

Diagnostic and phylogenetic significance of lateral field incisures, phasmids and other morphological characters of second-stage juveniles and males of Heteroderidae (Nematoda, Tylenchida), with notes on hosts and phylogeography

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Summary. Data of the current knowledge about the number of incisures in the lateral fields of second-stage juveniles and males, shape of phasmids and tip of spicules of the 158 recognised species in the 19 genera in the family Heteroderidae are reviewed and compiled. All characters are of diagnostic value in distinguishing genera and intrageneric species groups, but more detailed studies are needed. Differences in the number of incisures or in the size of phasmids among species of *Cryphodera*, *Meloidodera* and *Atalodera* are considered as an indication of paraphyly. In agreement with results of molecular analyses, three additional species groups are proposed for *Heterodera* species with Poales as hosts (*Cardiolata*, *Koreana* and *Orientalis* groups), and in *Globodera* designation of *Rostochiensis*, *Millefolii* and *Zelandica* groups. Information on host ranges and host reaction to parasitism has great relevance for the study of phylogenetic relationships and estimation of the age of taxa. Evaluation of biogeographical data restricted to ‘natural’ occurrence as well as consideration of geological and palaeoclimatic events are essential for the recovery of putative ancestral areas of origin of taxa. Heteroderid populations tentatively identified as *Meloidodera*, *Hylonema* and *Sarisodera* are briefly characterised from Africa (the first two genera) and Vietnam (the third genus). Other populations of unidentified species or representatives of still unknown genera are reported from Borneo, the Canary Islands, the Dominican Republic, New Zealand, Thailand, Tunisia and Vietnam.

Key words: Ataloderinae, *Cryphodera*, distribution, *Globodera*, *Heterodera*, Heteroderinae, *Hylonema*, *Meloidodera*, Meloidoderinae, morphology, plant hosts, Punctoderinae, *Sarisodera*, Verutinae, *Verutus*.

The family Heteroderidae is among the best studied taxa of tylenchid nematodes, with currently 158 recognised species in a total of 19 genera. Many species are of economic significance as plant parasites and require precise identification for their management in agriculture. The genera and species placed in the cyst-forming subfamily Heteroderinae and in the non-cyst forming subfamilies Meloidoderinae, Ataloderinae and Verutinae are mainly distinguished and characterised by morphological characters of cysts or females. More recent integrated morphological and molecular studies have shown that the significance of cyst characters has often been overestimated, which led

to non-acceptance of genera such as *Afenestrata*, *Bidera*, *Ephippiodera* and others and the transfer of individual species to other genera or to different species groups within a genus, particularly in the genus *Heterodera*. Species with descriptions exclusively based on cysts characteristics or lacking data on second-stage juveniles (J2) and males were commonly considered as *species inquirendae*. Morphological characters of males and J2 were mostly considered of secondary significance, but J2 features are presently more often used for distinction and identification of species. Differences in host preferences were other important characters used for changes in classification. For instance, the number

of incisures in the lateral fields of J2 and the size of phasmids were considered decisive for excluding *Heterodera bifenestra* from the *H. avenae* species group, phasmid size and host preference for excluding *H. turcomanica* from the same group (Wouts & Sturhan, 1995), and the number of lateral incisures for separating *Betulodera betulae* from the genus *Cactodera* (Sturhan, 2002).

In the present paper, data of our current knowledge on the number of longitudinal incisures in the lateral fields of J2 and males, on presence and size of phasmids in both developmental stages and on the shape of the tip of spicules are compiled for all genera and intrageneric groups currently placed in the family Heteroderidae. The number of lateral incisures is commonly used in Tylenchida as a significant diagnostic character for genera, in particular in Telotylenchidae and Merliniidae. In Heteroderidae the number of lateral field incisures ('lateral lines') has already often been used for distinction of species and occasionally also for distinction of species groups within the genus *Heterodera* (see Subbotin *et al.*, 2010a). Data on presence or absence of phasmids in males of Heteroderidae as potential diagnostic character for distinction of subfamilies have recently been compiled (Sturhan, 2016).

A compilation of known data on a few selected characters of motile life stages of heteroderids and their critical evaluation are presented to support and facilitate identification, based on some morphological characters that can generally be seen using light-microscopical examination of J2, which are often the only life stages available for identification. Thus, data on lip region characters, which were also used for the distinction of heteroderid taxa but difficult to discern in routine microscopical studies and only known for a comparatively low number of taxa, were not included in this paper.

Another objective of this publication is to confirm or to question congruence of the few selected morphological characters with available molecular data and eventually to indicate relationships or paraphylies that had not been demonstrated by previous molecular or biochemical analyses. The total number of species included into molecular studies to date is still relatively low. However, a high number of species is (still) placed into selected genera or species groups, such as Heteroderinae, exclusively on the basis of their morphological characters, especially those of cysts. Data on host plants, host reaction to parasitism and native geographical distribution are briefly added in the present paper, because such information is often

essential for identification of genera, species groups or individual species. These data are very useful for the elucidation and validation of potential phylogenetic relationships, which are so far mainly based on molecular studies. Moreover, another goal of compiling, discussing and reviewing the mentioned morphological characters and other data is to indicate the gaps in current knowledge and to provide a useful basis for further studies on Heteroderidae, which will hopefully stimulate future research.

MATERIALS AND METHODS

Original descriptions of the valid species in Heteroderidae and subsequent publications supplementing morphological data of individual species were critically reviewed and evaluated for information on the selected morphological characters of J2 and males. These characters include the numbers of incisures in the lateral fields, presence and size of phasmids and the shape of the spicule tip. Some previous data of such characters proved to be incorrect and had subsequently already been corrected in several publications; other characters were used as described or depicted in the original descriptions or in subsequent emending publications. The books published by Subbotin *et al.* (2010a, b) served in particular as valuable sources of information for the cyst-forming Heteroderinae.

Published data on lateral fields and the number of incisures in J2 are available for almost all valid heteroderid species, but not so in males of many species. Phasmids were often not precisely described or depicted. Mostly, no distinction was made between phasmidial opening to the outside (indistinct, small, distinct) and the phasmidial duct leading through the cuticle to the receptor cavity (narrow, with small lens-like extension, with large lens-like ampulla). Likewise, the shape of the spicules and spicule tips have often not been carefully or correctly described or depicted (pointed, bluntly rounded, notched, dentate, bidentate, tridentate). The significance of these characters is thus sometimes of only limited value and more detailed studies are required.

In the present paper, supplemental information on certain morphological characters is sometimes complemented by microscopical studies conducted by the author of type and other reliably identified specimens available in the German Nematode Collection (DNST), microscopical slides or other material obtained from several nematode collections or directly studied in other nematological research centres. Several presumably undescribed heteroderid

Table 1. Number of incisures in lateral fields and shape of phasmids in second-stage juveniles and males, shape of spicule tip, hosts and host response of Heteroderidae genera (detailed data for *Heterodera* in Table 2). Phasmids without lens-like ampulla are designated as “small”.

Subfamily/genus (no. of valid species, +: undescribed species known)	Lat. incisures		Phasmid shape		Spicule tip	Hosts (orders)	Host response: UG = uninucleate giant cell; SC = syncytium
	J2	♂	J2	♂			
Meloidoderinae							
<i>Cryphodera</i>							
<i>Zelandodera</i> group (3)	3	4	lens	lens	bluntly rounded	Pinales, Myrtales, Fagales	
other species (4+)	3	3	lens	lens	bluntly rounded	Pinales, Myrtales, Lamiales, Rosales	
<i>Meloidodera</i> (11+)	4	4	small/le ns	small/ lens/ absent	blunt/ notched	Pinales, Lamiales, Asterales, Fagales, Fabales, Caryophyllales, Rosales, Solanales, Saxifragales, Cucurbitales, Malpighiales, Malvales, Solanales, Poales	UG
Ataloderinae							
<i>Atalodera</i>							SC
group 1 (3)	3	4	lens	absent	pointed	Asterales, Fabales, Poales	
group 2 (6)	4	4	lens	absent	pointed/ notched	Asterales, Fabales, Caryophyllales, Solanales, Oxalidales, Malvales, Brassicales, Poales	
<i>Bellodera</i> (1)	4	4	lens	absent?	pointed	Rosales	UG
<i>Camelodera</i> (1)	3	4	small	absent?	notched	Carophyllales	?
<i>Ekphymatodera</i> (1)	4	4	small	absent	pointed	Poales	SC
<i>Hylonema</i> (1)	3	4	small	absent	pointed	Sapindales	UG
<i>Rhizonemella</i> (1)	4	4	lens	absent	pointed	Pinales, Sapindales, Fagales	UG
<i>Sarisodera</i> (1+)	4	4	lens	absent	blunt	Pinales, Rosales	UG
Verutinae							
<i>Verutus</i> (2+)	4	4	small	absent	notched	Myrtales, Gentianales, Poales	SC
<i>Bilobodera</i> (2)	4	4	small	?	notched	Caryophyllales, Poales	?
Heteroderinae							
<i>Betulodera</i> (1+)	3	4	small	absent?	notched	Brassicales, Fagales	SC
<i>Cactodera</i> (14)	4	4	small	absent	notched	Caryophyllales, Asterales, Poales	SC
<i>Dolichodera</i> (1)	4		small	(no ♂)		Poales?	?
<i>Globodera</i>							SC
<i>Zelandica</i> group (3+2)	4	4	small	absent	pointed	Myrtales, Fabales, Malvales, Ericales? Rosales?	
<i>Millefolii</i> group (2+1)	4	4	small	absent	pointed	Asterales	
<i>Rostochiensis</i> group (7)	4	4	small	absent	pointed	Solanales	
<i>G. mali</i>	?	?	?	?	?	Rosales	
<i>Paradolichodera</i> (1)	irreg.	4	small	absent	notched	Poales (Juncaceae)	?
<i>Punctodera</i> (4)	4	4	small	absent	pointed	Poales (Poaceae)	SC
<i>Vittatidera</i> (1)	4	4	small	absent	notched	Poales (Poaceae)	?
<i>Heterodera</i> (85+)	3/4	3/4	small/ lens	absent	notched	Monocots + Dicots	SC

MELOIDODERINAE GOLDEN, 1971***Cryphodera* Colbran, 1966**

Second-stage juveniles of all seven described species with three incisures in their lateral fields; in *C. nothophagi* (Wouts, 1973) presence of four incisures had been mentioned in the original description, but re-examination of paratype J2 revealed three incisures, the inner incisure occasionally diverging into two (Sturhan, 2010); three incisures in each lateral field were also found in J2 of several unidentified *Cryphodera* spp. from natural forests in Vietnam (Nguyen *et al.*, 2011), including one population tentatively identified later as *C. sinensis* Zhuo, Wang, Ye, Peng & Liao, 2014. In males of *C. brinkmani* Karssen & van Aelst, 1999, *C. eucalypti* Colbran, 1966, *C. sinensis* and unidentified *Cryphodera* spp. from Vietnam three incisures are present in each lateral field, while four incisures are present in males of the New Zealand species *C. coxi* (Wouts, 1973), *C. nothophagi* and *C. podocarpus* (Wouts, 1973). This character was confirmed for the latter of these species through studies of type specimens by the present author. In *C. kalesari* Bajaj, Walia, Dabur & Bhatti, 1989 from India males are unknown.

In all described *Cryphodera* species and in *Cryphodera* spp. from Vietnam (Nguyen *et al.*, 2011) phasmids in J2 are lens-like. Phasmids in males appear to be small or weakly lens-like; spicule tips appear to be generally bluntly rounded.

Based on differences in the number of lateral field incisures in males two species groups in *Cryphodera* are distinguished (Table 1): (1) A group with three species endemic to New Zealand and originally placed in the genus *Zelandodera* Wouts, 1973, which was later synonymised with *Cryphodera* by Luc *et al.* (1978). (2) Four described and several undescribed species known from Australia, east, south-east and south Asia.

Hosts of the three New Zealand species in group 1 are species of *Podocarpus* (Podocarpaceae, Pinales), *Metrosideros* (Metrosidereae, Myrtales) and *Nothofagus* (Nothofagaceae, Fagales); hosts of the species in group 2 are *Eucalyptus* spp. (Myrtaceae, Myrtales) for *C. eucalypti* from Australia, *Colebrookia* (Lamiaceae, Lamiales) and *Terminalia* (Combretaceae, Myrtales) for *C. kalesari* from India, *Boehmeria* (Urticaceae, Rosales) for *C. sinensis* from China, and *Pinus*

thunbergii (Pinaceae, Pinales) for *C. brinkmani* from Japan.

***Meloidodera* Chitwood, Hannon & Esser, 1956**

Second-stage juveniles with four incisures in each lateral field in all eleven valid species, including *M. sikhotealinensis* Eroshenko, 1978, which several authors considered as *species inquirenda*. Males of nine species in which males are known likewise with four incisures. Data on the size of the phasmids in J2 are diverging among the *Meloidodera* species: phasmids were described as distinct with lens-like ampulla in *M. alni* Turkina & Chizhov, 1986 (Sturhan, 2010), *M. floridensis* Chitwood, Hannon & Esser, 1956 (Wouts, 1973; Hirschmann & Triantaphyllou, 1973; Carta & Baldwin, 1990), *M. tianschanica* Ivanova & Krall, 1985, and also in the original descriptions of *M. eurytyla* Bernard, 1981 and *M. mexicana* Cid del Prado Vera, 1991. Phasmids with small lens-like ampulla in J2 were reported for *M. belli* Wouts, 1973 (original description and re-examination of paratype J2 by the present author) and *M. charis* Hopper, 1960 (Carta & Baldwin, 1990). These structures were reported as ‘pore-like’ and lacking a lens-like ampulla in the original descriptions of *M. astonei* Cid del Prado Vera & Rowe, 2000 and *M. zacanensis* Cid del Prado Vera, 1991. Similar to other heteroderid taxa (see below) phasmids with lens-like ampulla in J2 are situated a few body annuli posterior to the anus, whereas small ‘pore-like’ phasmids are generally situated more posterior and close to the middle of tail length. A similar range of phasmid appearance has been reported for males of *Meloidodera* (Sturhan, 2016); in *M. astonei* even absence of phasmids is included among the diagnostic characters (Cid del Prado Vera & Rowe, 2000), and phasmids have not been mentioned and depicted in the original description of *M. hissarica* Krall & Ivanova, 1992. Descriptions and figures of the distal ends of spicules are also variable among the nine species with males known, ranging from blunt to notched and wide.

