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An update of the catalogue of paraphyletic ‘Rhabditidae’ (Nematoda) after eleven years

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Abstract

Eleven years after publication, the catalogue on ‘Rhabditidae’ is herewith continued, presenting for subsequently described species information including synonyms, type locality and type habitat. Of the seven genus taxa proposed since 2011, five were judged to be synonymous, and of the 120 species described as new, 11 were suggested to be synonymous. The 109 new valid species are distributed across 25 genus taxa which each represent a side branch of the phylogenetic tree. Diagnostic features are mentioned for the new genera *Auanema* and *Tokorhabditis*. The increase in the number of nominal species mainly concerns *Caenorhabditis* (40 new species), *Oscheius* (12 new species) and *Pellioditis* (15 new species). New species were recruited mainly from India (29), Central and South America (17), Europe (15), Africa (9) and China (7 species). A list of *nomina nuda* is also given.

Keywords *Caenorhabditis* | *Heterorhabditis* | *Phasmarhabditis* | *Psychodorhabditis* | gastropod-pathogenic

Introduction

‘Rhabditidae’ is the paraphyletic assemblage consisting of the members of the clade Rhabditina from which *Agfa*, Angiostomatidae, *Carabonema*, Diplogastridae, *Noteodiplogaster*, Rhabdiasidae, and Strongylida are excluded (Sudhaus 2011, see fig. 2). Its species exhibit many characters of the old body plan that was built up in the lineage of the ancestors of Rhabditina which lived as saprobionts in ephemeral terrestrial habitats, feeding on bacteria. In six of these clades the body plan changed fundamentally in adaptation to a parasitic lifestyle. Although the Diplogastridae remained saprobiontic, a new body plan was constituted in its ancestral lineage too. The reasons for this are unclear, but innovations in digestive physiology can be assumed to have played a key role. The body plan of rhabditids, in contrast, remained reasonably stable (Sudhaus 2011: 120), though by thousands of speciation processes many divergent lineages arose. The separate lineages were designated with a genus name as required by the conventions of binomial species names. In the last revision of ‘Rhabditidae’ I accepted 38 genus clades and listed names of 368 valid species with 124 synonyms (Sudhaus 2011). Since then seven new genus names and 120 new species names have been proposed, whose validity and classification must be verified. This is the aim of the update.

History of research in ‘Rhabditidae’ systematics

In research into the diversity of rhabditid nematodes we can differentiate four overlapping periods. Starting with the creation by Dujardin (1844) of the genus name *Rhabditis* for *Rhabditis terricola*, the first period, which is ongoing, is characterised by the description of new species by many authors and only the odd comparative work by Maupas (1900) and Reiter (1928). The second

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period is determined by the systematisation of *Rhabditis* sensu lato by Osche (1952), and the elevation of ranks of his subgroups and nomenclatural corrections carried out by Dougherty (1955). A flurry of correspondence arose between Ellsworth Dougherty (in English) and Günther Osche (in German), resulting in a revision published by Dougherty alone. In a letter to Osche from December 2, 1952, Dougherty proposed writing a joint paper on the application of the nomenclatural rules in rhabditids, but Osche declined because he could not agree with the splitting of the genus taxon *Rhabditis* into several genus taxa as advocated by Dougherty. Their standpoints on classification were incompatible. Nevertheless, in extensive correspondence between December 1952 and May 1955 the splitter Dougherty and the lumper Osche collaboratively searched for all the species descriptions in the scattered literature and discussed their taxonomic status. Osche's expertise was acknowledged when Dougherty wrote (2.7.1954): 'It seems to me obvious ... that the profound contribution has been yours and that mine is but legalistic gingerbread.' And on January 13, 1953: 'If I cannot convert you largely to my nomenclatorial and taxonomic views in this matter, I shall ultimately publish them myself. However, I should be happier for you to carry through your own revision of the nomenclature of the group, for my contribution would be little more than parasitic on the vast amount of time and effort that you have already put into your studies on the Rhabditinae. ... As I have previously indicated, what I am basically interested in is a sound and reasonably stable system of nomenclature for a group of organisms that I feel will become important research material in experimental biology in the coming years.'

The last claim was prophetic. It became reality in the sixth decade of the last century when Sydney Brenner – based on the research by Victor Nigon and Dougherty – chose *Caenorhabditis elegans* as a model organism in developmental genetics. At nearly the same time, the third period in 'Rhabditidae' systematics began, a period that can be described as the change from a typological to a phylogenetic classification using synapomorphic morphological characters to hypothesise on sister group relationships between monophyletic taxa founded by apomorphies (Sudhaus 1976). This way of working was largely replaced from about 2000 by the reconstruction of phylogenetic diagrams using DNA sequence data, a method which continues to dominate the current fourth period (Kiontke et al. 2007). The work of the molecular phylogeneticists is supported by a living collection of a large number of species kept in the Caenorhabditis Genetics Center (founded in 1978) and various laboratories. All these periods are ongoing (Fig. 1).

In the last decade, fuelled by surveys intended to isolate biocontrol agents for pest insects (*Heterorhabditis* and *Oscheius*) and harmful slugs (*Pellioditis*), many new rhabditids have been discovered. Furthermore, members of the *C. elegans* community have been engaged in a hunt for hitherto unknown species of *Caenorhabditis* for scientific comparison. And, increasingly, nematologists worldwide have been investigating inhabitants of special biochores.

On species taxa

A species is constituted by members of a unique evolutionary lineage realising a special multidimensional ecological niche (econiche) and therefore became genetically isolated from members of other lineages by specific recognition mechanisms for mates. Identifying a specimen as a member of a described or undescribed (new) species using morphological, morphometric or molecular data is a hypothesis on the ecological and reproductive behaviour of that population of which it is

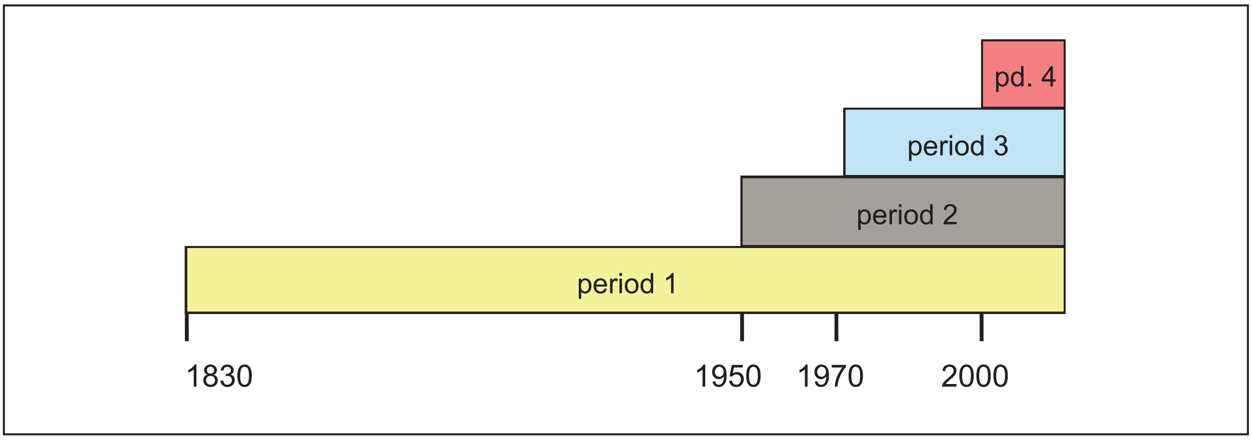

Figure 1. Four periods in phylogeny research of rhabditids: 1) discovery and description of species; 2) systematic grouping based on morphological similarity; 3) systematisation according to the cladistic method; 4) molecular phylogenetics.

