Subfamily Anaplectinae Zell, 1993
Genus *Anaplectus* De Coninck and Schuurmans Stekhoven, 1933
Anaplectus granulosus (Bastian, 1865) De Coninck and Schuurmans Stekhoven, 1933 (T)
Subfamily Wilsonematinae Chitwood, 1951
Genus *Wilsonema* Cobb, 1913
Wilsonema otophorum (de Man, 1880) Cobb, 1913 (T)
Genus *Tylocephalus* Crossman, 1933
Tylocephalus auriculatus (Bütschli, 1873) Anderson, 1966 (T)
Family Rhabdolaimidae Chitwood, 1951
Subfamily Rhabdolaiminae Chitwood, 1951
Genus *Rhabdolaimus* de Man, 1880
Rhabdolaimus terrestris de Man, 1880 (A)
Superfamily Metateratocephaloidea Eroshenko, 1973
Family Metateratocephalidae Eroshenko, 1973
Genus *Euteratocephalus* Andrássy, 1958
Euteratocephalus palustris (de Man, 1880) Andrássy, 1958 (T)
Euteratocephalus spiraloides (Micoletzky, 1913) Heyns, 1977 (A)

(continued)

Table 20.3 (continued)

Genus *Metateratocephalus* Eroshenko, 1973
Metateratocephalus crassidens (de Man, 1880) Eroshenko, 1973 (T)
Superfamily Plectoidea Örley, 1880
Family Chronogastridae Gagarin, 1975
Genus *Chronogaster* Cobb, 1913
Chronogaster africana Heyns and Coomans, 1980 (T and A)
Chronogaster glandifera Heyns and Coomans, 1980 (A)
Chronogaster longicauda Heyns and Coomans, 1980 (A)
Chronogaster multispinata Heyns and Coomans, 1980 (A)
Order Chromadorida Chitwood, 1933
Suborder Chromadorina Chitwood and Chitwood, 1937
Superfamily Chromadoroidea Filipjev, 1917
Family Selachinematidae Cobb, 1915
Genus *Cobbionema* Filipjev, 1922
Cobbionema capense Furstenberg and Heyns, 1987 (E)
Superfamily Cyatholaimoidea Filipjev, 1918
Family Cyatholaimidae Filipjev, 1918
Genus *Achromadora* Cobb, 1913
Achromadora ruricola (de Man, 1880) Micoletzky, 1925 (A, T)
Genus *Synonchium* Cobb, 1920
Synonchium capense Heyns and Swart, 1995 (T)
Order Desmodorida De Coninck, 1965
Suborder Desmodorina De Coninck, 1965
Superfamily Desmodoroidea Filipjev, 1922
Family Desmodoridae
Genus *Sibayinema* Swart and Heyns, 1991
Sibayinema natalensis Swart and Heyns, 1991 (A)

20.7 Conclusions

Non-parasitic nematodes are an integral part of the interlocking chain of nutrient conversions that occur in terrestrial and aquatic environments. They function in the recycling of carbon-containing substances, mineral nutrients and nitrogenous components. Likewise, they control explosions of microflora and microfauna and maintain the stability of life forms that constitute the delicate balance of nature. Viglierchio (1991) duly emphasised the fact that although non-parasitic nematodes are considered benign by mankind, they constitute one of the vital components in the preservation of the balance of life processes of our world.

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