Differences in the size and presence of the phasmids in J2 and males may be an indication of parafyly of the genus. Baldwin & Powers (1987) state that ‘inconsistent J2 lip patterns could suggest polyphyly of *Meloidodera*’. Lip pattern of *M. alni* J2 from Germany resembles that of type C in Fig. 2 of the cited publication and is similar also to the head region of *M. floridensis* (Othman & Baldwin, 1985) and the lip pattern of *Cryphodera eucalypti* shown by Stone (1975). Moreover, different chromosome



Fig. 2. Known distribution of the genus *Meloidodera* (putative identification of populations from Africa included).

numbers are considered as an indication that the genus may be paraphyletic: Triantaphyllou (1970) considered $n = 9$ chromosomes as the basic number of *Meloidodera*. The present author observed $n = 5$ chromosomes in oocytes of *M. alni* from Germany. Both diverging observations were already discussed by Triantaphyllou & Hirschmann (1980).

Hosts reported for *Meloidodera* species range from conifers (Pinaceae, Pinales), the angiosperm families Caryophyllaceae (Caryophyllales), Cucurbitaceae (Cucurbitales), Betulaceae and Fagaceae (Fagales), Euphorbiaceae and Salicaceae (Malpighiales), Paeoniaceae and Saxifragaceae (Saxifragales), Fabaceae (Fabales), Rosaceae (Rosales), Malvaceae (Malvales), Lamiaceae (Lamiales), Solanaceae (Solanales) and Asteraceae (Asterales) to the monocotyledon Poaceae (Poales). Both dicots and monocots as hosts were recorded for *M. astonei*, *M. charis*, *M. eurytyla* and *M. mexicana*.

Four of the *Meloidodera* species known and currently considered as valid are described and exclusively reported from Eurasia (Western Europe to the Russian Far East). These species include *M. sikhotealiniensis*, which is 'widespread in valley forests of broadleaf trees' in the Russian Far East (Eroshenko & Volkova, 2003). Additional seven

species are reported from North America (from Alaska to Mexico). Two unidentified species tentatively attributed to the genus *Meloidodera* were identified in Ethiopia and Cameroon (see below).

ATALODERINAE WOUTS, 1973

Atalodera Wouts & Sher, 1971

Nine species are known in the genus *Atalodera* (syn. *Sherodera* Wouts, 1974; *Thecavermiculatus* Robbins, 1978). Six of these species have J2 with four incisures in the lateral field; however, J2 of *A. gibbosa* Moreira de Souza & Huang, 1994, *A. trilineata* Baldwin, Bernard & Mundo-Ocampo, 1989 and *A. ucrici* Wouts & Sher, 1971 have each lateral field marked by three incisures. Males of both species groups have four incisures. No information on incisures in males is given in the original description of *A. lonicerae* (Wouts, 1974), but in paratype males four incisures were seen by the present author, with the inner incisures often indistinct. In *A. gracilancea* (Robbins, 1978) and *A. trilineata* males are unknown. The phasmids in J2 are lens-like in all species; they appear to be generally absent in males (Sturhan, 2016). Spicule tips were mostly described or depicted as pointed, for *A. andina* (Golden, Franco, Jatala & Astogaza, 1983) as notched.

Seven of the species were described from North America, among these *A. crassicrustata* (Bernard, 1981) described from the Aleutian Islands (Alaska) and recorded also from the Far East of Russia (Kazachenko, 1990); two species are only known from South America. Hosts are different eudicots and Poaceae. The presence of three or four lateral incisures in J2 is considered as an indication that the genus might be paraphyletic and that intrageneric species groups could or should be distinguished (Table 1).

***Bellodera* Wouts, 1985**

Second-stage juveniles and males in the only species of the genus, *B. utahensis* (Baldwin, Mundo-Ocampo & Othman, 1983) Wouts, 1985, with four incisures in each lateral field. Phasmids in J2 lens-like, situated rather closely posterior to the anus, they are reported as indistinct in the original description of the males. Spicules with pointed distal end. Described from *Rosa* sp. (Rosaceae, Rosales) in Utah, USA.

***Camelodera* Krall, Shagalina & Ivanova, 1988**

According to the original description of *C. eremophila* Krall, Shagalina & Ivanova, 1988 there are four lateral incisures in J2 and three in males, but re-examination of type specimens revealed only three incisures in a paratype J2 and four in the allotype male, but the inner incisures in the latter in part are closer together and appearing as a single line; phasmids in a paratype J2 are distinct, but obviously not lens-like, situated nine annuli posterior to the anus; allotype male with longitudinally striated lip annuli (Sturhan, 2010, and more recent studies of type specimens); spicules with notched tip. Described from *Calligonum arborescens* (Polygonaceae, Caryophyllales) in the Kara Kum desert of Turkmenistan.

***Ekphymatodera* Baldwin, Bernard & Mundo-Ocampo, 1989**

In both J2 and males of *E. thomasoni* Baldwin, Bernard & Mundo-Ocampo, 1989 four longitudinal incisures in each lateral field were observed; phasmids in J2 are small, pore-like; male spicules with pointed tip. Described from *Juncus effusus* (Juncaceae, Poales) from California, USA.

***Hylonema* Luc, Taylor & Cadet, 1978**

The only species in the genus, *H. ivorense*, has three and four incisures in each lateral field in J2 and males, respectively (Luc, Taylor & Cadet, 1978). J2 phasmids are pore-like. Male spicules

have pointed tip. Described from the tree *Turraeanthus africana* (Meliaceae, Sapindales) growing in a tropical rain forest in Ivory Coast. The only other record is from Cameroon (see below).

***Rhizonemella* Andrassy, 2007**

Four lateral incisures are reported in each lateral field of *R. sequoiae* males and J2 (Cid del Prado Vera, Lownsbery & Maggenti, 1983) Andrassy, 2007. The inner incisures in J2 at anterior and posterior ends of body are closer together and forming a single central line; phasmids in J2 are with lens-like structure, situated 3-6 annuli posterior to the anus; spicules with pointed tip. Described from *Sequoia sempervirens* (Cupressaceae, Pinales) in California, USA; developed to maturity also in species of *Libocedrus* and *Sequoiadendron* (Cupressaceae, Pinales), *Pseudotsuga* (Pinaceae, Pinales), *Acer* (Sapindaceae, Sapindales) and *Alnus* (Betulaceae, Fagales) (Cid del Prado Vera & Lownsbery, 1984). More species appear to exist in USA (Subbotin *et al.*, 2017).

***Sarisodera* Wouts & Sher, 1971**

In the only species of the genus, *S. hydrophila* Wouts & Sher, 1971 described from California and recorded also from Korea (Choi & Kim, 2001), four incisures are present in each lateral field in both males and J2. Phasmids in J2 with lens-like structure; male spicules with blunt distal end. Hosts are species of *Salix* and *Populus* (Salicaceae, Malpighiales) and *Lyonothamnus* (Rosaceae, Rosales) (original description and Mundo-Ocampo & Baldwin, 1983); in Korea found around the roots of *Fraxinus rhynchophylla* (Oleaceae, Lamiales). Specimens from *Pinus monticola* in Idaho found by Nickle (1960) were later identified as *Sarisodera* (Wouts & Sher, 1971). *Sarisodera* sp. identified in Vietnam (see below) was isolated from rhizosphere soil of an unidentified Fagaceae tree (Fagales) and wild banana.

VERUTINAE ESSER, 1981

***Verutus* Esser, 1981**

In both species described from USA, *V. volvingentis* Esser, 1981 and *V. californicus* Baldwin, Bernard & Mundo-Ocampo, 1989, and in a putatively undescribed species from Germany (see below), males and J2 have four lateral incisures. Phasmids in males absent, pore-like in J2 of *V. californicus* and *Verutus* sp. from Germany. In the original description of *V. volvingentis* J2, they were reported as 'not observed'. However, examination of J2 paratypes conducted by the present author

indicates that small and inconspicuous pores are present. Spicules of *V. californicus* with bifid tip, not precisely described or depicted for *V. volvingentis*, weakly notched in males from Germany. Hosts of *V. volvingentis* are members of Rubiaceae (Gentianales) and Onagraceae (Myrtales); only *Carex* sp. (Cyperaceae, Poales) is known as host of *V. californicus*; hosts of *Verutus* sp. from Germany are also Cyperaceae.

Verutus mesoangustus Minagawa, 1986 had been designated by Sharma & Siddiqi (1992) as type species of the genus *Bilobodera*, which is mainly characterised and distinguished from *Verutus* by a bilobed female body. Bajaj and Walia (1996) recorded *V. mesoangustus* from India, but subsequent studies by Bajaj & Dalal (1997) on the life cycle of the Indian population on a Poaceae host indicate that the population studied appears not in agreement with the genus diagnosis of *Bilobodera* but rather with that of *Verutus*.

***Bilobodera* Sharma & Siddiqi, 1986**

Lateral fields in J2 with four incisures in *B. flexa* Sharma & Siddiqi, 1992 described from India and in *B. mesoangusta* (Minagawa, 1986) described from Japan; four incisures present also in males of *B. mesoangusta*; males of *B. flexa* are unknown. Phasmids of J2 are pore-like in both species; no information about phasmids in males of *B. mesoangusta* available; tip of spicules probably slightly indented. Hosts are Poaceae (Poales) and Amaranthaceae (Caryophyllales).

HETERODERINAE FILIPJEV & SCHUURMANS STEKHOVEN, 1941

***Betulodera* Sturhan, 2002**

In *B. betulae* (Hirschmann & Riggs, 1969) three incisures in each lateral field in J2, four lateral incisures in males; J2 with phasmids small but distinct, not lens-like, 5-6 annuli posterior to the anus; male with spicules slightly bifid at distal end. Known host genera: *Betula* and *Alnus* (Betulaceae, Fagales), *Cleome* (Cleomaceae, Brassicales) and *Robinia* (Fabaceae, Fabales), but development observed on some more hosts, including Poaceae. The species has been found in several states of USA; a putative new species was collected from unidentified trees in California (Subbotin *et al.*, 2011).

***Cactodera* Krall & Krall, 1978**

Four incisures in each lateral field of J2 of the 14 species currently known in the genus and in the males (males unknown in three species); phasmids pore-like in J2, absent in males; spicules distally

notched (bifid). Type hosts of eleven *Cactodera* species are plants belonging to six families of the order Caryophyllales (see Sturhan, 2002). Hosts of *C. galinsogae* Tovar Soto, Cid del Prado Vera, Nicol, Evans, Sandoval Islas & Martinez Garza, 2003 are *Galinsoga* and *Bidens* species (Asteraceae, Asterales), barley and wild oats (Poaceae, Poales). *Hordeum vulgare* is the type host of *C. rosae* Cid del Prado Vera & Miranda, 2008. However, this species can also parasitise *Amaranthus hybridus* (Hernandez Gomez *et al.*, 2017). Hosts of *C. radiale* Chizhov, Udalova & Nasonova, 2008 described from Russia are unknown. Most *Cactodera* species have been described from the Americas, only *C. estonica* (Kirjanova & Krall, 1963) and *C. radiale* from the Palaearctic region. The type species *C. cacti* (Filipjev & Schuurmans Stekhoven, 1941) was described from cactus plants from a glasshouse in The Netherlands.

***Dolichodera* Mulvey & Ebsary, 1980**

According to the original description of *D. fluvialis* Mulvey & Ebsary, 1980 three lateral incisures in J2, but re-examination by Luc *et al.* (1988) revealed presence of four incisures in each lateral field; phasmids small without lens-like structure; males unknown. Only *Spartina pectinata* (Poaceae) is known as host (Ebsary & Eveleigh, 1983). The species is known from Canada only.

***Globodera* Skarbilovich, 1959**

Four incisures in each lateral field in both J2 and males; phasmids minute in J2, absent in males; spicules distally pointed. Three species groups can be distinguished in this genus based on host ranges and assumed geographical dispersal of their species. These groups are named after their longest known species:

1) *Rostochiensis* group, with currently seven valid species and hosts exclusively in Solanaceae (Solanales) and originated in the Americas. Several of the species recently dispersed worldwide, probably almost exclusively by human activities.

2) *Millefolii* group, with presently two valid species, viz *G. artemisiae* (syn. *G. hypolysi*), *G. millefolii* (syn. *G. achilleae*), and an undescribed species from Portugal (Sabo *et al.*, 2002). All of them are indigenous in the present Palaearctic faunal region, with hosts restricted to members of the family Asteraceae (Asterales).

3) *Zelandica* group, with *G. zelandica* Wouts, 1984, two undescribed species from New Zealand (Subbotin *et al.*, 2010a), and three species recently described from South Africa, *G. capensis* Knoetze, Swart & Tiedt, 2013, *G. agulhasensis* Knoetze,

Swart, Wentzel & Tiedt, 2017 and *G. sandveldensis* Knoetze, Swart, Wentzel & Tiedt, 2017. Hosts of *G. zelandica* are the trees *Fuchsia excorticata* (Onagraceae, Myrtales), *Sophora microphylla* (Fabaceae, Fabales) and *Plagianthus regius* (Malvaceae, Malvales), all three species native to New Zealand. Hosts of the two undescribed species from New Zealand are unknown; they were mainly recovered from rhizosphere soil of *Pentachondra pumila* (Ericaceae, Ericales) and *Acaena* sp. (Rosaceae, Rosales) from sites in alpine and subalpine areas of the South and the North Island, where no Solanaceae and only exceptionally Asteraceae were present (Wouts & Sturhan, unpubl.). The hosts of *G. capensis* and *G. sandveldensis* are unknown, but probably not belonging to Solanaceae; the only known host of *G. agulhasensis* is *Senecio burchelli* (Asteraceae). Species of the *Zelandica* and the *Millefolii* species groups are arranged in the same subclade in molecular studies conducted by Subbotin *et al.* (2011) and Knoetze *et al.* (2017a, b). However, for 'practical' purposes, it is proposed in the present paper to consider these two groups (*Millefolii* and polyphagous *Zelandica*) as separate entities.