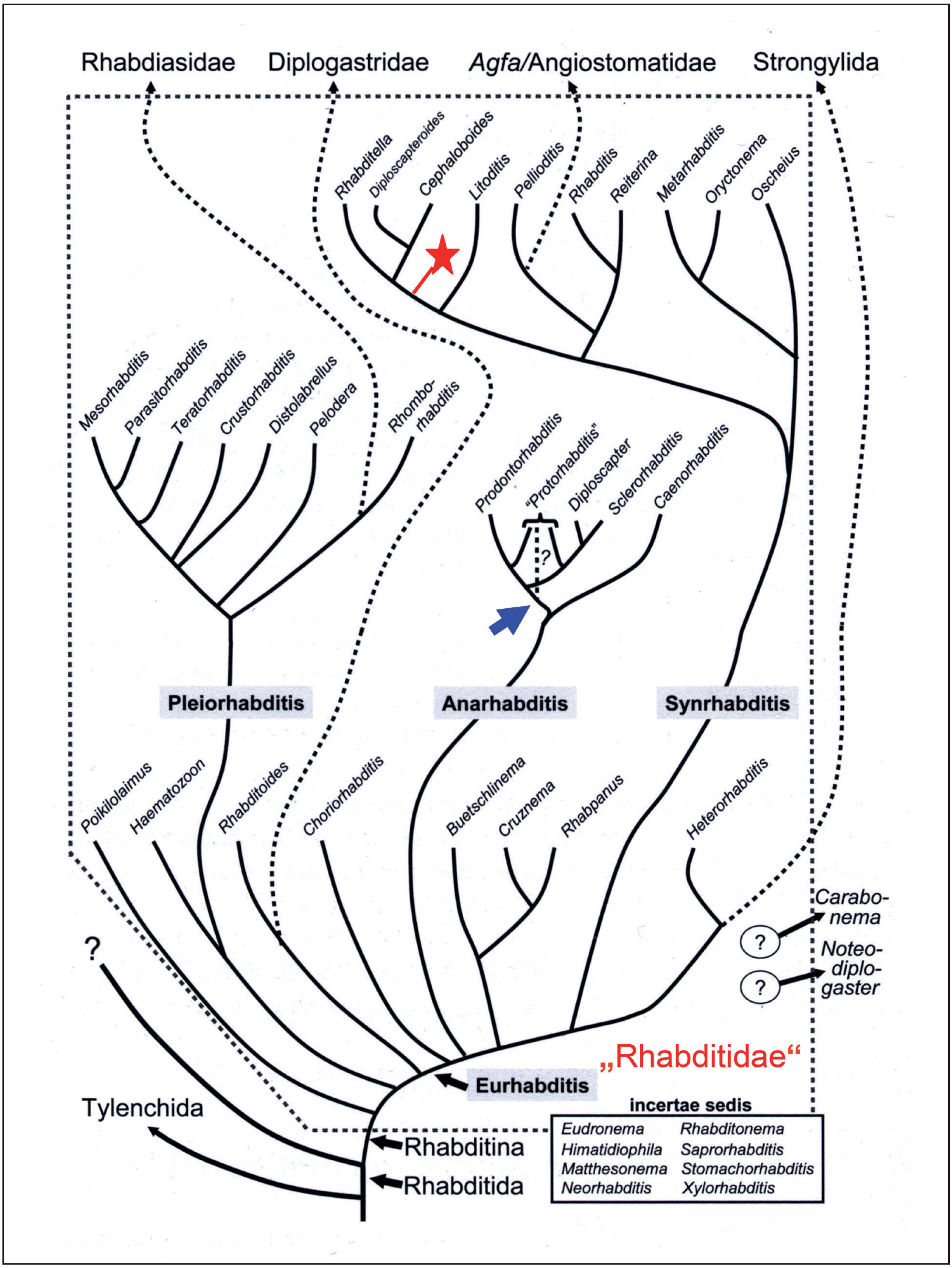

Figure 2. Phylogenetic diagram of the Rhabditina including the paraphyletic ‘Rhabditidae’ framed by a dotted line to show the relationships between the genus clades (based on Sudhaus 2014). The branch with the star indicate the position of the new genus taxa *Auanema* and *Tokorhabditis* (see fig. 3). The arrow marks the clade Protoscapter.

a member in the wild. Most rhabditids can be cultured in the laboratory, which offers favorable conditions under which to study their ecological requirements and life history in order to characterise the econiche of a species and – as far as males exist – conduct crossing experiments with closely related strains. In combination with sequence data these results will give a well-reasoned hypothesis on the species status of the strain in question. Several recent investigations take a multidimensional approach combining morphological, morphometric, molecular, biological, ecological and phylogenetic data. Though elaborate, this procedure is particularly necessary in view of the existence of morphologically nearly identical (cryptic) species, as demonstrated in *Caenorhabditis, Heterorhabditis, Oscheius, Parasitorhabditis, Pellioditis* and others, each following its own ecological program.

It is highly attractive to describe a species as new to science. But the reward is not the published description with the authors' name as part of the species name, it is when others can actually recognise the species from the description. A point of criticism regarding published proposals for new rhabditid species is that rarely are comparisons made with descriptions of species inquirendae or synonyms, though subjective synonymisations are still disposable and must be considered. In the last decade, for instance, only one of the descriptions of new *Pellioditis* species conducted a comparison with *P. incilaria, P. mairei, Rhabditis ikedai* and *R. ninomiyai* in order to establish that the new species were not identical with any of them (Huang et al. 2015). And too seldom are attempts made to recognise named but poorly described species in one's own material and – provided that the morphological characteristics and ecological data are compatible with the original description – to redescribe them, thus breathing new life into an anaemic name rather than creating a new one. This is the way older authors often proceeded. Félix and her team were exemplary in this regard in their work on *Mesorhabditis* (Launay et al. 2020).

On genus taxa

A typological (static) concept of the genus taxon is prevalent in nematology even today. Once a diagnosis of the genus has been formulated, it is rarely amended in the view of an 'aberrant' species. Instead, if 'important' characters in the species at hand do not fit with this diagnosis, a new genus name is suggested. However, the genus rank is not feature-related but justified phylogenetically. It is not the characteristics which are decisive, but the question of whether the taxon represents a separate clade. I refer to the criteria regarding genus taxa formulated in my last catalogue (Sudhaus 2011: 122). Whenever possible the genus taxon should represent a monophyletic group that exclusively includes all the species that descended from the same stemspecies. Accordingly, the main criterion for a genus taxon results from the phylogenetic diagram. Only proof of a new side

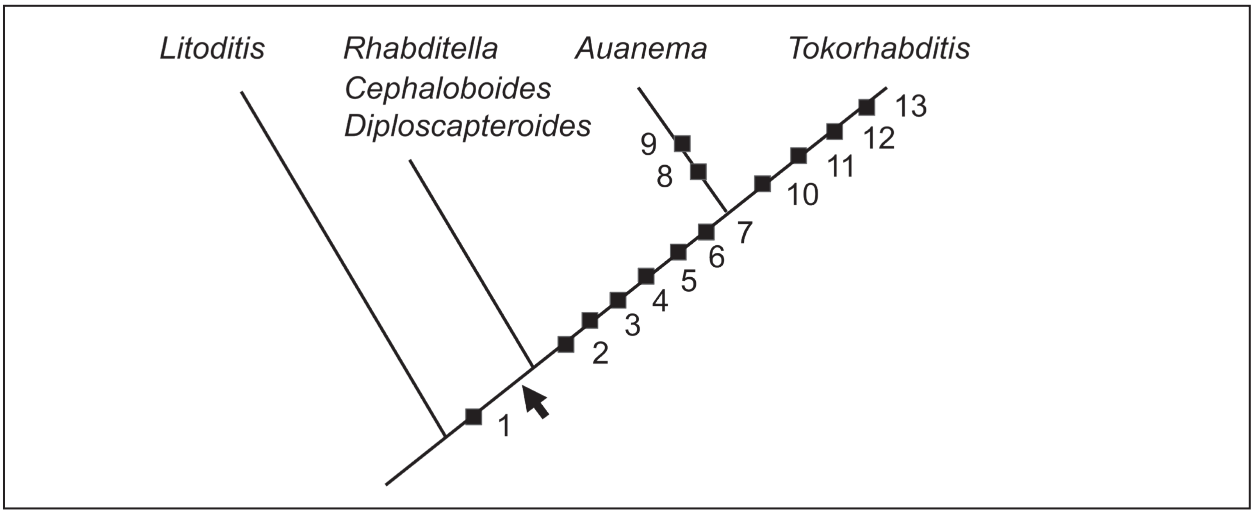

Figure 3. Cladogram to show the sister group relationship between *Auanema* and *Tokorhabditis* and their position in the phylogenetic tree of 'Rhabditidae'. Branching pattern based onAbolafia & Peña-Santiago (2019a) and Kanzaki et al. (2017, 2021b). Apomorphic characters are numbered: 1 = tube waving larvae; 2 = trioecious; 3 = one genital papilla lost (presumably the original GP7), only 8 GPs present on both sides, 6 GPs anterior of the posterior dorsal papilla; 4 = GP6 separate; 5 = males much smaller than females/hermaphrodites (dwarf males); 6 = mouth of adults triangular; 7 = bursa velum distally notched; 8 = GP3 shifted post/adcloacally; 9 = metarhabdia with one denticle each; 10 = viviparous (with nutrition of embryos); 11 = phasmid a simple pore in anterior position, behind GP6; 12 = GP1 shifted anterior of spicules; 13 = two metarhabdion denticles each. – Some characters oft the stemspecies of *Auanema rhodense* and *Rhabditella axei* (arrow): stoma cylindrical, bursa leptoderan, nine GPs on both sides, arranged as 1+2/3+3+ph, phasmid (ph) posterior of GPs, papilliform, GP5 and GP8 open on the dorsal surface of the fan, gonochoristic, oviparous, third stage juvenile exhibits tube waving behaviour.

branch can be accepted as the basis for a new genus taxon, not distinctive features that evolved within an otherwise uniform species group. This is how the previous genus clades came into being (Fig. 2) and why in my view most of the newly proposed genus names are not justified.

A genus clade cannot be defined by a diagnosis, but the characters of its stemspecies can be reconstructed. The aim of an analysis must thus be the reconstruction of this stemspecies pattern. Instead of attempting to formulate a diagnosis that encompasses all the species of that clade and therefore often includes contradictory terms, researchers should concentrate on producing a description of the stemspecies pattern in order to make obvious the possible derivations of a particular species of this clade. The stemspecies pattern consists of all the plesiomorphic characters of the ancestors and all the apomorphies that evolved in the ancestral lineage between the separation of the sister lineage and the stemspecies of the crown group encompassing exclusively all the descendants of this species. At the same time, these apomorphies constitute the monophyly of the group.

This approach is exemplified in Fig. 3 for the only two accepted new genus taxa *Auanema* Kanzaki et al., 2017 and *Tokorhabditis* Kanzaki et al., 2021. They are sister taxa, as constituted by a trioecious mating system consisting of males, females and self-fertilising hermaphrodites, and some further synapomorphies.

I reject Hodda’s (2022) unsubstantiated reinstatement of the genera *Colporhabditis* Andrássy, 1976, *Indorhabditis* Chaturvedi & Khera, 1979 and *Termirhabditis* Massey, 1971. His *Tetrarhabditis* is a lapsus for *Teratorhabditis* Osche, 1952.

A special remark is necessary on the description of fossil rhabditids by Poinar (2011). On the basis of feature-poor dauer juveniles in amber, Poinar named eight genera of Rhabditidae: † *Crustafila,* † *Palaeoarachnus,* † *Palaeorhabditis,* † *Prescafilotermes,* † *Proheterorhabditis,* † *Psocidonema,* † *Psychodorhabditis* and † *Tipulacomis.* Due to the lack of differentiating characteristics on the photos, however, I doubt that these taxa will ever be recognisable for comparison with recent ones. An exception is †*Psychodorhabditis*, the dauers of which wrap themselves around the body of mothflies (Psychodidae), documented by his fig. 169, as otherwise only known from *Choriorhabditis dubia* and *C. berolina* (Sudhaus & Kühne 1990). For this reason, I propose the following synonymisation and new combinations:

Choriorhabditis Osche, 1952
syn. nov. † *Psychodorhabditis* Poinar, 2011
† *C. attenuata* (Poinar, 2011) comb. n.
† *C. baltica* (Poinar, 2011) comb. n.
† *C. dominicana* (Poinar, 2011) comb. n.