The position of the imperfectly known species *G. mali* (Kirjanova & Borisenko, 1975), described from apple, *Malus domestica* (Rosaceae, Rosales), in Kazakhstan, remains unresolved.

***Heterodera* Schmidt, 1871**

Detailed data on this genus and the intrageneric species groups distinguished in *Heterodera* are given and discussed separately below.

***Paradolichodera* Sturhan, Wouts & Subbotin, 2007**

Lateral incisures irregular as shown by SEM studies of the extremely slender J2 of the only species in the genus, *P. tenuissima*; males with four incisures in each lateral field; phasmids in J2 punctiform without lens-like structure, absent in males; spicules tip rounded. Described from *Eleocharis gracilis* (Cyperaceae, Poales) growing at a coastal lagoon in New Zealand.

***Punctodera* Mulvey & Stone, 1976**

Four incisures in each lateral field in both J2 and males; phasmids small and punctiform in J2, absent in males; spicules distally pointed. Hosts of the four species described are exclusively members of Poaceae (Poales). *Punctodera punctata* (Thorne, 1928) and *P. matadorensis* Mulvey & Stone, 1976 were described from Canada, *P. chalcensis* Stone,

Sosa Moss & Mulvey, 1976 from Mexico, *P. stonei* Brzeski, 1998 from Europe, but recently reported also from Canada (see below).

***Vittatidera* Bernard, Handoo, Powers, Donald & Heinz, 2010**

Four incisures in each lateral field in both J2 and males of *V. zeaphila*, described from Tennessee, USA. Phasmids minute, midway between anus and tail tip in J2, not mentioned and depicted in males; spicules with bifid tips. The only known host is maize (Poaceae, Poales).

The genus *Heterodera* and its species groups

The genus contains the highest number of described and valid species (85) among the genera in Heteroderidae. Species groups in *Heterodera* have been distinguished and designated for a long time (Mulvey, 1972; many subsequent publications). Such groups were distinguished first exclusively based on cyst characteristics. Some of these species groups were later raised to the rank of genera (*Cactodera*, *Globodera*, *Punctodera*), which were validated by biochemical and molecular data. Other species groups, such as *Bidera*, *Ephippiodera* and more recently *Afenestrata*, were only temporarily considered as separate genera and subsequently returned to the genus *Heterodera*. Subbotin *et al.* (2010a) recognised seven species groups in *Heterodera*: *Afenestrata*, *Avenae*, *Cyperi*, *Goettingiana*, *Humuli*, *Sacchari* and *Schachtii* groups and presented a brief characterisation of each group, mainly based upon cyst characters, but included partially also the numbers of incisures in lateral fields of J2 and plants known as hosts. Molecular and biochemical studies of individual species placed in each group revealed close relationships. However, most of the known *Heterodera* species have been tentatively attributed to one of the species groups mainly on the basis of cyst characteristics only. The species groups and species arranged in these groups are critically reviewed below, some additional groups are proposed and several species are transferred to other species groups. Congruence between genetic and morphological characters was taken into consideration in proposing classification changes of these species groups. Results are summarised in Table 2.

***Afenestrata* group.** Based on results of morphological and molecular studies Mundo-Ocampo *et al.* (2008) synonymised the genus *Afenestrata* with *Heterodera* and placed six species,

Table 2. Number of incisures in lateral fields of J2 and males, shape of phasmids in J2, and plant hosts of *Heterodera* species groups and some individual species not placed into any group (*H. sojae* has not been included). Phasmids without lens-like ampulla are designated as “small”.

Species groups/species (number of species)	Lateral incisures		Phasmids	Host orders (families)
	J2	♂	J2	
<i>Sacchari</i> group (8)	3	3	lens	Poales (Poaceae)
<i>Koreana</i> group (4)	3	3	small lens	Poales (Poaceae)
<i>Cyperi</i> group (11)	3	4	small	Poales (Poaceae, Cyperaceae), Zingiberales (Musaceae)
<i>Cardiolata</i> group (4)	3	4	small	Poales (Poaceae)
<i>Orientalis</i> group (3)	4	4	small	Poales (Poaceae, Cyperaceae)
<i>Avenae</i> group (12)	4	4	lens	Poales (Poaceae)
<i>H. skohensis</i>	4	4	small	Poales (Poaceae)
<i>H. zaeae</i>	4	4	small	Poales (Poaceae)
<i>Goettingiana</i> group (16)	4	4	small	Saxifragales, Myrtales, Fabales, Malpighiales, Fagales, Rosales, Brassicales, Lamiales, Apiales
<i>Humuli</i> group (6)	4	4	small	Caryophyllales, Rosales
<i>Schachtii</i> group (16)	4	4	small	Caryophyllales, Fabales, Rosales, Brassicales, Lamiales etc.
<i>H. salixophila</i>	4	4	small	Malpighiales
<i>H. spinicauda</i>	4	(no ♂)	small	Unknown

within an *Afenestrata* group which they regarded as paraphyletic within *Heterodera*. The more recently described species *H. hainanensis* Zhuo, Wang, Ye Peng & Liao, 2013 was added as the seventh species to this group, which is characterised by cysts lacking a vulval fenestration. On the basis of juvenile and male morphological characters and supported by the molecular analyses of Mundo-Ocampo *et al.* (2008) and, in particular, those of Zhuo *et al.* (2013), the present author proposes the separation of the *Afenestrata* group into two distinct species groups, both named after the best characterised species in each group:

1) *Koreana* group – Four species characterised by three incisures in the lateral fields of J2 are placed in this group: *H. axonopi* (Souza, 1996), *H. bamboosi* (Kaushal & Swarup, 1988), *H. hainanensis* Zhuo *et al.*, 2013, and *H. koreana* (Vovlas, Lamberti & Choo, 1992). The latter two species were characterised molecularly by Zhuo *et al.* (2013, 2014b). Males of *H. bamboosi* with three lateral incisures; males of the other three species unknown. Phasmids in J2 mostly reported as pore-like, but lens-like in *H. koreana* as observed by the present author during studies of paratype J2 and other specimens collected in a nature reserve in Thailand (Sturhan, 2010). In specimens from Florida populations used for morphological and

molecular studies by Mundo-Ocampo *et al.* (2008) and in specimens from Iran only occasionally lens-like structures were seen (Inserra & Tanha Maafi, pers. comm.). Weakly lens-like extensions of the phasmidial ducts also were observed in J2 of *Heterodera* sp. A and *Heterodera* sp. B, found in several natural forests in Vietnam, and both morphologically close to *H. koreana* and *H. bamboosi* (Nguyen *et al.*, 2011). Males of *Heterodera* sp. A had lateral fields with three incisures, as it was observed in males recovered by the present author in a nature reserve in Thailand. Males from Vietnam and Thailand had a distinct cloacal tubus, which is absent in *H. bamboosi* (Kashual & Swarup, 1988) according to the original description. Three of the described species and the populations from Vietnam and Thailand, which were not definitely identified to one of the described species, had bamboo species as hosts or were recovered from the rhizosphere of various bamboo species (Poaceae); only *H. axonopi* described from Brazil has *Axonopus marginatus* (Poaceae) as host.

2) *Orientalis* group – It contains the three species: *H. africana* (Luc, Germani & Netcher, 1973), *H. orientalis* (Kazachenko, 1989) and *H. saccharophila* Mundo-Ocampo, Troccoli, Subbotin, Del Cid, Baldwin & Inserra, 2008 (= *Afenestrata sacchari* Kaushal & Swarup, 2008), which are

mainly characterised by the presence of four incisures in each lateral field in both J2 and males (males unknown in *H. orientalis*), punctiform phasmids in the J2 (not reported for *H. saccharophila*), and presence of a long cloacal tubus in the males (*H. africana* and *H. saccharophila*). Kleynhans (1992) observed only occasionally three lateral incisures in J2 of *H. africana*. Subbotin *et al.* (2010a) incorrectly reported presence of three incisures in both J2 and males of this species. In molecular studies, only *H. orientalis* isolates of different origin were included so far (Mundo-Ocampo *et al.*, 2008). Hosts of all three species are Poaceae, although *H. orientalis* parasitises also a *Carex* species. *Heterodera africana* was described from Africa, *H. saccharophila* from India and *H. orientalis* from the Far East of Russia. The populations of *H. orientalis* from Florida and Guatemala, which were used for studies by Mundo-Ocampo *et al.* (2008), were from imported plants.

Avenae group. Subbotin *et al.* (2010a) placed eleven species in this group, to which recently *H. sturhani* Subbotin, 2015 was added as the 12th species. Four longitudinal incisures present in each lateral field of J2, but outer incisures mostly less developed and occasionally indistinct in the ten species of the *avenae* complex, but generally well developed and distinct along the body in the two species of the *latipons* complex, *H. latipons* Franklin, 1969 and *H. hordecalis* Andersson, 1975. Phasmids distinct, lens-like in all 12 species, situated a few annuli posterior to the anus; males of all species with four incisures in each lateral field; tips of spicules notched. Hosts are exclusively cereals and grasses of Poaceae (Poales). Ten of the species were described from Eurasia. Records from few other geographical regions should be considered as ‘results’ of subsequent dispersals. Among these is the dissemination of *H. avenae* to Australia, which is assumed to have happened in the 1800s (Riley & McKay, 2009). Similarly, *H. australis* Subbotin, Rumpfenhorst, Sturhan & Moens, 2002, originally described from the southern regions of Australia and reported recently also from China (Subbotin, 2015), might have been introduced and subsequently established in Australia. Records of *H. aucklandica* Wouts & Sturhan, 1996 in Belgium and UK (Subbotin *et al.*, 2003) may indicate that this species described and known from very few sites within or close to towns in New Zealand (Wouts & Sturhan, 1996; unpubl. recent observations), is not a New Zealand endemite, but has been introduced to this remote country.

Cardiolata group. Subbotin *et al.* (2010a) placed *H. cardiolata* Kirjanova & Ivanova, 1969 (syn. *H.*

cynodontis Shahina & Maqbool, 1989), *H. graminis* Stynes, 1971, *H. longicolla* Golden & Dickerson, 1973 and *H. phragmitidis* Kazachenko, 1986 in a ‘*H. cardiolata* species complex’ within the *Cyperi* group. In molecular studies of Subbotin *et al.* (2001), Tanha Maafi *et al.* (2003), Mundo-Ocampo *et al.* (2008), Ma *et al.* (2008) and Wang *et al.* (2013), *H. cardiolata* clustered with *H. bifenestra* Cooper, 1955, which had not been placed by Subbotin *et al.* (2010a) into any species group; this species is here tentatively added to the *Cardiolata* group. Both *H. cardiolata* (*H. cynodontis*) and *H. bifenestra* were arranged in a subclade with species formerly placed in the *Afenestrata* group (now: *Koreana* and *Orientalis* species groups, see above).

In the five species mentioned above, J2 have three incisures in each lateral field. Males in four of the species have four lateral incisures, but males of *H. longicolla* only three. Phasmids of J2 have been described as very small, pore-like or ‘not visible’ in four of the species, but as ‘distinct’ in *H. longicolla*, which is tentatively transferred here to the *Sacchari* group (see below). Because the remaining four species (*H. cardiolata*, *H. graminis*, *H. phragmitidis*, *H. bifenestra*) are arranged in a clade well separated from species retained in the *Cyperi* group, a separate *Cardiolata* group is proposed. The justification of erecting a *Cardiolata* group needs further studies. The inclusion of *H. bifenestra* in this group may be controversial because it differs distinctly from the other species by cyst characteristics. Hosts of all species are Poaceae; type host of both *H. cardiolata* and *H. graminis* is *Cynodon dactylon*. Narbaev (1987) considered *H. graminis* as synonymous with *H. cardiolata*. The four species tentatively included in this group were described from Europe, Tajikistan, Russian Far East and Australia.

Cyperi group. Subbotin *et al.* (2010a) placed 14 species in this group to which the more recently described species *H. fengi* Wang, Zhuo, Ye, Zhang, Peng & Liao, 2013 and *H. guandongensis* Zhuo, Wang, Zhang & Liao, 2014 were added. The species *H. cardiolata*, *H. graminis* and *H. phragmitidis* of this group are transferred here to the *Cardiolata* group (see above) and *H. graminophila* Golden & Birchfield, 1972 and *H. longicolla* to the *Sacchari* group (see below).

Second-stage juveniles of all eleven species remaining in the *Cyperi* group show three incisures in each lateral field, but occasionally four incisures seen in *H. mothi* Khan & Husain, 1965 and *H. pakistanensis* Maqbool & Shahina, 1986. Males with four incisures in *H. cyperi* Golden, Rau & Cobb, 1962 sometimes appearing as three lines.

Males are unknown in *H. canadensis* Mulvey, 1979 and *H. delvii* Jairajpuri, Khan, Setty & Govinda, 1976. Phasmids of J2 appear to be generally small and indistinct. However, in the original descriptions of *H. oryzicola* Rao & Jayaprakash, 1978 and *H. raskii* Basnet & Jayaprakash, 1984 these structures were depicted as fairly large. Presence of a cloacal tubus is known from males of *H. fengi* and *H. oryzae* Luc & Brizuela, 1961. In molecular analyses, *H. cyperi* clustered with *H. elachista* Ohshima, 1974, *H. fengi*, *H. guangdongensis*, *H. mothi* and *H. oryzicola* (Subbotin *et al.*, 2001; Tanha Maafi *et al.*, 2003; Mundo-Ocampo *et al.*, 2008; Wang *et al.*, 2013; Zhuo *et al.*, 2014b).

Hosts of *H. canadensis*, *H. cyperi* and *H. raskii* are Cyperaceae (Poales), hosts of the other eight species are Poaceae (Poales). Besides Poaceae, bananas, *Musa* spp. (Musaceae, Zingiberales) were reported as hosts of *H. oryzae* and *H. oryzicola*. *Heterodera cyperi* was described from Florida, *H. canadensis* from Canada, *H. oryzicola* from Africa; the other eight species were described from South and East Asia.