To facilitate discussions on character evolution within *Caenorhabditis*, its sister taxon, encompassing *Diploscapter, Sclerorhabditis, Prodontorhabditis* and the paraphyletic *‘Protorhabditis’* (see Fig. 2), was given the name Protoscapter, a name without a categorical rank (Slos et al. 2017). As a result, the name Anarhabditis for the clade *Caenorhabditis*/Protoscapter no longer appears to be useful.

Information provided by this catalogue

In the information given and the order in which it appears I follow my catalogue on genus taxa and species of ‘Rhabditidae’, cited here as ‘catalogue 2011’. Genus taxa are presented in alphabetical order with the author and year and the type species. Diagnostic characters are only mentioned for genus taxa accepted as new. For the other genus taxa I refer to catalogue 2011. New species are listed alphabetically with author(s) and year of publication, type locality, type habitat or associate and, in rare cases, specific characteristics. The same applies to names accepted as synonyms. Publication year is the year in which the article was printed regardless of whether it was available online the year before. If sequence data are available, the strain designation of the type isolate is usually added. New combinations are marked ‘comb. n.’, while the original combination can be taken from the alphabetical list of epithets at the end.

Classification of new genus taxa and species described since 2011

> ‘While we may never complete the cataloguing
> and systematizing of life on our planet, it is deeply
> illuminating to attempt to do so’ (Blaxter 2016).

Auanema Kanzaki, Kiontke, Tanaka, Hirooka, Schwarz, Müller-Reichert, Chaudhuri & Pires-daSilva, 2017

Diagnostic characters: Trioecious, reproductive mode comprising males, females and self-fertilising hermaphrodites, n = 7 chromosomes, males are rare, stoma opening triangular, each sector of glottoid apparatus with **one denticle**, with pharyngeal sleeve, median bulb well developed, female/hermaphrodite tail elongated conical, males much smaller than females/

hermaphrodites, bursa open, peloderan or leptoderan, eight pairs of genital papillae, **precloacal only two GPs or even one**, GP5 and dorsally bent **GP7 open on the dorsal** surface of the velum, GP6 in isolated position, phasmids papilliform and terminal, spicules separate, dagger-shaped, cephalated, dauer juveniles exhibit tube waving behaviour, dauers develop into hermaphrodites. (Apomorphic characters bold.)

Habitats: Compost, decaying plants and fruits, rotten meat and insects.

Type species: *Auanema rhodense* Kanzaki et al., 2017

Six valid species:

- *A. freiburgense* Kanzaki, Kiontke, Tanaka, Hirooka, Schwarz, Müller-Reichert, Chaudhuri & Pires-daSilva, 2017 (type isolate SB372) – Freiburg, Germany; isolated from a dung pile in the animal enclosure Mundenhof.
- *A. melissense* Tandonnet, Haq, Turner, Grana, Paganopoulou, Adams, Dhawan, Kanzaki, Nuez, Félix & Pires-daSilva, 2022 (type isolate JU1783) – Saint Benoît (Melissa domain) of island of La Réunion; isolated from a rotting starfruit (*Averrhoa carambola*).
- *A. rhodense* Kanzaki, Kiontke, Tanaka, Hirooka, Schwarz, Müller-Reichert, Chaudhuri & Pires-daSilva, 2017 (type isolate SB347) – Kingston, Rhode Island, USA; from soil baited by blood-engorged deer ticks (*Ixodes scapularis*).

Three species primarily described as *Rhabditis* were transferred to *Auanema* by Kanzaki et al. (2017):

- *A. reciprocum* (Sudhaus, 1974)
- *A. seurati* (Maupas, 1916)
- *A. viguieri* (Maupas, 1900)

Buetschlinema Sudhaus, 2011

syn. nov. ***Chylorhabditis*** Kanzaki, Hamaguchi & Takeuchi-Kaneko, 2021: *C. epuraeae* Kanzaki, Hamaguchi & Takeuchi-Kaneko, 2021

It is obvious that *C. epuraeae* belongs to the same clade as *Buetschlinema* (Kanzaki et al. 2021a), The main difference is the pattern of genital papillae that point to the dorsal side of the bursa velum. This can change by shift of the anlagen of these papillae (Sudhaus & Fitch 2001). Even if *C. epuraeae* could be shown (which is not the case) to be the first branch and thus sister taxon to a group with all the other *Buetschlinema* species, this would not be a good argument to erect a new genus taxon in this place.

Type species: *Rhabditis buetschlii* de Man, 1876

Five valid species were listed in the catalogue 2011. Here a new one is added.

- *B. epuraeae* (Kanzaki, Hamaguchi & Takeuchi-Kaneko, 2021) comb. n. – Uji River, Yawata, Kyoto, Japan; from the beetle *Epuraea* (*Haptoncus*) *ocularis* from sap on the trunk of a Chinese elm (*Ulmus parvifolia*). – Special characters: arrangement of GPs 4 adcloacal and 1+1+3 postcloacal, GP5 and GP8 to the dorsal surface of bursal velum, spicules long and separated into two sections of equal length by a constriction.

Caenorhabditis Osche, 1952

Type species: *Rhabditis elegans* Maupas, 1899

Twenty valid species were listed in catalogue 2011. Here 40 new species are added.

- *C. afra* Félix, Braendle & Cutter, 2014 (= *C.* sp. 7; type isolate JU1199) – Begoro, South Ghana; from rotting citrus fruit.
- *C. agridulce* Sloat & Kiontke in Sloat, Noble, Paaby, Bernstein, Chang, Kaur, Yuen, Tintori, Jackson, Martel, Salome Correa, Stevens, Kiontke, Blaxter & Rockman, 2022 (= *C.* sp. 24; type isolate QG555) – Santa Barbara, California, USA; from a piece of rotting orange collected from a street tree in a planter.
- *C. astrocarya* Braendle & Cutter in Ferrari, Salle, Callemeyn-Torre, Jovelin, Cutter & Braendle, 2017 (= *C.* sp. 42; type isolate NIC1040) – Nouragues Natural Reserve, French Guiana; from inflorescence of *Astrocaryum* palm (likely *Astrocaryum paramaca*).
- *C. becei* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 29; type isolate QG704) – Barro Colorado Island, Panama; from a rotten flower of *Gustavia superba*.
- *C. castelli* Félix, Braendle & Cutter, 2014 (= *C.* sp. 12; type isolate JU1426) – Nouragues Forest, French Guiana; from rotting *Micropholis cayennensis* fruit.
- *C. chinkari* Mondal & Manna, 2015 – Alipore Zoological Garden Kolkata, India; from faeces of the Chinkara (*Gazella bennettii*).
- *C. dolens* Braendle & Cutter in Ferrari, Salle, Callemeyn-Torre, Jovelin, Cutter & Braendle, 2017 (= *C.* sp. 37; type isolate NIC394) – Nouragues Natural Reserve, French Guiana; from decaying fruit.
- *C. doughertyi* Félix, Braendle & Cutter, 2014 (= C. sp. 10; type isolate JU1333) – next to Periyar, Kerala, India; from rotting cacao fruit.