Goettingiana group. Subbotin *et al.* (2010a) arranged 16 *Heterodera* species in this group, mainly based on cyst characteristics and only seven species with supporting biochemical or molecular characterisation. Several of the species appear to be incorrectly placed in the *Goettingiana* group; *H. turangae* Narbaev, 1988 and *H. uzbekistanica* Narbaev, 1980, both parasitising members of the family Salicaceae (Malpighiales), might be better arranged in the *Humuli* group, because in cyst characters they are closer to species in this group (Sturhan, 2010).

Second-stage juveniles and males with four incisures in each lateral field; phasmids in J2 pore-like; spicules distally notched. Hosts are from Saxifragaceae (Saxifragales), Onagraceae (Myrtales), Fabaceae (Fabales), Salicaceae (Malpighiales), Betulaceae (Fagales), Rosaceae (Rosales), Urticaceae (Rosales), Brassicaceae (Brassicales), Lamiaceae and Plantaginaceae (Lamiales), Apiaceae (Apiales). All 16 species were described from Eurasia and only a few of these were subsequently recorded for other geographical regions.

Humuli group. Six species were placed in this group by Subbotin *et al.* (2010a). Their relationships are well supported by morphological and molecular data. All species with four incisures in each lateral field in J2 and males; phasmids of J2 punctiform; spicules tip notched. Hosts of *H. humuli* Filipjev, 1934, *H. fici* Kirjanova, 1954, *H. ripae* Subbotin, Sturhan, Rumpfenhorst & Moens, 2003 and *H.*

vallicola Eroshenko, Subbotin & Kazachenko, 2001 are from species belonging to the families Cannabaceae, Moraceae, Ulmaceae and Urticaceae, all in the order Rosales. Type and only known host of *H. litoralis* Wouts & Sturhan, 1996 is *Sarcocornia quinqueflora* (Amaranthaceae, Caryophyllales). The only reliable host reported for *H. turcomanica* Kirjanova & Shagalina, 1965 is *Calligonum* sp. (Polygonaceae, Caryophyllales) (Sturhan & Wouts, 1995). The species *H. fici*, *H. humuli*, *H. ripae*, *H. turcomanica* and *H. vallicola* were described from Eurasia and only the first two species have been recorded also from other regions. *Heterodera litoralis* is known from a few coastal sites around Auckland and Nelson, New Zealand (Wouts & Sturhan, 1996).

Sacchari group. Subbotin *et al.* (2010a) placed six species to this group. Molecular analyses indicated close relationships for *H. sacchari* Luc & Merny, 1963, *H. goldeni* Handoo & Ibrahim, 2002, *H. sinensis* Chen & Zheng, 1994 and *H. sorghi* Jain, Sethi, Swarup & Srivastava, 1982 (Tanha Maafi *et al.*, 2007; Mundo-Ocampo *et al.*, 2008; Subbotin *et al.*, 2010b), while *H. gambiensis* Merny & Netscher, 1976 and *H. leuceilyma* Di Edwardo & Perry, 1964 have not been included in such studies because no topotype material of these two species to be used for molecular analyses has been found so far. Tentatively, *H. longicolla* and *H. graminophila* are transferred here from the *Cyperi* group to the *Sacchari* group because of shared J2 and male characters (lateral fields in males with three incisures, phasmids of J2 distinct and lens-like).

In the eight species placed in the *Sacchari* group now, both J2 and males have three incisures in each lateral field (occasionally four seen in males of *H. longicolla*). Phasmids in J2 appear to be mostly distinct and more or less lens-like; they were described or depicted as prominent in five of the species (original descriptions; Netscher *et al.*, 1969; Tanha Maafi *et al.*, 2007). In original descriptions of *H. sorghi* and *H. gambiensis*, J2 phasmids are located closely posterior to the anus and are lens-like in shape. However, a lens-like swelling of the phasmideal duct was less distinct in *H. sorghi*, which had a basal position in a molecular tree of the *Sacchari* group (Tanha Maafi *et al.*, 2007). No information on phasmid size of J2 is available for *H. sinensis*. Males mostly with a cloacal tubus, spicules tip described or depicted as blunt or crenate. The morphological characterisation of the *Sacchari* group by Subbotin *et al.* (2010a), mainly based on cyst characters such as presence of finger-like projections of the bullae, is no longer valid because these structures are only known from three of the

species. Furthermore, bullae are absent in three of the eight species in this group. Hosts of all species in this group are Poaceae. *Heterodera sacchari*, *H. gambiensis* and *H. goldeni* were described from Africa, *H. leuceilyma*, *H. graminophila* and *H. longicolla* from USA, *H. sorghi* from India and *H. sinensis* from China.

Schachtii group. All 16 species currently placed in this group (Subbotin *et al.*, 2010a) with four incisures in each lateral field of J2, likewise in all males described; phasmids of J2 generally pore-like; spicules tips described as notched or dentate. Hosts are known from Caryophyllales, Fabales, Rosales, Brassicales, Lamiales and other orders of dicotyledon plants. The validity of *H. agrostis* Kazachenko, 1993, reported from *Agrostis tenuis* (Poaceae) in Russia, needs confirmation (Subbotin *et al.*, 2010a). *Heterodera lespedezae* Golden & Cobb, 1963 is known from USA only (described from field soil). All other species were described from Eurasia and appear to be still restricted in their occurrence to this area; only *H. schachtii* Schmidt, 1871, *H. trifolii* Goffart, 1932 and *H. glycines* Ichinohe, 1952 are widely dispersed.

Heterodera species not placed in any of the species groups. Five *Heterodera* species had not been attributed to any species group by Subbotin *et al.* (2010a). One of these, *H. bifenestra*, is tentatively placed here in the *Cardiolata* species group (see above), the remaining four species are mentioned below. *Heterodera sojae* Kang, Eun, Ha, Kim, Park, Kim & Choi, 2016, recently described as a parasite of soybean in Korea, could not be included in the studies of the present paper because of inappropriate morphological characterisation (no information on incisures in lateral fields and phasmids in J2 and males, no precise description of spicules tip, vague data on bullae and underbridge in the cysts, cyst fenestration not depicted) and inadequate differential diagnosis. Molecular analyses placed this species close to the *Cyperi* group (Kang *et al.*, 2016), which contains species that parasitise exclusively monocots.

Heterodera salixophila Kirjanova, 1969: Second-stage juveniles and males with four incisures in each lateral field; phasmids in J2 pore-like, small but distinct, and located in about mid-tail region; spicules tip dentate. Hosts are *Salix* spp. and *Populus* spp. (Salicaceae, Malpighiales). Described from the Baltic coast of Russia, recorded also from Ukraine, Slovakia, Poland, Estonia, Germany and Belgium. Phylogenetic analyses mostly placed *H. salixophila* close to the *Humuli* group (Ma *et al.*, 2008; Subbotin *et al.*, 2001, 2010b).

Heterodera skohensis Kaushal, Sharma & Singh, 2000: Second-stage juveniles with four incisures in the lateral fields; phasmids pore-like, located near or just anterior to anus level (according to original description). Males are unknown. This species was described in India, where it parasitises *Oryza sativa* (Poaceae, Poales). No biochemical and molecular data are available.

Heterodera spinicauda Wouts, Schoemaker, Sturhan & Burrows, 1995: J2 with four incisures in the lateral fields and small phasmids without a lens-like structure in cuticle, situated in mid-tail region. Males are unknown. The type population was found around *Phragmites australis* and “other permanent vegetation” close to the coast in the south-western part of The Netherlands. It appears unlikely that reed is the host of this species, which is considered by the present author as a neozoon of unknown origin. The species had first been considered as a member of the *Avenae* group but was later excluded from this group, mainly because of the pore-like shape of the J2 phasmids, which are moderately lens-like in the *Avenae* group. No biochemical and molecular data are available. The *Heterodera* species reported by Kaushal (1996) from India as *H. spinicauda* was later described as *H. skohensis* (Kaushal *et al.*, 2000).

Heterodera zae Koshy, Swarup & Sethi, 1971: Both J2 and males with four incisures in the lateral fields; phasmid opening of J2 very small but conspicuous; spicules with pointed tips, non-dentate. Described from *Zea mays* (Poaceae, Poales) in India and reported from some other countries; this species parasitises many other members of Poaceae. Records of various dicotyledonous plants as hosts require verification. In phylogenetic analyses, *H. zae* could not be placed into any of the distinguished species groups but was mostly close to *H. salixophila* and the *Humuli* group (Subbotin *et al.*, 2010b; Zhuo *et al.*, 2013; Sekimoto *et al.*, 2017).

Undescribed or unidentified taxa and new records. Heteroderid juveniles and occasionally cysts, which could not be identified to species because of only limited sampling material available, were found by the author at many localities and in several countries, among others, *Heterodera* J2 with three lateral incisures in lateral fields in Italy, Morocco, Tunisia and Turkey. Only of some of the unidentified and, in part, probably undescribed species or genera are listed with some detailed information below. Some more material and other sampling data are available for these unidentified heteroderids. Preserved slide material also is retained in DNST at Julius Kühn-Institut in Münster. Details about the sampling sites are given

below to enable and facilitate eventual future re-collecting.

***Cryphodera* sp. from Borneo (unpubl.)**

Besides many heteroderid juveniles of an unidentified genus, which were isolated from a soil sample collected close to a natural rainforest in Sarawak, Malaysia (see below), a single second-stage juvenile was found with morphological characters in agreement with that of *Cryphodera*: lateral fields with three incisures, phasmids lens-like, high pointed arches of the basal plate of the cephalic framework. In the following characters the second-stage juvenile differs from all described *Cryphodera* species and several populations briefly characterised from Vietnam (Nguyen *et al.*, 2011): body almost straight, 435 μm long, cephalic region only weakly offset, tail slender-conical; stylet 36 μm long with stylet base 6 μm in diameter, knobs weakly concave and rather flat, DGO 6.7 μm behind stylet base; outer lateral incisures crenate, inner incisure less developed, cuticle annuli 1.4 μm wide at midbody; tail 79 μm long, H = 49 μm , with offset terminal mucron, phasmids situated 69 μm from tail end.

***Heterodera* sp. from Canary Islands (unpubl.)**

Cysts, females, males and J2 of a *Heterodera* species with typical characters of the *Goettingiana* group were recovered by the author from soil samples taken mid-March 1966 in the laurel forest Parque Nacional de Garajonay close to the road leading to Las Hayas and Chipude in the island La Gomera, and in a small laurel stand above the settlement Frontera in the island El Hierro. White females with an egg sac were found attached to the roots of *Geranium purpureum* and *G. rotundifolium*, but not on other plants growing at the sampling sites. Members of the family Geraniaceae (Geraniales) appear to be unknown as hosts of heteroderids so far.

Main morphological characters. Cysts lemon-shaped, ambifenestrate, underbridge very weak, no bullae. – Males: Stylet = 29, 30, 31 μm , spicules = 34 μm . J2 (n = 10): L = 440 (410-475) μm , tail = 57 (53-61) μm , H = 30 (25-34) μm , stylet = 27 (26-29) μm ; 5-6 small lip annuli, stylet knobs weakly concave, lateral fields with four incisures and irregular areolation, tail end narrow, phasmids small but distinct.

***Heterodera* sp. from Tunisia (unpubl.)**

Second-stage juveniles, males and cysts of an unidentified species of the *Schachtii* group were isolated from a soil sample collected by the author

in April 1984 north-east of Nekta east of the road to Sfax. The collective sample was taken from the rhizosphere of *Arthrocnemum* sp. (Chenopodiaceae) growing on a coastal plain with sandy to fine-textured moist soil; no other plants growing at the sampling site. Stylet of males 28-29 μm long, stylet of J2 around 27-28 μm . J2 and males with four lateral incisures, phasmids of J2 small.

***Heterodera* sp. from New Zealand (unpubl.)**

Cysts, males and J2 of this unidentified *Heterodera* species were isolated from soil samples taken by the author in November 2005 from around two unidentified grasses (Poaceae) in coastal dunes at Whatipu west of Auckland and at a site west of Helensville, and from coastal vegetation at Waihi Beach, Bay of Plenty, all three sites located in the northern part of North Island.

Main morphological characters. Cysts: Lemon-shaped with projecting vulval cone, dark brown, afenestrate but appearing ambifenestrate at lower vulval level, dark underbridge with central swelling, bullae present at some distance from vulval slit. Males: Body C-shaped, twisted; lateral fields with three incisures, areolated; cephalic region offset, with four lip annuli and perioral disc; stylet = 32.5-35 μm long, stylet base 6.5 μm in diameter, knobs weakly concave; spicules about 39 μm long. J2: L = 580-675 μm , stylet = 29-31 μm , tail = 65-79 μm , H = 38-47 μm ; lateral fields with three distinct incisures, areolated; stylet cone shorter than posterior part of stylet, stylet knobs thick and distinctly concave, stylet base 6.5-7 μm in diameter; cephalic region offset, with two annuli and elongate labial disc; pharyngeal glands extending for five to nine body widths posterior to the pharyngo-intestinal junction; tail bluntly rounded at tip, phasmids large, situated 3-5 annuli posterior to the anus level.

In the number of incisures in the lateral fields in J2 and males, size of phasmids in J2, presence of a central thickening of the underbridge in cysts, and grasses as putative hosts, this species is close to members of the *H. sacchari* species group. There is, however, a distinct surface cover with wrinkled cuticle markings on both sides of the vulval slit, and the morphometrics of J2 are greater, especially the stylet length.

***Hylonema* sp. from Cameroon (unpubl.)**

In one of four soil samples collected by the author in a rainforest in the south of Cameroon, south of Kribi, in March 1994, some heteroderid J2 were found (together with juveniles of an undescribed *Meloidodera* species, see below), with

morphological characters close to those of *Hylonema ivorense* Luc, Taylor & Cadet, 1978 described from a forest reserve near Abidjan, Ivory Coast.