- *C. guadeloupensis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 20; type isolate NIC113) – Soufrière Forest trail, Guadeloupe; from rotten *Heliconia* flowers.
- *C. hystrisi* Mondal & Manna, 2013 (2013a) – Alipore Zoological Garden, Kolkata, India; from faecal samples of the Porcupine (*Hystrix indica*).
- *C. imperialis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 14; type isolate EG5716) – Moorea, French Polynesia; from a rotten horse chestnut (Tahitian chestnut?).
- *C. inopinata* Kanzaki, Tsai, Tanaka, Hunt, Liu, Tsuyama, Maeda, Namai, Kumagai, Tracey, Holroyd, Doyle, Woodruff, Murase, Kitazume, Chai, Akagi, Panda, Ke, Schroeder, Wang, Berriman, Sternberg, Sugimoto & Kikuchi, 2018 (= *C.* sp. 34; type isolate NK74SC) – Ishigaki Island, Okinawa, Japan; in syconia of *Ficus septica*, pollinated by the fig wasp *Ceratosolen bisulcatus*.
- *C. kamaaina* Félix, Braendle & Cutter, 2014 (= *C.* sp. 15; type isolate QG122) – near Hanalei Bay, Kauai, Hawaii; from rotten fruit.
- *C. krikudae* Sloat & Kiontke in Sloat, Noble, Paaby, Bernstein, Chang, Kaur, Yuen, Tintori, Jackson, Martel, Salome Correa, Stevens, Kiontke, Blaxter & Rockman, 2022 (= *C.* sp. 57; type isolate QG3050) – Barro Colorado Island, Panama; from a rotten fig.
- *C. latens* Félix, Braendle & Cutter, 2014 (= C. sp. 23; type isolate VX88) – Jiufeng Village, Wuhan City, Hubei Province, China; from soil near the lotus pond.
- *C. macrosperma* Félix, Braendle & Cutter, 2014 (= C. sp. 18; type isolate JU1857) – Nouragues Forest, French Guiana; rotting *Hyeronima taxiflora* fruits.
- *C. microvilli* (Zhou, Yang, Wang, Bao, Wang, Hou, Lin, Yedid & Zhang, 2017) comb. n. (isolate CM19) – Chongming Island, Shanghai, China; from soil, collected by baiting with *Galleria mellonella* larvae. – Abolafia & Peña-Santiago (2019a) compared the species with *C. sinica*. The sequence is from a species of *Oscheius* which is very close to *O. myriophilus*, that was probably in the same sample.
- *C. monodelphis* Slos & Sudhaus in Slos, Sudhaus, Stevens, Bert & Blaxter, 2017 (= *C.* sp. 1, type isolate SB341) – Berlin Grunewald, Germany; galleries of the beetle *Cis castaneus* inside the fungus *Ganoderma applanatum* on the stump of a common beech.
- *C. nigoni* Félix, Braendle & Cutter, 2014 (= *C.* sp. 9; type isolate JU1325) – Zoo/Botanical Garden of Trivandrum, Kerala, India; from rotting flowers and leaves.
- *C. niphades* Sun, Kanzaki, Dayi, Maeda, Yoshida, Tanaka & Kikuchi, 2022 (= *C.* sp. 36; type isolate NKZ391) – Tama Forest Science Garden, Forestry and Forest Products Research Institute, Hachioji, Tokyo, Japan; isolated from adult wood-boring weevils (*Niphades variegatus,* Curculionidae) from the dead log of Masson’s pine (*Pinus massoniana*).
- *C. nouraguensis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 17; type isolate JU1825) – Nouragues Forest, French Guiana; from rotten fruit (said of *Barokia* sp.).
- *C. oiwi* Crombie, Zdradjevic, Cook, Tanny, Brady, Wang, Evans, Hahnel, Lee, Rodriguez, Zhang, van der Zwagg, Kiontke & Andersen, 2019 (type isolate ECA821) – Island of Oahu, Hawaii; from a cluster of freshly fallen flowers.
- *C. panamensis* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 28; type isolate QG702) – Snyder-Molino trail on Barro Colorado Island, Panama; from a rotting palm fruit.
- *C. parvicauda* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 21; type isolate NIC134) – island Sainte Marie, Madagascar; from a rotting fruit.
- *C. pini* Shah & Vaid, 2017 (2017a) – Dera Ki Gali forests, district Poonch, Jammu and Kashmir, India; in soil near the roots of *Pinus wallichiana.*
- *C. portoensis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 6; type isolate EG4788) – Amares, Portugal; from a rotting apple.
- *C. quiockensis* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 38; type isolate JU2745) – Quiock river trail, Guadeloupe; from a rotting fruit.
- *C. ratufae* Mondal & Manna, 2013 (2013b)– Alipore Zoological Garden Kolkata, India; stool samples of the giant squirrel (*Ratufa indica*).
- *C. scuri* Mondal & Manna, 2013 (2013a)– Alipore Zoological Garden Kolkata, India; from faeces of the Indian giant squirrel (*Ratufa indica*, Sciuridae).
- *C. sinica* Huang, Ren, Qiu & Zhao, 2014 (= *C.* sp. 5, type isolate ZZY0401) – Luofo Mountain, Huizhou City, Guangdong Province, China; from a rotting fruit.

- *C. sulstoni* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 32; type isolate SB454) – from an insect market in Berlin; from faeces of the East African millipede *Archispirostreptus gigas* after transfer into a clean terrarium.
- *C. tribulationis* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 40; type isolate JU2774) – Danbulla Road, south of Cape Tribulation, Queensland, Australia; from humus below a fig tree (*Ficus destruens*).
- *C. tropicalis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 11; type isolate JU1373) – Saint-Benoît, La Réunion; from rotting torch ginger (*Etlingera elatior*) flowers.
- *C. uteleia* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 31; type isolate JU2469) – Madre de Dios, Peru; from a rotting kumquat-like fruit.
- *C. virilis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 13; type isolate JU1528) – Orsay, France; from a rotting apple in an orchard.
- *C. vivipara* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 43; type isolate NIC1070) – Chichén Itzá, Yucatán, Mexico; from rotting red berries.
- *C. waitukubuli* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 39; type isolate NIC564) – Morne Trois Pitons, Dominica; from a rotting *Clusia* fruit.
- *C. wallacei* Félix, Braendle & Cutter, 2014 (= *C.* sp. 16; type isolate JU1873) – Sanda Center, Bali, Indonesia; rotting cacao fruit.
- *C. yunquensis* Félix, Braendle & Cutter, 2014 (= *C.* sp. 19; type isolate EG6142) – El Yunque, Puerto Rico; from a rotten fruit of Ausubo tree (*Manilkara bidentata*).
- *C. zanzibari* Stevens & Félix in Stevens, Félix, Beltran, Braendle, Caurcel, Fausett, Fitch, Frézal, Gosse, Kaur, Kiontke, Newton, Noble, Richaud, Rockman, Sudhaus & Blaxter, 2019 (= *C.* sp. 26; type isolate JU2161) – Dole district, Zanzibar, Tanzania; from a rotting mandarine fruit on a farm.

Comment: The validity of four very similar species of *Caenorhabditis* (*C. chinkari, C. hystrisi, C. ratufae, C. scuri)* in the same location (Alipore Zoological Garden Kolkata) and the same habitat (faeces of mammals) as claimed by Mondal and Manna should be reexamined.

The phylogenetic trees in Stevens et al. (2019, 2020), Dayi et al. (2021), Sloat et al. (2022) and Sun et al. (2022) show several clades.

Elegans clade (15 species): *C. brenneri, C. briggsae, C. clavopapillata, C. doughertyi, C. elegans, C. inopinata, C. kamaaina, C. latens, C. nigoni, C. remanei, C. sinica, C. tribulationis, C. tropicalis, C. wallacei, C. zanzibari.*

Japonica clade (11 species): *C. afra, C. becei, C. imperialis, C. japonica, C. macrosperma, C. niphades, C. nouraguensis, C. panamensis, C. sulstoni, C. waitukubuli, C. yunquensis.*

Guadeloupensis clade (2 species): *C. guadeloupensis, C. uteleia.*

Drosophilae superclade (10 species): *C. agridulce, C. angaria, C. astrocarya, C. castelli, C. dolens, C. drosophilae, C. portoensis, C. quiockensis, C. virilis, C. vivipara.*

Basal branches (7 species): *C. auriculariae, C. bovis, C. krikudae, C. monodelphis, C. parvicauda, C. plicata, C. sonorae.*

Not yet placed (15 species): *C. anthobia, C. avicola, C. chinkari, C. craspedocercus, C. formosana, C. fruticicolae, C. genitalis, C. hystrisi, C. microvilli, C. oncomelaniae, C. oiwi, C. perrieri, C. pini, C. ratufae, C. scuri.*

Cephaloboides Rahm, 1928

Type species: *Rhabditis (Cephaloboides) musicola* Rahm, 1928

Six valid species were listed in catalogue 2011. One of them is treated here as a new synonym and one new and one reinstated species are added, resulting in seven valid species in this genus taxon.

- *C. anisospiculus* Tahseen, Hussain, Ahlawat, Mustaqim & Khan, 2017 – Lado Saray, New Delhi, India; from green manure.
- *C. parapapillosus* (Schuurmans Stekhoven, 1951) was reinstated and redescribed by Tahseen et al. (2017).
- *Flagicaudoides pawani* Khan, Singh & Baird, 1999 was suggested as a new synoym of *Cephaloboides curvicaudatus* (Schneider, 1866) by Tahseen et al. (2017).

Crustorhabditis Sudhaus, 1974

Type species: *Rhabditis* (*Crustorhabditis*) *riemanni* Sudhaus, 1974

Five valid species were listed in catalogue 2011. Here a new one is added.

- *C. dunicola* Ruiz-Cuenca & Abolafia, 2022 – Riumar beach, Ebro Delta Natural Park, Spain; in sand coastal dunes from the rhizosphere of xerophile plants (*Medicago littoralis*).

Cruznema Artigas, 1927

Type species: *Cruznema cruznema* Artigas, 1927

Eight valid species were listed in catalogue 2011. Here two new species are added.

- *C. helalii* Tahseen, Sultana, Khan & Hussain, 2012 – Keoladeo National Park, near Bharatpur, Rajasthan, India; soil from the bank of a pond.
- *C. minimum* Sultana & Pervez, 2019 – Firoz Shah's tomb, Hauz Khas Lake, New Delhi, India; from leaf debris.

Diploscapter Cobb, 1913

Type species: *Rhabditis coronata* Cobb, 1893

15 valid species were listed in catalogue 2011. Here one new species is added.

- *D. formicidae* Zhao, Davies, Brenton-Rule, Grangier, Gruber, Giblin-Davis & Lester, 2013 – St Arnaud, South Island, New Zealand; from the heads of worker ants of *Prolasius advenus.*

Diploscapteroides Rahm, 1928

syn. nov. ***Quercorhabditis*** Shah, Hussain & Vaid, 2013: *Q. rajouriensis* Shah, Hussain & Vaid, 2013

The species *Q. rajouriensis* shares apomorphic characteristics with *Diploscapteroides* like heavily sclerotised and arched cheilorhabdions and anterior bursal papillae shifted postcloacally, and like its sister group *Cephaloboides* has spicules with a dorsal thorn and a ventral prong proximally, and its adults are ensheathed as they retain the cuticle of the last juvenile stage.

Type species: *Diploscapteroides brevicauda* Rahm, 1928

Six valid species were listed in catalogue 2011. Here two new species are added.

- *D. persicus* Ghaemi, Pourjam, Álvarez-Ortega, Pedram & Atighi, 2015 – Golestan province, northern Iran; from rotten wood in the forest.
- *D. rajouriensis* (Shah, Hussain & Vaid, 2013) comb. n. – Rajouri, Jammu and Kashmir, India; from inside a hollow cavity in the trunk of an oak tree (*Quercus leucotrichophora*).

Distolabrellus Anderson, 1983

Type species: *Distolabrellus veechi* Anderson, 1983

Three valid species were listed in catalogue 2011. Here one new species is added.

- *D. vulvatus* Khatoon & Ahmad, 2021 – Aligarh, Uttar Pradesh, India; from decaying leaves in a ditch.

Comment: The four species *D. magnivulvatus* Abolafia & Peña–Santiago, 2011, *D. scarabaeus* (Sudhaus, 1978), *D. veechi* Anderson, 1983 and *D. vulvatus* Khatoon & Ahmad, 2021 look almost the same. The main named differences are features of the vulva and vagina, which are not convincing enough to establish separate species status. A comparative study is necessary. – Distribution map in Tahseen et al. (2009: 824).

Haematozoon Leisering, 1865

syn. nov. ***Loffienema*** Shah, Allie, Vaid & Handoo, 2018: *L. dhanoriense* Shah, Allie, Vaid & Handoo, 2018

In *L. dhanoriense* the male tail with a narrow bursa velum, arrangement of genital papillae and particularly the very characteristic shape of the spicules and gubernaculum are (nearly) identical with these characters in *Haematozoon subulatum.*

Type species: *H. subulatum* Leisering, 1865

Two valid species were listed in catalogue 2011. Here one new species is added.

- *H. dhanoriense* (Shah, Allie, Vaid & Handoo, 2018) comb. n. – University campus, Dhanore Rajouri, Jammu and Kashmir, India; from soil mixed with mature compost. – Perhaps identical to *H. subulatum.*

Heterorhabditis Poinar, 1976

Type species: *H. bacteriophora* Poinar, 1976

21 valid species were listed in catalogue 2011. Here, four new species are added and three species names mentioned in catalogue 2011 are shown to be new synonyms, resulting in 22 species in this genus taxon now.

- *H. beicherriana* Li, Liu, Nermuť, Půža & Mráček, 2012 – Beijing area, China; soil from a cherry orchard, isolated with the *Galleria mellonella* baiting technique.

- *H. noenieputensis* Malan, Knoetze & Tiedt, 2014 (type isolate SF669) – on the farm Springbokvlei, near Noenieput, South Africa; soil from beneath a fig tree, using the trapping method with larvae of *Galleria mellonella*.
- *H. ruandica* Machado, Bhat, Abolafia, Muller, Bruno, Fallet, Arce, Turlings, Bernal, Kajuga, Waweru & Toepfer, 2021 (type isolate Rw14_N-C4a) – near Kanyirandori village, Nyamagabe district, Southern province, Rwanda; cropland, isolated from soil samples by the *Galleria* baiting technique.
- *H. zacatecana* Machado, Bhat, Abolafia, Muller, Bruno, Fallet, Arce, Turlings, Bernal, Kajuga, Waweru & Toepfer, 2021 (type isolate MEX-39) – Villanueva, Zacatecas, Mexico; soil from maize field, isolated by the *Galleria* baiting technique.

I accept the synonymisations given by Dhakal et al. (2021) for the following three species dealt with in catalogue 2011.

- *H. baujardi* Phan, Subbotin, Nguyen & Moens, 2003
  syn. *H. somsookae* Maneesakorn, An, Grewal & Chandrapatya, 2015 (= *H.* sp. MP68) – Amphoe Srisawat, Kanchanaburi province, Western Thailand; soil.
- *H. indica* Poinar, Karunakar & David, 1992
  syn. *H. gerrardi* Plichta, Joyce, Clarke, Waterfield & Stock, 2009
  – *H. pakistanensis* Shahina, Tabassum, Salma, Mehreen & Knoetze, 2016 – Malir, Karachi, Pakistan; soil around the roots of Bermuda grass (*Cynodon dactylon*), isolated by baiting with *Galleria mellonella* larvae.
  – *H. brevicaudis* Liu, 1994
- *H. taysearae* Shamseldean, Abou El-Sooud, Abd-Elgawad & Saleh, 1996
  syn. *H. sonorensis* Stock, Rivera-Orduño & Flores-Lara, 2009

So far sequence data were available, the species group into three clades (Dhakal et al. 2021, Machado et al. 2021).

Bacteriophora clade (5 species): *H. bacteriophora, H. beicherriana, H. georgiana, H. ruandica, H. zacatecana.*

Indica clade (7 species): *H. amazonensis, H. baujardi, H. floridensis, H. indica, H. mexicana, H. noenieputensis, H. taysearae.*

Megidis clade (6 species): *H. atacamensis, H. downesi, H. marelata, H. megidis, H. safricana, H. zealandica.*

Not assigned to a group (4 species): *H. egyptii, H. hambletoni, H. hoptha, H. poinari.*

Mesorhabditis Osche, 1952

Type species: *Rhabditis spiculigera* Steiner, 1936

34 valid species were listed in catalogue 2011. Here five new species are added.

Monhystera clade (now 18 species)

Besides the vestigial bursa, the following characters are apomorphic: **low frequency of males, small sperm cells, pseudogamy, females produced by gynogenesis and males by amphimixis** (Launay et al. 2020). – Distribution map for several species in Launay et al. (2020).

- *M. bifurcata* Launay, Félix, Dieng & Delattre, 2020 (type isolate JU2902) – Botanical Garden University of Florence, Italy; from rotting pseudostem of Japanese banana (*Musa basjoo*).
- *M. denticulata* Mahboob & Jahan, 2021 – Domariaganj, district Siddharthnagar, Eastern Uttar Pradesh, India; from a larva of a longhorn beetle (Cerambycidae) inside the dead log of North Indian rosewood (*Dalbergia sissoo*).
- *M. okuensis* Launay, Félix, Dieng & Delattre, 2020 (type isolate JU3143) – Oku Mountain, Cameroon; from rotting wood.

Spiculigera clade (now 21 species)

This might be a paraphyletic group (Launay et al. 2020).

- *M. acidophila* Borgonie, Dierick, Houthoofd, Willems, Jacobs & Bert, 2010 – sulfur cave Cueva de Villa Luz, near Tapijulapa, Tabasco, Mexico; in extreme acidic conditions of snottites (mucuous mats of extremophiic bacteria hanging from the walls and ceiling).
- *M. acuticauda* Ahmad, Shah & Mahamood, 2010 – Jawahar Park, Aligarh, Uttar Pradesh, India; from farmyard manure.

Metarhabditis Tahseen, Hussain, Tomar, Shah & Jairajpuri, 2004

Type species: *Metarhabditis andrassyana* Tahseen, Hussain, Tomar, Shah & Jairajpuri, 2004

Seven valid species were listed in catalogue 2011. Here two new species are added.

- *M. giennensis* Abolafia & Peña-Santiago, 2019 (2019b) – Puente de la Sierra, Jaén province, Southern Spain; from decaying wood from dead *Populus alba* in a riverbank forest (Quiebrajano river).
- *M. suklaae* (Mondal & Manna, 2014) comb. n. (= *Rhabditis suklai* Mondal & Manna, 2014; emended because named after a woman, Sukla) – Alipore Zoological Garden Kolkata, India; from faeces of Sambar deer (*Cervus unicolor*).

I accept the following synonymisations by Asif et al. (2013) and Bhat et al. (2020):

- *M. amsactae* (Ali, Pervez, Andrabi, Sharma & Verma, 2011) – already dealt with in catalogue 2011 (description published in January 2011). *Oscheius amsactae* in Ali et al. (2007, 2010) and Ahmad et al. (2009) is a *nomen nudum*.

  syn. *Oscheius ciceri* Shaheen, Ali and Asif, 2011 (description published in June 2011) – village Akbarpur, Kanpur district, Uttar Pradesh, India; soil from the rhizosphere of chickpea (*Cicer arietinum),* isolated by the insect baiting technique and maintained on larvae of the moth *Corcyra cephalonica*.

  – *Oscheius hussainii* Shaheen, Ali & Asif, 2011 (description published in June 2011) – Indian institute of Pulses Research, Kanpur, Uttar Pradesh, India; soil from rhizosphere of pigeonpea (*Cajanus cajan*), collected by the insect baiting technique and maintained on *Corcyra cephalonica* larvae.

  – *Oscheius gingeri* Pervez, Eapen, Devasahayam & Jacob, 2013 – Experimental farm, Peruvannamuzhi, Calicut district, Kerala, India; soil from the rhizosphere of ginger (*Zingiber officinale*), baited with *Galleria mellonella*.

  – *Metarhabditis longicaudata* Tabassum, Salma & Nasir, 2019 – Malir cantonment, Karachi, Sindh, Pakistan; soil below Mango tree (*Mangifera indica*), baited using last instars of *Galleria mellonella*.

Neorhabditis Schuurmans Stekhoven, 1954

Type species: *Pararhabditis flagellicaudata* Schuurmans Stekhoven, 1951

One valid species was mentioned in catalogue 2011. Here one new species is added.

- *Neorhabditis andrassyii* Tabassum, Nasir & Shahina, 2021 – Saeedabad, Karachi, Pakistan; soil around the roots of chikoo (*Manilkara zapota*) tree, baited with wax moth larvae (*Galleria*).

Oscheius Andrássy, 1976

Type species: *Rhabditis insectivora* Körner, 1954

27 valid species were listed in catalogue 2011. Here twelve new species are added.

Dolichura clade (now 16 species)

- *O. karachiensis* Nasir & Tabassum, 2018 – Saeedabad, Karachi, Pakistan; soil around the roots of chicko tree (*Manilkara zapota*), baited with *Galleria mellonella* larvae.
- *O. onirici* Torrini, Mazza, Carletti, Benvenuti, Roversi, Fanelli, De Luca, Troccoli, & Tarasco, 2015 – cave ‘Grotta del Lago’ in the Monti Pisani area, Pisa province, Italy; soil, using the *Galleria mellonella* bait method.
- *O. saproxylicus* Abolafia & Peña-Santiago, 2019 (2019a) – Puente de la Sierra, Jaén province, Southern Spain; from decaying wood (white poplar tree) from an orchard.

Insectivorus clade (now 23 species)

Some of the here listed species are supposed to be synonymous (see Rana et al. 2021).