Main morphological characters of J2: L = 550-580 μm , body and tail straight or slightly curved to the ventral side, anterior end occasionally with distinct narrowing at level of middle of stylet; body annuli at mid-body almost 2 μm in diameter; lateral fields with three incisures, irregularly areolated, in particular, at anterior and posterior ends, outer lateral incisures extending to mid-stylet region, where the lateral fields are widened to about half corresponding body diameter; stylet 34-37.5 μm long, conus and basal part of the same length, with basal stylet portion 6-7 μm in diameter and knobs weakly concave, dorsal gland orifice 4-5 μm posterior to the knobs; lip region rounded and offset by incisure, 10 μm wide and 5 μm high, with 4-6 annuli; head skeleton very strong, with high arches; valve of median pharyngeal bulb small, isthmus very slender, pharyngeal glands extending about two corresponding body widths posterior to the pharyngo-intestinal junction; tail 60-63 μm long, H = 34-38 μm , tail in posterior part coarsely annulated, with finely rounded terminus; phasmid with distinct opening, but duct without lens-like extension, situated *ca* 8 annuli posterior to the anus.

***Meloidodera* sp. from Cameroon (unpubl.)**

Heteroderid second-stage juveniles recovered from four soil samples collected by the author in a rainforest in the southern region of Cameroon, south of Kribi, were tentatively identified as representatives of *Meloidodera*, but cannot be attributed to any described species (or species of any other heteroderid genera).

Main morphological characters of J2: Body 490-560 μm long, heat-relaxed specimens C-shaped; lateral fields with four incisures, areolated; stylet 30-31 μm long with slightly forwardly directed relatively flat knobs; lip region with five annuli and indistinct labial disc, stoma opening situated in a depression; valve of median pharyngeal bulb rather small, pharyngeal glands relatively short (*ca.* 2 body widths long); tail = 50-52 μm , H = 29-30 μm , tail more or less hook-like, with finer annulation in its posterior part and extending to almost tail terminus; phasmid opening very large, 6-8 annuli posterior to the anus.

***Meloidodera* sp. from Ethiopia (unpubl.)**

From four collective soil samples taken from around coffee plants at three localities in different regions of Ethiopia, heteroderid J2 and males were

isolated and tentatively identified as *Heterodera* sp. (Mekete, 2007; Mekete *et al.*, 2008; Mekete, pers. comm.). Subsequent morphological studies by the present author revealed that the nematodes can probably be attributed to the genus *Meloidodera* and are obviously representing a still undescribed species. It is not known, whether *Coffea arabica*, shade trees or other plants growing close to coffee plants are hosts.

Main diagnostic characters. J2: L = 390-450 μm , body of heat-relaxed specimens slightly C-shaped; lateral fields with four incisures with the inner two often closer together, areolated; stylet 29-31 μm long, knobs with concave anterior surfaces, basal part of stylet *ca.* 6 μm in diameter; lip region weakly offset, with three annuli and a wide, not offset perioral disc, cephalic framework heavy; dorsal pharyngeal gland with distinct nucleus, subventral glands broadly rounded posteriorly; tail conoid with indistinct annulation towards the finely rounded tip, 44-50 μm long, hyaline part 20-28 μm long; phasmids large lens-like, 5-6 annuli posterior to the anus. Males: Body 450 and 460 μm long, twisted; cephalic region with a broad posterior annulus, a second annulus of about half this diameter and a wide offset labial disc; stylet 24-25 μm long with relatively small and flat knobs; valve of median pharyngeal bulb small or indistinct; testis well developed; phasmids distinct, lens-like.

***Sarisodera* sp. from Vietnam = *Genus indet. A* of Nguyen *et al.* (2011)**

Heteroderid J2 recovered in two natural forests in the northern part of Vietnam, with four equally spaced incisures in each lateral field and large phasmids with lens-like extension in the cuticle situated 7-10 annuli posterior to the anus, as their main morphological characteristics, could not be attributed to any of the known genera in Heteroderidae.

Morphological details in addition to those mentioned by Nguyen *et al.* (2011): Stylet conus slightly longer than shaft plus knobs; labial framework with high arches extending to almost half length of the lip region; procorpus of pharynx constricted anterior to the median bulb, isthmus narrow; pharyngeal glands filling body cavity, extending 4-5 corresponding body widths posterior to the pharyngo-intestinal junction, broadly rounded at posterior end; cuticle annuli at mid-body about 1.4 μm in diameter; phasmids 46-64 μm from tail terminus. For more details, see Nguyen *et al.* (2011).

In most characters the Vietnam specimens closely agree with those of *Sarisodera hydrophila*

described from California (Wouts & Sher, 1971) and of a population recorded from Korea (Choi & Kim, 2001); they are considered here as representatives of the genus *Sarisodera*. Differences in morphometrics and few other characteristics indicate that eventually several species can be distinguished in the genus. Mean measurements of J2 from California/Korea/Vietnam (n = 25/17/10, respectively): L = 579/490/464 μm , tail = 54/55.2/66 μm , H = 31/18.7/39 μm , stylet = 40/34.6/36 μm . Wouts & Sher (1971) estimated presence of at least five *Sarisodera* species in California.

***Verutus* sp. from Germany**

Females, males and J2 attributed to the genus *Verutus* were recovered from moist biotopes at many localities in Germany, ranging from Schleswig-Holstein in the north to Bayern in the south, with *Scirpus sylvaticus* identified as host. These specimens from Germany can be distinguished by some morphological characters from the two described *Verutus* species known from USA (Sturhan, 2006, 2014b). In J2 and males, four incisures are present in each lateral field. Phasmids of J2 are small and often inconspicuous, they are lacked in males, which have spicules with broad, weakly notched tip. Subbotin *et al.* (2010b, 2017) used specimens of a population from Germany for molecular analyses; the two described *Verutus* have not been included in such studies so far. It appears justified to consider the *Verutus* populations from Germany as representatives of a separate species, which should be formally described and named. *Carex acutiformis* (Cyperaceae, Poales) has been identified as an additional host.

***Genus indet.* from Borneo (unpubl.)**

Many second-stage heteroderid juveniles isolated from a loamy soil sample collected by J. and M. Sturhan in the northern part of Borneo (Sarawak, Malaysia) from a rainforest near Gunung Mulu National Park, are characterised by the following main morphological features: Body shape similar to that of most heteroderid J2, 455-525 μm long, mostly C-shaped to semi-circular in relaxed specimens. Lateral fields with four incisures, cuticle annulation extending into both outer bands, inner band with irregular areolation; cuticle annuli at mid-body 1.5 μm wide. Lip region continuous with body contour, rounded, with five annuli; cephalic framework moderately developed. Stylet 20-22.5 μm long with rounded knobs; dorsal gland orifice 11-12 μm behind stylet base. Pharynx with oval median bulb with valve 2.5 μm in diameter located

around 50 μm behind stylet base; terminal pharyngeal lobe broadly rounded, in a more or less ventral position, extending for slightly more than one corresponding body width posterior to the pharyngo-intestinal junction. Tail elongate-conoid, 60-72 μm long, with a conspicuous 32-39 μm long hyaline portion; tail terminus sharply pointed with slightly demarcated refractive tip of 10-11 μm length. Phasmids situated 49-54 μm from tail tip, with distinct opening and without lens-like ampulla.

The juveniles studied could not be attributed to any of the known genera in Heteroderidae. The continuous lip region and the moderately developed cephalic framework suggest putative placement in the subfamily Verutinae. An orifice of the dorsal gland located at about half stylet length behind the stylet base has also been observed in second-stage juveniles of *Bilobodera flexa* Sharma & Siddiqi, 1992, described from India and in males of *B. mesoangusta* (Minagawa, 1986), described from Japan. Other morphological characters are distinctly different from those of all species known in Verutinae.

***Genus indet.* from Dominican Republic (unpubl.)**

From soil samples collected by the author in the Dominican Republic in November 1977, heteroderid J2 were isolated with the following main morphological characteristics: L = 400-470 μm , tail = 46-63 μm , H = 21-34 μm , stylet = 30-34 μm , width of stylet base = 6-6.5 μm , DGO = 2.5-3 μm . Body of heat-relaxed specimens mostly slightly bent ventrad; lip region almost continuous with body contour, 10 μm wide and 5 μm high, weakly conoid, only posterior lip annulus discernible; anterior and posterior stylet parts of equal length, knobs massive, anchor-shaped; cephalic framework heavy, with high arches of its basal part; median pharyngeal bulb and valve well developed; pharyngeal glands 2-3 corresponding body widths long, filling body cavity and broadly rounded at posterior end; lateral fields with three distinct incisures, often irregularly areolated; annuli along mid-body about 2 μm wide; tail conoid with pointed tip, coarsely annulated in its anterior part, in hyaline region almost smooth; phasmids 2-6 annuli posterior to the anus, with distinct opening and duct but without lens-like ampulla.

The J2 found cannot be attributed to any known heteroderid genus. In genera with J2 characterised by three lateral incisures and small phasmids (Tables 1 & 2) all species described so far distinctly differ in other morphological characteristics of J2, among others, in shape of the cephalic framework. The unidentified species is most probably a member

of the cystoid heteroderids and can eventually be included in Meloidoderinae.

Many juvenile specimens were isolated from rhizosphere sandy soil taken from two coconut seedlings in a long-used coconut tree nursery situated within a coconut tree plantation close to the coast at Los Yayales south-east of Nagua in the north-eastern part of the Dominican Republic, and from a collective second soil sample taken from around coconut trees growing close to the first site immediately at the edge of the littoral vegetation strip; no other plants were present at the first sampling site. However, unidentified grasses and specimens of *Ipomoea* sp. were present at the second site. From 250 ml soil samples from both sites more than 30 J2 were isolated. The findings suggest *Cocos nucifera* as a potential host; palms appear to have never been observed as heteroderid hosts so far.

Genus indet. from Thailand (unpubl.)

Cysts (n = 2): Globular with slightly projecting vulval cone, measuring 895 × 770 µm and 770 × 610 µm, dark brown, cuticle very thick with distinct punctation and with more or less distinct ridges or annuli around vulva; anus situated laterally at the vulval cone; vulval area circumfenestrate, no underbridge, few bullae-like structures may be present at some distance from fenestra. J2 (n = 12): L = 480 (440-520) µm, tail = 72 (68-77) µm, H = 50 (45-55) µm, stylet = 33 (31-34) µm; stylet cone shorter than posterior stylet part, stylet base 6 µm in diameter, stylet knobs concave; cephalic region flatly rounded, slightly offset, 10 µm in diameter and 4.5-5 µm high, 3-4 lip annuli plus labial disc; lateral fields with four incisures, inner two faint and closer together, mostly only three incisures visible in mid-body region, irregular areolation present; pharyngeal overlap ca. five body widths long; phasmids small but distinct, 6-8 annuli posterior to the anus, no lens-like structures; tail slender in terminal part. The species can eventually be attributed to the genera *Globodera* or *Cactodera*. Collected by the author in February 1999 in Khao Sok National Park, at Bang Hua Raed, southern part of Thailand, from sandy soil with various unidentified woody plants growing along the Sok River. Second-stage juveniles of the *H. koreana* species group were found in the same soil sample.

Genus indet. B from Vietnam (Nguyen *et al.*, 2011)

Second-stage juveniles and males found in soil samples collected in a mountain forest in the central part of Vietnam could not be attributed to any of the

19 currently recognised Heteroderidae genera. Main diagnostic characters of J2: Body > 600 µm long, stylet 26-28 µm, lip region not offset, with five annuli and labial disc, lateral fields with three incisures, tail long and slender with pointed tip, phasmids with distinct opening and large globular structure of 2.5 µm diameter in cuticle, 3-4 annuli posterior to the anus. Males with four indistinct lateral incisures, lateral fields areolated, stylet 26-29 µm long, spicules 39-40 µm long, with crenate tips; a long cloacal tubus present. Additional morphological details given by Nguyen *et al.* (2011).

DISCUSSION

Morphological characters. The compilation of morphological data in Tables 1 and 2 shows that three incisures in each lateral field are present in second-stage juveniles in six genera of Heteroderidae and in four species groups of *Heterodera*; four incisures are found in a higher number of genera and intrageneric groups. In males three incisures are only exceptionally present within Heteroderidae; in most cases, taxa with three incisures in J2 had four incisures in males. Similar to several Merliniidae genera, in which juveniles had fewer incisures than adults (Sturhan, 2012), the lower number of lateral incisures in juveniles is considered as a plesiomorphic character. Only in the *Zelandodera* species group of *Cryphodera* and in the *Koreana* and *Sacchari* species groups of the genus *Heterodera* the number of three incisures is retained in the males. It seems that the character ‘three incisures’ developed in different subfamilies and the species groups in *Heterodera* independently. The presence of fewer incisures in males than in juveniles has not been observed.

The number of incisures in each lateral field is in general a stable character within a species, but occasionally a splitting or amalgamation of the inner incisures has been observed in some *Heterodera* species, e.g. in *H. africana*, *H. cyperi*, *H. mothi* and *H. pakistanensis*. Within the *H. avenae* group, species of the *H. avenae* complex have mostly well developed inner incisures and indistinct outer incisures; in species of the *H. latipons* complex all four incisures in each lateral field are generally distinct along the central part of the body.

Phasmids are present and lens-like in males of *Cryphodera* and males of several *Meloidodera* species, but appear to be absent in males of all (most?) other Heteroderidae genera (Sturhan, 2016). These morphological structures are lens-like also in J2 of *Cryphodera*, some species of *Meloidodera* and in species of five genera in Ataloderinae. Phasmids

are also moderately lens-like with mostly distinct opening to the outside in J2 of three species groups of *Heterodera*. However, phasmids were often not precisely described or depicted and no distinction was made between opening and presence of a subcuticular lens-like ampulla. Verification of shape and size of phasmids is required for several heteroderid taxa.

Both morphological characters – lateral incisures and phasmids – can mostly be observed using light-microscopy and are thus of diagnostic value, at least in identifying or distinguishing genera by using morphological features. They are particularly important in cases when only J2 are available for identification. For instance, in central and northern Europe, J2 of the *H. avenae* group are easily distinguished from all other heteroderids (except *Meloidodera alni*) known to occur in this geographical region by presence of four lateral incisures plus lens-like phasmids. In the same geographical region, *Heterodera bifenestra* is the only species of Heteroderidae with only three lateral incisures in J2 (Sturhan, unpubl. key). Wouts & Weischer (1977) were among the first authors to present a key (on commonly occurring heteroderid species in Western Europe) based on selected J2 characters, such as lateral incisures and phasmids.