- *O. basothovii* Lephoto & Gray, 2019 – Heidelberg at the Suikerbosrand Nature Reserve, South Africa; grassland, isolated from the soil by the bait method using *Galleria mellonella* larvae
- *O. citri* Tabassum, Shahina, Nasira & Erum, 2016 – Gadap, Sindh, Pakistan; soil around the roots of citrus (*Citrus* sp.), baited using *Galleria mellonella* larvae. – I follow the synonymisations by Rana et al. (2021). (This name has page priority.)

  syn. *O. cobbi* Tabassum, Shahina, Nasira & Erum, 2016 – University of Karachi, Karachi, Pakistan; from soil around the roots of bermuda grass (*Cynodon dactylon*), baited using *Galleria mellonella* larvae.

  – *O. cynodonti* Tabassum, Shahina, Nasira & Erum, 2016 – Islamabad, Pakistan; soil around the roots of bermuda grass (*Cynodon dactylon*), baited using *Galleria mellonella* larvae.

  – *O. esculentus* Tabassum, Shahina, Nasira & Erum, 2016 – Azad Jammu and Kashmir, Pakistan; soil around the roots of okra (*Abelmoschus esculentus*), baited using *Galleria mellonella* larvae.

  – *O. punctatus* Tabassum, Shahina, Nasira & Erum, 2016 – University of Karachi, Karachi, Pakistan; soil around the roots of bermuda grass (*Cynodon dactylon*), baited using *Galleria mellonella* larvae.

  – *O. sacchari* Tabassum, Shahina, Nasira & Erum, 2016 – Nawabshah, Sindh, Pakistan; from a dead moth from sugarcane (*Saccharum officinarum*) field.
- *O. cyrus* Kuhestani, Karimi, Shokoohi & Makhdoumi, 2022 – Dalkhani forest, Ramsar city, Mazandaran Province, Iran; moist soil from forest heights, baited with last instar larvae of *Galleria mellonella*; dominant associated bacterium is *Ochrobactrum pseudogrignonense*.

- *O. indicus* Kumar, Jamal, Somvanshi, Chauhan & Mumtaz, 2019 – district Cachar, Assam, India; extracted from soil of fallow field.
- *O. nadarajani* Ali, Asif & Shaheen, 2011 – village Kurmikhera, Unnao district, Uttar Pradesh, India; soil from the rhizosphere of lentil (*Lens culinaris*), isolated by insect baiting technique and cultured on larvae of the moth *Corcyra cephalonica.*
- *O. niazii* Tabassum & Shahina, 2010 – Niaz Manzil, North Nazimabad, Karachi, Sindh, Pakistan; soil around roots of palm tree (*Cocos nucifera*), baited using *Galleria mellonella* larvae.
- *O. rugaoensis* (Zhang, Liu, Tan, Wang, Qiao, Yedid, Dai, Qiu, Yan, Tan, Su, Lai & Gao, 2012) = *Heterorhabditidoides rugaoensis* Zhang, Liu, Tan, Wang, Qiao, Yedid, Dai, Qiu, Yan, Tan, Su, Lai & Gao, 2012 (type isolate RG081015) – near Rugao, Jiangsu province, China; soil from farmland, using the *Galleria mellonella* baiting method. – *Oscheius rugaoensis* newly was proposed as a junior synonym of *O. chongmingensis* (Zhang, Liu, Xu, Sun, Yang, An, Gao, Lin, Lai, He, Wu & Zhang, 2008) by Bhat et al. (2021).
- *O. safricanus* Serepa-Dlamini & Gray, 2018 – Brits, North West province of South Africa; isolated from soil of a citrus farm using the *Galleria mellonella* bait method. – As the authors had a mixture of different species, the description is inherently contradictory.
- *O. siddiqii* Tabassum & Shahina, 2010 – Karachi University, Karachi, Sindh, Pakistan; soil around the roots of rose (*Rosa damascena*) bush, baited using Galleria mellonella larvae.

Without presenting new material Abolafia & Peña-Santiago (2019a) reinstated *O. debilicauda* (Fuchs, 1937) and *O. oxyuris* (Claus, 1862) and excluded *O. pheropsophi* (Smart & Nguyen, 1994) from *Oscheius*. I cannot agree with any of these proposals. With respect to the lips, lateral ridges, pharynx corpus, excretory duct, female rectum and arrangement and orientation of 9 bursal papillae plus terminal phasmids *O. pheropsophi* belongs to the Dolichura group of *Oscheius*. The fused spicules are certainly unique.

Pellioditis Dougherty, 1953

syn. ***Phasmarhabditis*** Andrássy, 1976: *Pelodera papillosa* Schneider, 1866

Type species: *Pelodera pellio* Schneider, 1866

Based on morphology there is a clade encompassing *Pellioditis pellio* and the species labelled *Phasmarhabditis* which Sudhaus (1976) called the Papillosa group (Sudhaus & Fitch 2001). This systematisation has never been taken into account, however, and the synonymy of *Phasmarhabditis* has been ignored. However, sequence data for the type species *P. pellio* will be soon published, showing that it belongs to the same clade as *Phasmarhabditis*. According to the systematic position of *Agfa* and Angiostomatidae, *Pellioditis* is possibly paraphyletic (Nermuť et al. 2016a, 2017, Tandingan De Ley et al. 2016, Pieterse et al. 2021, Gorgadze et al. 2022, Ivanova et al. 2023). However, the phylogenetic position of *Angiostoma* has not yet been convincingly shown, especially since only representatives of the Gastropoda bound Limacis group are analysed and not the Plethodontis group living parasitic in Tetrapoda.

The *Pellioditis* species are necromenic in earthworms and terrestrial gastropods. Dauer juveniles can survive in soil. Some species live like parasitoids, first being parasitic and finally killing their former hosts (Sudhaus 2008). In analogy to entomo-pathogenic nematodes, this life-cycle might be called ‘gastropod-pathogenic’. They are thus used as biological control agents for slugs and snails.

Seven valid species were listed in catalogue 2011, *P. tawfiki* (Azzam, 2003) with reservations (Sudhaus 2018) (see ‘Comments on dubious species’ p. 110). Since then 15 species have been described as new.

- *P. akhaldaba* (Ivanova, Gorgadze, Lortkhipanidze & Spiridonov, 2021) comb. n. – Akhaldaba, Georgia; in the slug *Deroceras reticulatum*; also baited with *Galleria* cadavers from garden soil. – In cupola-shaped females phasmids open on the spine.
- *P. apuliae* (Nermuť, Půža & Mráček, 2016) comb. n. – Bari, southern Italy; from the slug *Milax sowerbyi* in the garden of the University.
- *P. bohemica* (Nermuť, Půža, Mekete & Mráček, 2017) comb. n. – near Chelčice, Czech Republic; from *Deroceras reticulatum* from a red currant plantation; also baited from soil samples with *Galleria* larvae.
- *P. bonaquensis* (Nermuť, Půža, Mekete & Mráček, 2016) comb. n.; emendation of *Phasmarhabditis bonaquaense* Nermuť, Půža, Mekete & Mráček, 2016 by D. J. Hunt (Nematology 24, 2022, p. 232) – České Švýcary, near Dobrá Voda, Czech Republic; from the slug *Malacolimax tenellus.*
- *P. californica* (Tandingan De Ley, Holovachov, Mc Donnell, Bert, Paine & De Ley, 2016) comb. n. – Eureka, California, USA; obtained from a cadaver of the slug *Deroceras reticulatum*.
- *P. circassica* (Ivanova, Geraskina & Spiridonov, 2020) comb. n. – Nickel settlement, Adygea Republic, Russia; from the snail *Oxychilus* cf. *difficilis*, in deciduous forest.

- *P. clausiliiae* (Ivanova, Geraskina & Spiridonov, 2020) comb. n. – near Georgievsk, Stavropol district, Russia; from Clausiliidae snails (cf. *Quadriplicata* sp.) in decidous forest.
- *P. huizhouensis* (Huang, Ye, Ren & Zhao, 2015) comb. n. – Kowloon Peak of Huizhou City, Guangdong Province, China; in rotting leaves.
- *P. kenyaensis (Pieterse,* Rowson, Tiedt, Malan, Haukeland & Ross, 2021) comb. n. – Nairobi, Kenya; from the slug *Polytoxon robustum* in a garden.
- *P. meridionalis* (Ivanova & Spiridonov, 2017) comb. n. – Cát Tiên National Park, southern Vietnam; from the land snail *Quantula striata.*
- *P. quinamensis* (Ivanova & Spiridonov, 2022) comb. n. – Cát Tiên National Park, southern Vietnam; from the land snail *Sesara* sp.. Further isolates from seven additional genus taxa of terrestrial snails in that National Park. – Special is three separate lips by fusion in pairs and GP1 shifted anteriorly to beginning of bursa velum.
- *P. safricana* (Ross, Pieterse, Malan & Ivanova, 2018) comb. n. – near George, Western Cape province, South Africa; from the slug *Deroceras reticulatum* from a nursery.
- *P. thesamica* (Gorgadze, Troccoli, Fanelli, Tarasco & De Luca, 2022) comb. n. – Tezami, East Georgia; from a dead *Deroceras reticulatum* slug in a raspberry garden.
- *P- villasmundi* (Ivanova, Clausi, Leone & Spiridonov. 2023) comb. n. – Nature Reserve 'Speleological Complex Villasmundo – S. Alfio', Syracuse Province, Sicily; from the slug *Milax nigricans*, found in 7 further gastropod species.
- *P. zhejiangensis* (Zhang & Liu, 2020) comb. n. – Ningbo, Zhejiang province, China; from the slug *Meghimatium* **(**= *Philomycus***)** *bilineatum* from a vegetable garden.

Pelodera Schneider, 1866

Type species: *Pelodytes strongyloides* Schneider, 1860

24 valid species were listed in catalogue 2011. Here two new species are added.

Coarctata clade (now 11 species)

- *P. aligarhensis* Tahseen, Akram, Mustaqim & Ahlawat, 2014 – Harduaganj, Aligarh, Uttar Pradesh, India; from land fill area.

Strongyloides clade (now 11 species)

- *P. scrofulata* Tahseen, Akram, Mustaqim & Ahlawat, 2014 – Quarsi, Aligarh, Uttar Pradesh, India; soil from a drain.

Poikilolaimus Fuchs, 1930

Type species: *Poikilolaimus micoletzkyi* Fuchs, 1930

15 valid species were listed in catalogue 2011. Here one new species is added.

Oxycercus clade (now 8 species)

- *P. gangulyi* Sultana, 2015 – surroundings of Hauz Khas lake, New Delhi, India; in decaying leaf debris. – Probably identical with *P. oxycercus* (de Man, 1895).

Prodontorhabditis Timm, 1961

Type species: *Prodontorhabditis pluvialis* Timm, 1961

Five valid species were listed in catalogue 2011. Here two new species are added.

- *P. grandistoma* Mumtaz, Fatima, Jamal, Ahlawat, Tahseen & Ahmad, 2020 – Harduaganj, Aligarh, Uttar Pradesh, India; from decaying organic matter in a small ditch.
- *P. robusta* Mumtaz, Fatima, Jamal, Ahlawat, Tahseen & Ahmad, 2020 – near Aligarh fort, Aligarh, Uttar Pradesh, India; from rotting banana rhizome.

'Protorhabditis' Osche in Dougherty, 1955

syn. nov. ***Distorhabditis*** Shah, Vaid, Hussain & Ahmad, 2015: *D. poonchiana* Shah, Vaid, Hussain & Ahmad, 2015

D. poonchiana exhibits the apomorphic characters oft he Xylocola group (only 8 pairs of bursal papillae, arranged as 1+1/1+3+2, spicules sickle-shaped with dorsal lamella, female tail short conoid) and therefore belongs to paraphyletic *Protorhabditis*. It is unique in being monodelphic with a posterior vulva.

Type species: *Rhabditis* (*Protorhabditis*) *xylocola* Körner, 1954

15 valid species were listed in catalogue 2011. Here three new species are added.

Oxyuroides clade (now 8 species)

- *P. parva* Shah & Vaid, 2017 (2017a) – Kallar village, Poonch district, Jammu and Kashmir, India; farmyard manure.

Xylocola clade (now 8 species)

- *Protorhabditis hortulana* Abolafia & Peña-Santiago, 2016 – Puente de la Sierra, Jaén province, Spain; from domestic compost in an orchard. – Hermaphroditic, gonads without flexure.
- *Protorhabditis poonchiana* (Shah, Vaid, Hussain & Ahmad, 2015) comb. n.

= *Distorhabditis poonchiana* Shah, Vaid, Hussain & Ahmad, 2015 – Dera Ki Gali forest, Topa village, Poonch district, Jammu and Kashmir, India; from litter of forest soil containing decaying leaves and bird droppings. – Special character: reproductive system monoprodelphic and vulva position far posterior (at 81-84 % of body length).

Rhabpanus Massey, 1971

Type species: *Rhabpanus ossiculus* Massey, 1971

One valid species was listed in catalogue 2011. Here two new species are added.

- *R. poonchianus* Shah & Vaid, 2017 – Loran Mandi area, Poonch district, Jammu and Kashmir, India; from decayed wood of pine tree (*Pinus roxburghii*).
- *R. uniquus* Tahseen, Sultana, Khan & Hussain, 2012 – Lake Fulmor, California, USA; from the shore, semiaquatic.

Sclerorhabditis Ahmad, Shah & Mahamood, 2007

Type species: *Sclerorhabditis tridentata* Ahmad, Shah & Mahamood, 2007

One valid species was listed in catalogue 2011. Here two new species are added.

- *S. miniata* Shah & Vaid, 2015 – Dera Ki Gali forest, district Poonch, Jammu and Kashmir, India; from soil near the roots of an oak tree (*Quercus leucotrichophora*).
- *S. neotropicalis* Esquivel, Abolafia, Hanson & Pinto, 2012 – near La Selva Biological Station, Costa Rica; paste-like tissue material from the inner walls of the internode of a *Cecropia obtusifolia* tree containing an ant nest of *Azteca constructor*.

Stomachorhabditis Andrássy, 1970

syn. nov. ***Stegorhabditis*** Shah, Hussain, Vaid & Ahmad, 2015: *S. abursata* Shah, Hussain, Vaid & Ahmad, 2015

Like *Stomachorhabditis, S. abursata* exhibits a long stoma, setose metastegostom denticles, amphid pores more than a labial diameter posterior the lips (!), long filiform tails in both sexes, absence of bursa, two precloacal pairs of genital papillae and slender spicules.

Type species: *S. vietnamica* Andrássy, 1970

Three valid species were listed in catalogue 2011. Here one species is added.

- *S. abursata* (Shah, Hussain, Vaid & Ahmad, 2015) comb. n. – Kotli village, Rajouri district, Jammu and Kashmir, India; inside the trunk of an oak (*Quercus leucotrichophora*).

Teratorhabditis Osche, 1952

Type species: *Rhabditis dentifera* Völk, 1950

Eight valid species were listed in catalogue 2011. Here one new species is added.

- *T. giraffae* Mondal & Manna, 2012 – Alipore Zoological Garden Kolkata, India; from faeces of *Giraffa camelopardalis.*

Tokorhabditis Kanzaki, Yamashita, Lee, Shih, Ragsdale & Shinya, 2021

Diagnostic characters: Trioecious mating system comprising males, females and self-fertilising hermaphrodites, dauer juveniles develop into hermaphrodites, female and hermaphrodite tail elongate conoid tapering, morphologically not distinguishable, both **obligately viviparous with nutrition** from their mother and embryonic growth in utero, adults lips not offset, mouth triangular, metarhabdions each bearing **two denticles**, pharyngeal sleeve, median bulb, one excretory-secretory cell, males much smaller than females/hermaphrodites, open leptoderan bursa with a spike, eight pairs of genital papillae (GPs), 3 or 4 pairs precloacal, **GP1 anterior of spicules**, GP5 and GP7 point dorsally, GP6 separate, **phasmid pore anterior GP7**, testis length only about half intestine length with short ventral flexure, gubernaculum nearly half of spiculum length. (Characters in bold are apomorphies.)

Habitats: Edge of lake and associated with dung beetles as carrier.

Type species: *Tokorhabditis tufae* Kanzaki, Yamashita, Lee, Shih, Ragsdale & Shinya, 2021

Three valid species.

- *T. atripennis* Ragsdale, Kanzaki, Yamashita & Shinya, 2022 (type isolate NKZ329) – Tsukuba, Japan; from a dung beetle (*Onthophagus* sp.).
- *T. tauri* Ragsdale, Kanzaki, Yamashita & Shinya, 2022 (type isolate EJR13) – Hillsborough, North Carolina, USA; from the dung beetle *Onthophagus taurus* from a dairy farm, dauer juveniles beneath the elytra.
- *T. tufae* Kanzaki, Yamashita, Lee, Shih, Ragsdale & Shinya, 2021 (type isolate PS8402) – Mono Lake, California, USA; from soil at the bank of the alkaline, hypersaline, and arsenic-rich lake. – Four

GPs anterior cloaca in two doublets, first doublet far anterior.

Manuscript names and lapsi

Several new names which appear in nematode descriptions in theses put onto the internet for some time must be regarded as *nomina nuda.* Besides this, there are various volatility errors in articles and *nomina nuda* in abstracts of meetings, although special care is required with taxon names.

Rhabditis aligarhensis Shah, 2005 thesis
Rhabditis aliporensis Mondal, 2012 thesis
Parasitorhabditis alistina in Lortkipanidze et al. (2020) is a nomen nudum (see Sudhaus 2011: 151)
Metarhabditis amplirectum Khan, 2009 thesis
Mesorhabditis andrassyi Hussain, 2006 thesis
Pelodera angularis Shah, 2005 thesis
Mesorhabditis anisospicula Mustaqim, 2017 thesis
Mesorhabditis bicollumellatus Shah, 2005 thesis
Rhabditella bilineata Shah, 2005 thesis
Oscheius carlianonsis in Pervez et al. (2013); lapsus for *O. carolinensis*
Cuticularia conica Tabassum (2006) and 2010 thesis
Cruznema curtivelatum Khan, 2009 thesis
Protorhabditis curvatus Shah, 2005 thesis
Teratorhabditis cuspilabia Sultana, 2005 thesis
Protorhabditis defecta Ahlawat, 2013 thesis
Sclerorhabditis devprayaga Kumar, 2012
Oscheius dimorpha Khan, 2009 thesis
Metarhabditis distincta Ahlawat, 2013 thesis
Curviditis diversispicula Sultana, 2005 thesis
Oscheius dolichuraisda respectively *O. dolichurastra* in Zhang et al. (2012); lapsus for *O. dolichura*
Mesorhabdtis environmental Ghaemi et al. (2015)
Protorhabditis filicaudatus Shah, 2005 thesis
Rhabditoides fungicola Goodey, 1942 or *Rhabditella fungicola*: lapsus for *Rhabditoides frugicolus*
Rhabditella garhwali Kumar, 2012 thesis
Bursilla gossypii Shah, 2005 thesis
Caenorhabditis heptalineata Mustaqim, 2017 thesis
Metarhabditis indica Kumar, 2012 thesis
Dorsorhabditis indicus Shah, 2005 thesis
Curviditis jammuvi Shah, 2005 thesis
Caenorhabditis kashmirensis Sha, 2001 thesis
Rhabditella kashmirensis Shah, 2005 thesis
Oscheius keethamensis Mustaqim, 2017 thesis
Poikilolaimus laxothecus Sultana, 2005 thesis
Oscheius leptodera Shah, 2005 thesis
Curviditis longicaudata Hussain, 2006 thesis; name mentioned in Ryss & Petrov (2021)
Cruznema longispicula Kumar, 2012 thesis
Cuticularia macrodentata Hussain, 2006 thesis; name mentioned in Ryss & Petrov (2021)
Teratorhabditis mangiferae Sha, 2001 thesis
Mesorhabditis manipuriana Shah, 2005 thesis
Rhabditella masculata in Taha et al. (2019) is a *nomen nudum*; most likely lapsus for *Rhabditella muscicola* (compare Abdein et al. 2020)
Curviditis microspicula Ahlawat, 2013 thesis
Mesorhabditis minicaudata Kumar, 2012 thesis
Protorhabditis minirobustus Shah, 2005 thesis
Heterorhabditis minutus Prabhuraj, Viraktamath & Kumar, 2002
Protorhabditis minutus Hussain, 2006 thesis
Protorhabditis mucronata Mustaqim, 2017 thesis
Protorhabditis neoxylocola Shah, 2001 thesis
Phasmarhabditis pakistanensis Shahina, Tabassum & Soomro, Pak patent 141630
Curviditis parilis Hussain, 2006 thesis; name mentioned in Ryss & Petrov (2021)
Phasmarhabditis phasmarhabditis Huang, Ye, Ren & Zhao, 2015; lapsus for *P. hermaphrodita*
Protorhabditis phoudelus Shah, 2005 thesis
Protorhabditis pini Shah, 2005 thesis
Parasitorhabditis poinari in Kakuliya, Devdariani & Maglakelidze (1980) is a *nomen nudum*
Metarhabditis polydentatus Shah, 2005 thesis
Distolabrellus poonchianus Shah, 2005 thesis
Bursilla quadripapillata Sultana, 2010
Heterorhabditis riobravus in Costa & Furlong (2006) and Costa et al. (2007) is a *nomen nudum*
Oscheius rugaolensis Darsouei & Karimi (2014) is a *nomen nudum*
Bursilla shekhaensis Ahlawat, 2013 thesis
Coarctadera sparsus in Nemaplex
Distolabrellus sudhausi Hussain, 2006 thesis
Cruznema uniquus Hussain, 2006 thesis