Head morphology of J2, which had been proposed as a valuable diagnostic character of genera (Stone, 1975, and other authors) and the number of lip annuli occasionally used in keys (Wouts & Weischer, 1977, and few other authors) have not been considered in the present studies, because these structures can be best seen only in SEM studies and are thus less suitable for (routine) light-microscopic identification. Moreover, reliable data about such characters are not available for a high number of species in Heteroderidae, and lip region patterns may be diverse within species and populations and unreliable for phylogenetic analyses (Baldwin & Powers, 1987; Baldwin & Schouest, 1990).

The shape of the tip of spicules has not been precisely described or depicted in many heteroderid species, and thus the data compiled for this character in Table 1 often require verification. There is, however, evidence that the tips of the spicules are generally pointed or bluntly rounded in certain genera (e.g. *Cryphodera*, *Globodera*, *Punctodera*) and notched in other genera (e.g. *Cactodera*, *Heterodera*). More detailed studies are needed to check the diagnostic significance of this morphological character.

The compilation of characters in Table 1 shows that the genera *Cryphodera* and *Atalodera* consist of

two species groups, each group with species having different numbers of incisures in the J2 and male lateral fields. One of these groups in *Cryphodera* coincides with the former genus *Zelandodera* described from New Zealand. Future molecular analyses including more species of both taxa will hopefully show if these differences are of diagnostic or phylogenetic significance. Obvious differences in the shape of phasmids among *Meloidodera* species might also be an indication of parphyly of this genus. In the genus *Heterodera*, species of the former *Afenestrata* group were placed into two new groups, an *Orientalis* group and a *Koreana* group, a decision based on differences in the number of lateral incisures in the J2 and supported by molecular analyses. The separation of the *Cardiolata* group from the *Cyperi* group, both with three lateral incisures in J2 and four incisures in males, was based on the results of molecular analyses. These actions increase the number of species groups in *Heterodera* to nine (Table 2). A morphological distinction of species groups in *Heterodera* using lateral incisures of J2 and males and the shape of phasmid appears often to be more reliable than using cyst characters alone. More molecular studies will hopefully support distinction of the species groups and correct placement of species within each group.

Hosts and phylogeography. Data on host ranges of species and, in particular, on geographical distribution are not only useful for a correct identification but also for the determination of the origin and phylogeny of heteroderid taxa, provided that only reliable data on hosts are used, plant ‘associations’ are excluded, only data on ‘natural’ or ‘native’ distribution are considered, and geographical records attributed to man’s activities are not included. Heteroderids dispersed by man include those in arable soils (*G. rostochiensis*, *G. pallida*, *H. avenae*, *H. schachtii*, *H. glycines* etc.) and species parasitising specific cultivated plants (e.g. *H. humuli*, *C. cacti*). The present geographical distribution of the potato cyst nematodes *G. rostochiensis* and *G. pallida* shows how fast a worldwide dispersal by man can take place!

A critical evaluation and interpretation of distribution data of genera in Heteroderidae must take into account that cysts of Heteroderinae (with their protected contents of eggs and unhatched juveniles) are more easily dispersed by wind, birds, migrating mammals and other means of dispersal than species of the ‘cystoid’ Meloidoderinae, Ataloderinae and Verutinae with females more susceptible to desiccation and often only few eggs

retained in female body. Moreover, polyphagous species will mostly become more easily established at 'new' locations or in distant and remote areas than species with narrow host ranges (e.g. *Heterodera trifolii* with widely distributed Fabales and many other plants as hosts and *Heterodera* species parasitising Poaceae vs *H. carotae* and *H. fici*). Widespread presence of potential hosts (such as Poaceae) will more effectively support an establishment and further dispersal than less widely occurring and less common potential hosts (such as Solanaceae). In previous studies on the origin of heteroderid taxa in space and time often no clear distinction was made between putative areas of 'native' occurrence and subsequent dispersal by natural means and more recently by man, particularly, in *Heterodera* species groups and other cyst-forming nematodes (Ferris, 1979).

The genera *Cryphodera* and *Meloidodera* are generally considered as ancestral heteroderids, among others, because parasitism of gymnosperms as hosts might have developed already before angiosperms developed since Cretaceous, almost 140 million years ago. *Cryphodera brinkmani*, *C. podocarp*i and *M. floridensis* have members of Coniferales as hosts. The genus *Cryphodera* is exclusively known so far from East, South-East and South Asia, Australia, and New Zealand. In India, *C. calesari* was recovered in two northern states (Bajaj *et al.*, 1989; Bajaj & Walia, 2000). In Vietnam *Cryphodera* spp. were found in eleven of the 16 natural forests studied. Three species were distinguished by molecular data, several more species by morphological characters (Nguyen *et al.*, 2011); one of these species was later considered as conspecific with *C. sinensis* (Zhuo *et al.*, 2013). The recent finding of an undescribed species in Borneo (this paper) extends the known range of distribution of the genus. *Cryphodera* may have developed in the geological period, in which Laurasia in the north was temporarily connected by a land bridge or a range of islands with the Australia/New Zealand region of Gondwanaland in the south (Fig. 1). Seven of the *Meloidodera* species considered as valid, have been described from North America (from Alaska to Mexico) and four from the Eurasian region, which may indicate a Laurasian origin of this ancestral genus. If the two African heteroderid populations mentioned in the present paper can be identified definitively as members of *Meloidodera*, this may be considered as another indication of very ancient origin, which might date back to a geological period even prior to breakup of Pangaea, around 180 million years ago (Fig. 2).

Among the Ataloderinae, *Rhizonemella sequoiae* parasitises several conifers but is known to have also *Acer* and *Alnus* as hosts. Also *Sarisodera hydrophila*, originally described from California, has a conifer (*Pinus monticola*) among its hosts (Wouts & Sher, 1971). Trees of different angiosperm families are known or assumed to be hosts of *Sarisodera* populations from California, Korea and Vietnam (see above). Not much is known of the host ranges of *Bellodera* and *Ekphymatodera*, both described from North America, and of *Hylonema* known from Africa and of *Camelodera* described from Central Asia. The genus *Atalodera* (with seven species to date) probably developed in Laurentia (now North America) and dispersed further to South America (with two species known) after unification of North and South America or even earlier through migrating birds or wind. *Atalodera crassicrustata*, described from the Aleutian Islands of Alaska, extended its distribution to the (geographically close) Russian Far East (Kazachenko, 1990) (Fig. 1). It is remarkable that four of the nine *Atalodera* species appear to parasitise exclusively grasses (Poaceae, Poales), which are considered as the youngest larger angiosperm group.

The subfamily Verutinae with the genera *Verutus* and *Bilobodera* is mostly considered as the most ancestral heteroderid taxon (Wouts, 1985; many subsequent publications; Subbotin *et al.*, 2017). Characteristics such as the absence of phasmids in males, small phasmids in J2, induction of a syncytium as host response to parasitism, and Poales as hosts of all known species (with the exception of *V. volvingentis*) appear not to support the hypothesis. The few geographical records of members of the subfamily from USA, Japan, India and Germany do not allow speculations on the putative origin of Verutinae (Fig. 3).

The genera *Betulodera*, *Dolichodera* and *Vittatidera* in the subfamily Heteroderinae, with only one species each, are known from North America only. *Paradolichodera tenuissima* was described from New Zealand (see notes below). A remarkable fact is that all *Heterodera* species with three lateral incisures in J2 have cereals or other Poaceae as hosts. Several species of the *Cyperi* group are specialised to Cyperaceae in the order Poales and some even parasitise members of the related Zingiberales. Among the species with four lateral incisures in J2, all members of the *Avenae* group are specialised to Poaceae, likewise the species *H. skohensis* and *H. zaeae*. There appear to be no reliable records that members of the *Goettingiana*, *Humuli* and *Schachtii* species groups parasitise Poaceae or other monocotyledon plants.



Fig. 3. Known distribution of the genera *Sarisodera* (■) and *Verutus* + *Bilobodera* (●).

Among the other genera in Heteroderidae five are known exclusively from Poales, and some species of *Meloidodera*, *Atalodera*, *Cactodera*, *Verutus* and *Bilobodera* are known to have Poales as hosts (Table 1).

The ability to parasitise Poales has obviously developed independently several times in *Heterodera* evolution, as well as the character ‘three incisures’ in lateral fields. This is well documented by biochemical and molecular analyses, which arrange the *Heterodera* species groups specialised to Poales in different positions in phylogenetic trees (Subbotin *et al.*, 2010b). *Heterodera* species sharing the characters ‘three incisures’ in lateral fields of J2 plus parasitism of Poales were first considered as members of a *bifenestra* species group (Sturhan, 1998), but subsequent molecular analyses arranged such species in distant clades or subclades (Mundo-Ocampo *et al.*, 2008), a fact which can be considered as an enigma.

Among the cyst-forming nematodes, which are placed in the present paper in the subfamily Heteroderinae, several authors arranged genera characterised by circumfenestrate cysts in a separate subfamily Punctoderinae and leaving only the genus *Heterodera* with bifenestrate, ambifenestrate and afenestrate cysts in Heteroderinae. Former suggestions that the genus *Globodera* in Punctoderinae originated in Gondwanaland (Stone, 1979; Sturhan, 2007) is supported by recent findings

of more species besides *G. zelandica* in New Zealand and the description of three species from South Africa. Recovery of indigenous *Globodera* species also in Australia/Tasmania may be expected. Records of *Globodera* spp. parasitising non-solanaceous plants in South America (Jatala *et al.*, 1979; several other authors) are to be confirmed (Stone, 1979). The polyphagy of the *Zelandica* group may be considered as an ancestral character and is supporting the hypothesis of Gondwana origin of *Globodera*. The *Rostochiensis* group specialised to Solanaceae probably separated early from the Gondwana group, and the species in this group considered as valid or their ancestors developed in South America and (subsequently) further diversified in North America. There appears to be no evidence of any ‘native’ occurrence of populations from this group outside the New World. The *Millefolii* group specialised to Asteraceae, which clustered with the *Zelandica* (Gondwana) species group (Subbotin *et al.*, 2011; Knoetze *et al.*, 2017a), probably separated later. Ancestors of this group eventually spread from Gondwana to Eurasia via island chains and land bridges in South-Eastern Asia (or eventually by hurricanes or migrating birds?).

The next genus to develop and diversify in Punctoderinae was *Cactodera* with 12 species described from the Americas and probably without

any reliable record of native occurrence outside this geographical region. Ancestors of the two *Cactodera* species described from Europe, *C. estonica* (Kirjanova & Krall, 1963) and *C. radicale* Chizhov, Udalova & Nasonova, 2008, might have dispersed to Europe and Asia during times of historic land connections or by long-distance dispersal by wind or migrating birds. Krall & Krall (1978) wrote that *C. estonica* ‘was found to be a tropical amphimictic species’, without giving details or references. The subsequent record of *C. estonica* in field soil in Wisconsin, USA (Norgren & Goldon, 1986), might be an indication of native occurrence of the species in North America. Whereas most of *Cactodera* species are specialised to Caryophyllales as hosts, *C. galinsogae* Tovar Soto, Cid del Prado Vera, Nicol, Evans, Sandoval Islas & Martinez Garza, 2003 parasitises Asteraceae and Poaceae, and *C. rosae* Cid del Prado Vera & Miranda, 2008 is known from barley (*Hordeum vulgare*) and pigweed (*Amaranthus hybridus*, Caryophyllales) is reported as another host (Hernandez Gomez *et al.*, 2017).

The extension of host range among *Cactodera* species to include Poaceae may have led to development of Punctoderinae genera specialised to Poales, which are among the major most recently evolved angiosperms. Three of the *Punctodera* species were described from North America, *P. stonei* from Poland. The recent discovery of the latter species in Canada (Dobosz *et al.*, 2013) is considered as evidence that also this fourth species in the genus might have developed and originated in North America.

The related genus *Dolichodera* with Poaceae as suspected hosts is known from Canada only. *Paradolichodera tenuissima*, described from a coastal lagoon in New Zealand and with Cyperaceae as hosts, is more likely an introduced species to this ‘remote’ geographical area, far away from that of related taxa, than an endemic New Zealand species. Dispersal may have taken place by ships ballast or any soil-contaminated cargo transported by ships, like the assumed disseminations of *Longidorus andalusicus* Gutiérrez-Gutiérrez *et al.*, 2013 and *Telomerlinius mellumensis* Siddiqi & Sturhan, 2014 (Sturhan, 2014a, 2015). Discovery of *P. tenuissima* may be expected in North America, where the related taxa obviously originated.

The hypothesis of Subbotin *et al.* (2011) that Punctoderinae and the North American genus *Betulodera* occupies a phylogenetically basal position in Punctoderinae and that Punctoderinae originated in North America with possible further long-distance dispersal to South America, Africa and other regions is not supported by the analysis of

phylogeography and host ranges, which most probably evolved from polyphagy to host specialisation and from ancient plant taxa to phylogenetically younger taxa parasitised by Punctoderinae, among others Poales and Solanaceae. The phylogenetic basal position of *Betulodera* in Punctoderinae has already been questioned by Bernard *et al.* (2010) and the inclusion of *Vittatidera*, described from North America and specialised to Poales, in Punctoderinae was considered as doubtful. Recent molecular studies (Zhuo *et al.*, 2014b; Subbotin *et al.*, 2017) appear to confirm that both genera cannot be considered as most ancestral representatives of Punctoderinae. Moreover, *B. betulae* is the only species in Punctoderinae with three incisures in each lateral field, and there are differences from other cyst-forming nematodes in the number of chromosomes (Triantaphyllou, 1970).

In *Heterodera*, the only other genus among the cyst nematodes, the *Schachtii*, *Goettingiana* and *Humuli* species groups are polyphagous, with dicotyledonous plants as hosts; there appears to be no reliable record of Poales parasitised. All other species groups in the genus *Heterodera* parasitise monocotyledon plants, mostly members of Poaceae (Table 2). In phylogenetic trees based on molecular analyses, the *Goettingiana* occupies mostly a basal position (Subbotin *et al.*, 2001). It is a remarkable fact that all 16 species currently placed in this group were described from Eurasia and records from other geographical regions are relatively few. Similarly, almost all species in the *Schachtii* group were described from the Palaearctic region and records of few of the species in other regions might be a result of dispersal. Five of the six species in the *Humuli* group were also described from Eurasia; *H. litoralis* is known only from New Zealand, where the species was recovered at a few coastal sites in both the North and the South Island (Wouts & Sturhan, 1996; unpubl. observations). A putative dispersal to New Zealand cannot be excluded, like that assumed for *P. tenuissima*.

Members of the *Avenae* group are widely distributed in Eurasia and ten of the 12 species were described from this geographical region, including the Mediterranean area. *Heterodera aucklandica*, originally described from New Zealand and so far known from very few localities in New Zealand (Wouts & Sturhan, 1995; unpubl. observations), has been identified in Belgium and England (Subbotin *et al.*, 2003). It is unlikely that this species specialised to grasses evolved in New Zealand, which separated from other parts of the former Gondwanaland some 80 million years ago, prior to

the evolution of Poaceae. *Heterodera australis*, described from the southern parts of Australia and recently recorded also from China (Subbotin *et al.*, 2010a), may have been introduced by man to Australia, like *H. avenae* as suggested for the latter species by Meagher (1977) and Riley & McKay (2009).

Species of the other *Heterodera* groups and the individual species specialised to Poales (Table 2) have been described and recorded from various countries worldwide and speculations about the putative ancestral areas are impossible with our current knowledge.

Heterodera salixophila with trees as hosts is known from Central Europe to the western parts of Russia. Origin and hosts of *H. spinicauda* are unknown (see above).

The geological and palaeoclimatic history must be taken into account as an important factor in speculations about the areas of origin of genera and species. Thus, species originally described from the northern parts of Europe (and with their type localities in this area) most probably cannot have developed in this geographical area, for instance, *H. spinicauda* in The Netherlands, *H. humuli* and *H. cruciferae* in England, *H. hordecalis* in Sweden, *H. salixophila* in the western part of Russia, *C. estonica* in Estonia, *H. schachtii*, *H. daverti*, *H. avenae* and *H. goettingiana* in Germany, but must have invaded these regions only after the last glacial period, following the recolonisation of this geographical area by their respective host plants.

It is not surprising to find a high biodiversity of species and genera in geographical areas with largely unchanged climatic and geological conditions during long geological periods. The mentioned findings of undescribed taxa particularly in natural forests in south-east Asia and Africa may serve as examples. Mountaineous regions, which enable vegetational zones to 'evade' in periods of changing climate to altitudes with adequate climatic conditions, also favour survival of plant parasites. The *Globodera* species found at different altitudes in New Zealand and the records of an undescribed *Heterodera* species from the laurisilva in the Canary Islands may confirm this assumption. Extended diverse mountain regions also favour speciation and survival of taxa, as shown by Grenier *et al.* (2010) for the Andes and by Subbotin *et al.* (2017) for the mountains in California. Likewise, tropical rainforests and similar biotopes with high plant diversity favoured development of species, which is well documented by the studies of Nguyen *et al.* (2011) in Vietnam and the records of heteroderid taxa discovered in Cameroon, Thailand and Borneo mentioned in the present paper.

Concluding remarks

The brief compilation of our current knowledge of selected morphological characters, hosts and host reactions of all taxa presently arranged in the family Heteroderidae, summarised in Tables 1 and 2, reveals that – beyond features of females or cysts – the number of incisures in the lateral fields of J2 is an essential morphological character to distinguish genera and species groups. This character in J2 facilitates the identification of these taxa since J2 are more commonly available than adults, females and cysts. It allows and supports, for instance, distinction of *Cryphodera* and *Meloidodera*, in the genus *Heterodera* the *Koreana* and the *Orientalis* species groups, both formerly placed in the genus *Afenestrata*. In *Atalodera* differences in the number of incisures might be an indication of parphyly or intrageneric species groups. Considering also the number of lateral incisures in males, species groups might be distinguished in *Cryphodera*, and in the genus *Heterodera* the *Cyperi* and *Cardiolata* species groups can be distinguished from the *Sacchari* and the *Koreana* species groups by this morphological character.

Phasmids and their shape – present *vs* absent, small/indistinct *vs* distinct, with lens-like structure in the cuticle – are additional useful morphological characters for the distinction of taxa within Heteroderidae, among others, of species groups within the genus *Heterodera*. Both pore-like and lens-like phasmids reported for *Meloidodera* species might be an indication that intrageneric groups also could/should be distinguished, like in the genus *Heterodera*. The phasmids appearance is, however, often imperfectly described or even unknown, which restricts the use of this character. Based mainly on comparative fine structural studies of phasmids in J2 of Heteroderidae, Baldwin & Powers (1987) considered lens-like phasmids as plesiomorphic.

Like phasmids, the shape of spicules has quite often not been precisely described. Different spicule shapes have been reported for, *e.g.* among species of the genera *Meloidodera* and *Atalodera*. Spicules with notched tip in *Heterodera* and *Cactodera*, against pointed tips in *Globodera*, *Punctodera* and other genera, may prove to be an additional morphological character useful for the distinction of genera. The significance of such spicule characters for phylogenetic analyses has still to be explored (Baldwin & Powers, 1987).

The compilation of known data on a few selected characters, indication of gaps in knowledge and of characters to be studied in more detail, to be confirmed or corrected, is considered as a basis for

further studies and will hopefully stimulate future research. The extension of molecular analyses with inclusion of more species (in general, traditionally identified by morphological characteristics!) in such studies is considered as essential for recovering relationships and evaluating phylogenies. Congruence of molecular data with morphological features, biological or ecological characteristics and supported by phylogeographic analyses, will hopefully provide a good basis for a 'stable' phylogeny of Heteroderidae. Such an integrated approach should be favoured in studying nematode diversity and for solving taxonomic problems (Luc *et al.*, 2010).

Recent discovery of many heteroderid species and even of genera new to science, in-particular, in mountaineous, tropical and subtropical regions and environments, suggests that presumably only a small fraction of the actually existing heteroderid taxa is known so far (Sturhan, this paper; Nguyen *et al.*, 2011; Zhuo *et al.*, 2014a; Subbotin *et al.*, 2017). There are still large geographical areas insufficiently studied or even so far not at all explored for their nematological diversity!

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REFERENCES

- ANGIOSPERM PHYLOGENY GROUP. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: AGP IV. *Botanical Journal of the Linnean Society* 181: 1-20.
- BAJAJ, H.K. & DALAL, M.R. 1997. Life cycle of *Verutus mesoangustus* Minagawa (Nematoda: Heteroderidae) on *Vetiveria zizanioides* (L.) Nash. (Gramineae). *Fundamental and Applied Nematology* 20: 191-196.
- BAJAJ, H.K. & WALIA, R.K. 1996. *Verutus mesoangustus* Minagawa, 1986 (Nematoda: Heteroderidae), a new record from India. *Indian Journal of Nematology* 25: 48-51.
- BAJAJ, H.K. & WALIA, R.K. 2000. Host response to *Cryphodera kalesari* (Heteroderidae: Nematoda). *Nematologia Mediterranea* 28: 197-199.
- BAJAJ, H.K., WALIA, R.K., DABUR, K.R. & BHATTI, D.S. 1989. *Cryphodera kalesari*, a new heteroderid nematode species from Haryana, India. *Systematic Parasitology* 14: 113-116.
- BALDWIN, J.G. & POWERS, T.O. 1987. Use of fine structure and nucleic acid analysis in systematics. In: *Vistas on Nematology* (J.A. Veech & D.W. Dickson Eds). pp. 336-345. Society of Nematologists Inc., Hyattsville, Maryland, USA.
- BALDWIN, J.G. & SCHOUDEST JR., L.P. 1990. Comparative detailed morphology of the Heteroderinae Filipjev & Schuurmans Stekhoven, 1941, *sensu* Luc *et al.* (1988): phylogenetic systematics and revised classification. *Systematic Parasitology* 15: 81-106.
- BALDWIN, J.G., BERNARD, E.C. & MUNDO-OCAMPO, M. 1989. Four new species of Heteroderidae including *Ekphymatodera* n. gen. from California. *Journal of Nematology* 21: 48-68.
- BERNARD, E.C. 1981. Three new species of Heteroderoidea (Nematoda) from the Aleutian Islands. *Journal of Nematology* 13: 499-513.
- BERNARD, E.C., HANDOO, Z.A., POWERS, T.O., DONALD, P.A. & HEINZ, R.D. 2010. *Vittatidera zeaphila* (Nematoda: Heteroderidae), a new genus and species of cyst nematodes parasitic on corn (*Zea mays*). *Journal of Nematology* 42: 139-150.
- CARTA, L.K. & BALDWIN, J.G. 1990. Ultrastructure of phasmid development in *Meloidodera floridensis* and *M. charis* (Heteroderinae). *Journal of Nematology* 22: 362-385.
- CID DEL PRADO VERA, I. 1991. Description of *Meloidodera mexicana* n. sp. (Nemata: Heteroderinae) with key to species. *Revue de Nématologie* 14: 537-542.
- CID DEL PRADO VERA, I. & LOWNSBERY, B.F. 1984. Histopathology and host range studies of the redwood nematode *Rhizonema sequoiae*. *Journal of Nematology* 16: 68-72.
- CID DEL PRADO VERA, I. & MIRANDA, B.L. 2008. A second cyst-forming nematode parasite of barley (*Hordeum vulgare* L.var. Esmeralda) from Mexico. *Nematropica* 38: 105-114.
- CID DEL PRADO VERA, I. & ROWE, J.A. 2000. *Cactodera evansi* sp. n. and *Meloidodera astonei* sp. n. (Tylenchida: Heteroderidae) from Mexico. *International Journal of Nematology* 10: 159-168.
- CID DEL PRADO VERA, I., LOWNSBERY, B.F. & MAGGENTI, A.R. 1983. *Rhizonema sequoiae* n. gen. n. sp. from Coast Redwood *Sequoia sempervirens* (D. Don) Endl. *Journal of Nematology* 15: 460-467.

- CHOI, Y.-E. & KIM, S.-E. 2001. Two unrecorded species, *Globodera hypolysi* and *Sarisodera hydrophila* (Nematoda: Heteroderidae) from Korea. *Korean Journal of Applied Entomology* 40: 5-13.
- DOBOSZ, R., WINISZEWSKA, G., MALEWSKI, T., RYBARCZYK-MYDŁOWSKA, K., TEREBA, A., KOWALEWSKA, K., GAWLAK, M. & BOGDANOWICZ, W. 2013. Morphological and molecular features of *Punctodera stonei* Brzeski, 1998 (Nematoda: Heteroderidae) – Species associated with roots of grasses. *Annales Zoologici* 63: 157-162.
- EBSARY, B.A. & EVELEIGH, E.S. 1983. *Meloidogyne aquatilis* n. sp. (Nematoda: Meloidogynidae) from *Spartina pectinata* with a key to the Canadian species of *Meloidogyne*. *Journal of Nematology* 15: 349-353.
- EROSHENKO, A.S. 1978. [New species of *Meloidodera* (Nematoda, Heteroderidae) from the Primorsky Territory]. *Parazitologiya* 12: 456-459 (in Russian).
- EROSHENKO, A.S. & VOLKOVA, T.V. 2003. Distribution of plant-nematodes in the Russian Far East. *Russian Journal of Nematology* 11: 135-136.
- ESSER, R.P. 1981. *Verutus volvingentis* n. gen., n. sp. (Heteroderidae: Tylenchida) in Verutinae n. subf., a phytoparasitic nematode infesting buttonweed in Florida. *Proceedings of the Helminthological Society of Washington* 48: 220-240.
- FERRIS, V.R. 1979. Cladistic approaches in the study of soil and plant parasitic nematodes. *American Zoologist* 19: 1195-1215.
- GRENIER, E., FOURNET, S., PETIT, E. & ANTHOINE, G. 2010. A cyst nematode ‘species factory’ called the Andes. *Nematology* 12: 163-169.
- HERNANDEZ GOMEZ, Y.I., CID DEL PRADO VERA, I., YAÑEZ JIMÉNEZ, P., & GARCI ESTEVA, A. 2017. Comparative histology of feeding sites induced by *Cactodera rosae*, *Globodera mexicana*, *Globodera* sp. and *Meloidodera astonei* (Nematoda: Heteroderidae). *Nematropica* 47: 114-119.
- HIRSCHMANN, H. & TRIANTAPHYLLOU, A.C. 1973. Postembryogenesis of *Meloidodera floridensis* with emphasis on the development of the male. *Journal of Nematology* 5: 185-195.
- JATALA, P., FRANCO, J., VILCA, A. & CORNEJO, W. 1979. Nonsolanaceous hosts of *Globodera* in the Andes. *Journal of Nematology* 11: 210-211.
- KANG, H., EUN, G., HA, J., KIM, Y., PARK, N., KIM, D. & CHOI, I. 2016. New cyst nematode, *Heterodera sojiae* n. sp. (Nematoda: Heteroderidae) from soybean in Korea. *Journal of Nematology* 48: 280-289.
- KAUSHAL, K.K. 1996. A report on *Heterodera spinicauda* from India. *Indian Journal of Nematology* 26: 272-274.
- KAUSHAL, K.K., SHARMA, S.B. & SINGH, M. 2000. *Heterodera skohensis*, a new cyst nematode species (Nematoda: Heteroderidae) from Kangra valley of Himachal Pradesh, India. *International Journal of Nematology* 10: 67-70.
- KAZACHENKO, I.P. 1990. [Morphology of the rare cyst-forming nematode species *Thecavermiculatus crassicrustata* Bernard (Nematoda: Tylenchida) from the Far East of the USSR]. *Parazitologiya* 24: 446-450 (in Russian).
- KIRJANOVA, E.S. & BORISENKO, A.V. 1975. [A cyst forming nematode – *Heterodera (Globodera) mali* sp. n. – a parasite of apple trees in Kazakhstan.] *Parazitologiya* 9: 335-338 (in Russian).
- KLEYNHANS, K.P.N. 1992. Cyst-forming nematodes in South Africa: *Afenestrata africana* (Luc, Germani & Netscher, 1973) Baldwin & Bell, 1985 (Nematoda: Heteroderidae). *Phytophylactica* 24: 307-311.
- KNOETZE, R., SWART, A. & TIEDT, L.R. 2013. Description of *Globodera capensis* n. sp. (Nematoda: Heteroderidae) from South Africa. *Nematology* 15: 233-250.
- KNOETZE, R., SWART, A., WENTZEL, R. & TIEDT, L.R. 2017a. Description of *Globodera agulhasensis* n. sp. (Nematoda: Heteroderidae) from South Africa. *Nematology* 19: 305-322.
- KNOETZE, R., SWART, A., WENTZEL, R. & TIEDT, L.R. 2017b. Description of *Globodera sandveldensis* n. sp. (Nematoda: Heteroderidae) from South Africa. *Nematology* 19: 805-816.
- KRALL, E.L. & KRALL, H.A. 1978. [Revision of the plant nematodes of the family Heteroderidae on the basis of trophic specialization of these parasites and their co-evolution with their host plants]. In: *Fitogel'mintologicheskie Issledovaniya*. pp. 39-56. Moscow, USSR, Nauka (in Russian).
- KRALL, E., SHAGALINA, L. & IVANOVA, T. 1988. [A new desert-inhabiting genus and species of nematodes *Camelodera eremophila* gen. n., sp. n. (Nematoda, Heteroderidae, Ataloderinae)]. *Proceedings of the Academy of Sciences of the Estonian SSR, Biology* 37: 27-35 (in Russian).
- LUC, M., TAYLOR, D.P. & CADET, P. 1978. Description of a new tropical Heteroderidae, *Hylonema ivorense* n. gen., n. sp., and a new outlook on the family Heteroderidae (Nematoda: Tylenchida). *Revue de Nématologie* 1: 73-86.
- LUC, M., DOUCET, M.E., FORTUNER, R., CASTILLO, P., DECRAEMER, W. & LAX, P. 2010. Usefulness of morphological data for the study of nematode biodiversity. *Nematology* 12: 495-504.
- MA, H., OVERSTREET, R.M. & SUBBOTIN, S.A. 2008. ITS2 secondary structure and phylogeny of cyst-forming nematodes of the genus *Heterodera* (Tylenchida: Heteroderidae). *Organisms, Diversity & Evolution* 8: 182-193.
- MEAGHER, J.W. 1977. World dissemination of the cereal cyst nematode (*Heterodera avenae*) and its potential