Comments on dubious species

- *Pellioditis mairei* (Maupas, 1919): In the short description the only figures provided are of the male bursa and spicules. The measurements of one female are given. The shape of the female tail is not mentioned, but it is presumably long conical (c = 23.6). The species is gonochoristic. Though very similar to *P. pellio* and also found in an earthworm (Maupas isolated his *P. pellio* from slugs!), *P. mairei* is different. In crossing experiments between the two species conducted by Maupas (1919), copulations and sperm transfer occurred in both directions, and in the combination *P. pellio* males X *P. mairei* females development and segmentation were even triggered, but this came to an end after a few steps. So it can be concluded that these species are isolated.

- *Pellioditis tawfiki* (Azzam, 2003): Several described characters indicate that it is not a *Pellioditis* species: The arrangement of rays, 2/1+2+1+3, is reminiscent of the *Pelodera* Teres group, if GP1 is overlooked. The spicules have a head, the stoma is long, embryonating eggs are in a single row, and the copula astonishingly follows the spiral type (Azzam 2003, 2004). A redescription is necessary.

Alphabetical list of genus group names of 'Rhabditidae'

From the six genus names described as new in the period under review I accept two as valid (names in bold), so that in my view we currently have 40 valid clades or groups in the rank of genera in 'Rhabditidae'.

Auanema
Chylorhabditis: syn. of *Buetschlinema*
Distorhabditis: syn. of *Protorhabditis*
Loffienema: syn. of *Haematozoon*
Quercorhabditis: syn. of *Diploscapteroides*
Stegorhabditis: syn. of *Stomachorhabditis*
Tokorhabditis

Alphabetical llst of species epitheta of 'Rhabditidae'

abursata, Stegorhabditis → Stomachorhabditis
afra → Caenorhabditis
acidophila → Mesorhabditis
acuticauda → Mesorhabditis
agridulce → Caenorhabditis
akhaldaba, Phasmarhabditis → Pellioditis
aligarhensis → Pelodera
andrassyii → Neorhabditis
anisospiculus → Cephaloboides
apuliae, Phasmarhabditis → Pellioditis
astrocarya → Caenorhabditis
atripennis → Tokorhabditis
attenuata, † Psychodorhabditis → Choriorhabditis
baltica, † Psychodorhabditis → Choriorhabditis
basothovii → Oscheius
becei → Caenorhabditis
beicherriana → Heterorhabditis
bifurcata → Mesorhabditis
bohemica, Phasmarhabditis → Pellioditis
bonaquaense, Phasmarhabditis → emended to *Pellioditis bonaquensis*
bonaquensis, Phasmarhabditis → Pellioditis
brevicaudis, Heterorhabditis → syn. of *Heterorhabditis indica*
californica, Phasmarhabditis → Pellioditis
castelli → Caenorhabditis
chinkari → Caenorhabditis
ciceri, Oscheius → syn. of *Metarhabditis amsactae*
circassica, Phasmarhabditis → Pellioditis
citri → Oscheius
clausiliiae, Phasmarhabditis → Pellioditis
cobbi, Oscheius → syn. of *Oscheius citri*
cynodonti, Oscheius → syn. of *Oscheius citri*
cyrus → Oscheius
denticulata → Mesorhabditis
dhanoriense, Loffienema → Haematozoon
dolens → Caenorhabditis
dominicana, † Psychodorhabditis → Choriorhabditis
doughertyi → Caenorhabditis
dunicola → Crustorhabditis
epuraeae, Chylorhabditis → Buetschlinema
esculentus, Oscheius → syn. of *Oscheius citri*
formicidae → Diploscapter
freiburgense → Auanema
gangulyi → Poikilolaimus
gerrardi, Heterorhabditis → syn. of Heterorhabditis indica
giennensis → Metarhabditis
gingeri, Oscheius → syn. of *Metarhabditis amsactae*
giraffae → Teratorhabditis
grandistoma → Prodontorhabditis
guadeloupensis → Caenorhabditis
helalii → Cruznema
hortulana → Protorhabditis
hussainii, Oscheius → syn. of *Metarhabditis amsactae*
huizhouensis, Phasmarhabditis → Pellioditis
hystrisi → Caenorhabditis
imperialis → Caenorhabditis
indicus → Oscheius
inopinata → Caenorhabditis
kamaaina → Caenorhabditis
karachiensis → Oscheius
kenyaensis, Phasmarhabditis → Pellioditis

krikudae → *Caenorhabditis*
latens → *Caenorhabditis*
longicaudata, Metarhabditis → syn. of *Metarhabditis amsactae*
macrosperma → *Caenorhabditis*
melissense → *Auanema*
meridionalis, Phasmarhabditis → *Pellioditis*
microvilli, Oscheius → *Caenorhabditis*
miniata → *Sclerorhabditis*
minimum → *Cruznema*
monodelphis → *Caenorhabditis*
nadarajani → *Oscheius*
neotropicalis → *Sclerorhabditis*
niazii → *Oscheius*
nigoni → *Caenorhabditis*
niphades → *Caenorhabditis*
noenieputensis → *Heterorhabditis*
nouraguensis → *Caenorhabditis*
oiwi → *Caenorhabditis*
okuensis → *Mesorhabditis*
onirici → *Oscheius*
pakistanensis, Heterorhabditis → syn. of *Heterorhabditis indica*
panamensis → *Caenorhabditis*
parapapillosus, Rhabditis → *Cephaloboides*
parva → *Protorhabditis*
parvicauda → *Caenorhabditis*
pawani, Flagicaudoides → syn. of *Cephaloboides curvicaudatus*
persicus → *Diploscapteroides*
pini → *Caenorhabditis*
poonchiana, Distorhabditis → *Protorhabditis*
poonchianus → *Rhabpanus*
portoensis → *Caenorhabditis*
punctatus, Oscheius → syn. of *Oscheius citri*
quinamensis, Phasmarhabditis → *Pellioditis*
quiockensis → *Caenorhabditis*
rajouriensis, Quercorhabditis → *Diploscapteroides*
ratufae → *Caenorhabditis*
reciprocum, Rhabditis → *Auanema*
rhodense → *Auanema*
robusta → *Prodontorhabditis*
ruandica → *Heterorhabditis*
rugaoensis, Heterorhabditidoides → *Oscheius*
sacchari, Oscheius → syn. of *Oscheius citri*
safricana, Phasmarhabditis → *Pellioditis*
safricanus → *Oscheius*
saproxylicus → *Oscheius*
scrofulata → *Pelodera*
scuri → *Caenorhabditis*
seurati, Rhabditis → *Auanema*
siddiqii → *Oscheius*
sinica → *Caenorhabditis*
somsookae, Heterorhabditis → syn. of *Heterorhabditis baujardi*
sonorensis, Heterorhabditis → syn. of *Heterorhabditis taysearae*
suklaae, Rhabditis → *Metarhabditis*
sulstoni → *Caenorhabditis*
tauri → *Tokorhabditis*
thesamica, Phasmarhabditis → *Pellioditis*
tribulationis → *Caenorhabditis*
tropicalis → *Caenorhabditis*
tufae → *Tokorhabditis*
uniquus → *Rhabpanus*
uteleia → *Caenorhabditis*
viguieri, Rhabditis → *Auanema*
villasmundi, Phasmarhabditis → *Pellioditis*
virilis → *Caenorhabditis*
vivipara → *Caenorhabditis*
vulvatus → *Distolabrellus*
waitukubuli → *Caenorhabditis*
wallacei → *Caenorhabditis*
yunquensis → *Caenorhabditis*
zacatecana → *Heterorhabditis*
zanzibari → *Caenorhabditis*
zhejiangensis, Phasmarhabditis → *Pellioditis*

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