- as a pathogen of wheat. *Journal of Nematology* 9: 9-15.
- MEKETE, T. 2007. *Presence and frequency of occurrence of plant parasitic nematodes on coffee (Coffea arabica L., Rubiaceae) in Ethiopia and the importance of endophytic microorganisms for biocontrol*. MSc Thesis, University of Bonn, Bonn, Germany, 153 pp.
- MEKETE, T., SIKORA, R.A., KIEWNICK, S. & HALLMANN, J. 2008. Plant-parasitic nematodes associated with coffee (*Coffea arabica* L., Rubiaceae) in Ethiopia. *Nematopica* 38: 177-186.
- MINAGAWA, N. 1986. Description of *Verutus mesoangustus* n. sp. (Tylenchida: Heteroderidae) from Japan. *Applied Entomology and Zoology* 21: 277-282.
- MULVEY, R.H. 1972. Identification of *Heterodera* cysts by terminal and cone top structures. *Canadian Journal of Zoology* 50: 1277-1292.
- MUNDO-OCAMPO, M. & BALDWIN, J.G. 1983. Host response to *Sarisodera hydrophila* Wouts and Sher, 1971. *Journal of Nematology* 15: 259-268.
- MUNDO-OCAMPO, M. & BALDWIN, J.G. 1984. Comparison of host response of *Cryphodera utahensis* with other Heteroderidae, and a discussion of phylogeny. *Proceedings of the Helminthological Society of Washington* 51: 25-31.
- MUNDO-OCAMPO, M., TROCCOLI, A., SUBBOTIN, S.A., DEL CID, J., BALDWIN, J.G. & INSERRA, R.N. 2008. Synonymy of *Afenestrata* with *Heterodera* supported by phylogenetics with molecular and morphological characterisation of *H. koreana* comb. n. and *H. orientalis* comb. n. (Tylenchida: Heteroderidae). *Nematology* 10: 611-632.
- NARBAEV, Z.N. 1987. [Redescription of the cyst nematode *Heterodera cardiolata* Kirjanova & Ivanova, 1969]. *Uzbekskii Biologicheskii Zhurnal* 6: 44-48 (in Russian).
- NETSCHER, C., LUC, M. & MERNY, G. 1969. Description du mâle d'*Heterodera sacchari* Luc & Merny, 1963. *Nematologica* 15: 156-157.
- NGUYEN, C.N., STURHAN, D. & SUBBOTIN, S.A. 2011. Studies on the occurrence and diversity of Heteroderidae and Meloidogynidae (Nematoda: Tylenchida) in natural forests of Vietnam. *Russian Journal of Nematology* 19: 159-172.
- NICKLE, W.R. 1960. Nematodes associated with the rootlets of western white pine in northern Idaho. *Plant Disease Reporter* 44: 470-471.
- NORGREN, R.L. & GOLDON, A.M. 1986. First report of *Cactodera estonica* in the United States. *Plant Disease* 70: 1159.
- OTHMAN, A.A. & BALDWIN, J.G. 1985. Comparative morphology of *Meloidodera* spp. and *Verutus* sp. (Heteroderidae) with scanning electron microscopy. *Journal of Nematology* 17: 297-309.
- RILEY, I.T. & MCKAY, A.C. 2009. Cereal cyst nematode in Australia: biography of a biological invader. In: *Cereal Cyst Nematodes: Status, Research and Outlook* (I.T. Riley, J.M. Nicol & A.A. Dababat Eds). pp. 23-28. Ankara, Turkey, CIMMYT.
- SABO, A., REIS, L.G.L., KRALL, E., MUNDO-OCAMPO, M. & FERRIS, V.R. 2002. Phylogenetic relationships of a distinct species of *Globodera* from Portugal and two *Punctodera* species. *Journal of Nematology* 34: 263-266.
- SEKIMOTO, S., UEHARA, T. & MIZUKUBO, T. 2017. Characterisation of populations of *Heterodera trifolii* Goffart, 1932 (Nematoda: Heteroderidae) in Japan and their phylogenetic relationships with closely related species. *Nematology* 19: 543-558.
- SHARMA, S.B. & SIDDIQI, M.R. 1992. *Bilobodera flexa* gen. n., sp. n. (Nematoda: Heteroderidae) from Andhra Pradesh, India. *Afro-Asian Journal of Nematology* 2: 59-63.
- SIDDIQI, M.R. 1986. *Tylenchida: Parasites of Plants and Insects*. UK, Commonwealth Agricultural Bureaux. 645 pp.
- SIDDIQI, M.R. 2000. *Tylenchida: Parasites of Plants and Insects*. UK, CAB International. 833 pp.
- SOUZA, R.M. 1996. *Afenestrata axonopi* n. sp. (Nemata: Heteroderidae) from Brazil. *Fundamental and Applied Nematology* 19: 35-42.
- STONE, A.R. 1975. Head morphology of second-stage juveniles of some Heteroderidae (Nematoda: Tylenchoidea). *Nematologica* 21: 81-88.
- STONE, A.R. 1979. Co-evolution of nematodes and plants. *Symbolae Botanicae Upsaliensis* 22: 46-61.
- STURHAN, D. 1998. Notes on the taxonomy and phylogeny of Heteroderidae parasitising Gramineae. *Nematologica* 44: 585-586.
- STURHAN, D. 2002. Notes on the genus *Cactodera* Krall & Krall, 1978 and proposal of *Betulodera betulae* gen. nov., comb. nov. (Nematoda: Heteroderidae). *Nematology* 4: 875-882.
- STURHAN, D. 2006. Zystenbildende Nematoden und verwandte Heteroderiden in Deutschland. *Aktuelle Beiträge zur Nematodenforschung* 404: 18-30.
- STURHAN, D. 2007. Wirte, Verbreitung und Verwandtschaftsbeziehungen von *Globodera* und verwandten Zystennematoden. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes* 59: 16.
- STURHAN, D. 2010. Notes on morphological characteristics of 25 cyst nematodes and related Heteroderidae. *Russian Journal of Nematology* 18: 1-8.
- STURHAN, D. 2012. Contribution to a revision of the family Merliniidae Ryss, 1998, with proposal of Pratylenchoidinae subfam. n., *Paramerlinius* gen. n., *Macrotylechus* gen. n. and description of *M. hylophilus* sp. n. (Tylenchida). *Journal of Nematode*

- Morphology and Systematics* 15: 127-147.
- STURHAN, D. 2014a. Native – indigenous – endemic? On occurrence, dispersal and origin of some phytonematodes. *Journal of Plant Diseases and Protection* 121: 188.
- STURHAN, D. 2014b. Plant-parasitic nematodes in Germany – an annotated checklist. *Soil Organisms* 86: 177-198.
- STURHAN, D. 2015. Ein erster nach Mellum benannter Organismus: *Telomerlinius mellumensis*. *Natur- und Umweltschutz (Mellumrat)* 14: 11-12.
- STURHAN, D. 2016. On the presence or absence of phasmids in males of Heteroderidae (Tylenchida). *Nematology* 18: 23-27.
- STURHAN, D. & WOUTS, W.M. 1995. On the identity of *Heterodera turcomanica* Kirjanova & Shagalina, 1965 and the synonymy of the genus *Ephippiodera* with *Heterodera* (Nematoda: Heteroderidae). *Nematologica* 41: 566-574.
- STURHAN, D., WOUTS, W.M. & SUBBOTIN, S.A. 2007. An unusual cyst nematode from New Zealand, *Paradolichodera tenuissima* gen. n., sp. n. (Tylenchida, Heteroderidae). *Nematology* 9: 561-571.
- SUBBOTIN, S.A. 2015. *Heterodera sturhani* sp. n. from China, a new species of the *Heterodera avenae* species complex (Tylenchida: Heteroderidae). *Russian Journal of Nematology* 23: 145-152.
- SUBBOTIN, S.A., VIERSTRAETE, A., DE LEY, P., ROWE, J., WAEYENBERGE, L., MOENS, M. & VANFLETEREN, J.R. 2001. Phylogenetic relationships within the cyst-forming nematodes (Nematoda, Heteroderidae) based on analysis of sequences from the ITS region of ribosomal DNA. *Molecular Phylogenetics and Evolution* 21: 1-16.
- SUBBOTIN, S.A., MUNDO-OCAMPO, M. & BALDWIN, J.G. 2010a. *Systematics of Cyst Nematodes (Nematoda: Heteroderinae)*. *Nematology Monographs and Perspectives*, 8B (Series Eds: D.J. Hunt & R.N. Perry). The Netherlands, Brill. 511 pp.
- SUBBOTIN, S.A., MUNDO-OCAMPO, M. & BALDWIN, J.G. 2010b. *Systematics of Cyst Nematodes (Nematoda: Heteroderinae)*. *Nematology Monographs and Perspectives*, 8A (Series Eds: D.J. Hunt & R.N. Perry). The Netherlands, Brill. 351 pp.
- SUBBOTIN, S.A., CID DEL PRADO VERA, I., MUNDO-OCAMPO, M. & BALDWIN, J.G. 2011. Identification, phylogeny and phylogeography of circumfenestrate cyst nematodes (Nematoda: Heteroderidae) as inferred from analysis of ITS-rDNA. *Nematology* 13: 805-824.
- SUBBOTIN, S.A., AKANWARI, J., NGUYEN, C.N., CID DEL PRADO VERA, I., CHITAMBAR, J.J., INSERRA, R.N. & CHIZHOV, V.N. 2017. Molecular characterisation and phylogenetic relationships of cystoid nematodes of the family Heteroderidae (Nematoda: Tylenchida). *Nematology* 19: 1065-1081.
- TANHA MAAFI, Z., SUBBOTIN, S.A. & MOENS, M. 2003. Molecular identification of cyst-forming nematodes (Heteroderidae) from Iran and a phylogeny based on ITS-rDNA sequences. *Nematology* 5: 99-111.
- TANHA MAAFI, Z., STURHAN, D., HANDOO, Z., MORDECHAI, M., MOENS, M. & SUBBOTIN, S.A. 2007. Morphological and molecular studies of *Heterodera sacchari*, *H. goldeni* and *H. leuceilyma* (Nematoda: Heteroderidae). *Nematology* 9: 483-497.
- TOVAR SOTO, A., CID DEL PRADO VERA, I., NICOL, J.M., EVANS, K., SANDOVAL ISLAS, J.S. & MARTÍNEZ GARZA, A. 2003. *Cactodera galinsogae* n. sp. (Tylenchida: Heteroderinae) on barley (*Hordeum vulgare* L.) of the high valleys of Mexico. *Nematropica* 33: 41-54.
- TRIANANTAPHYLLOU, A.C. 1970. Cytogenetic aspects of evolution of the family Heteroderidae. *Journal of Nematology* 2: 26-32.
- TRIANANTAPHYLLOU, A.C. & HIRSCHMANN, H. 1980. Cytogenetics and morphology in relation to evolution and speciation of plant-parasitic nematodes. *Annual Review of Phytopathology* 18: 333-359.
- VOVLAS, N., LAMBERTI, F. & CHOO, H.Y. 1992. Description of *Afenestrata koreana* n. sp. (Nematoda: Heteroderinae), a parasite of bamboo in Korea. *Journal of Nematology* 24: 553-559.
- WANG, H., ZHUO, K., YE, W., ZHANG, H., PENG, D. & LIAO, J. 2013. *Heterodera fengi* n. sp. (Nematoda: Heteroderinae) from bamboo in Guangdong Province, China – a new cyst nematode in the *Cyperi* group. *Zootaxa* 3652: 179-192.
- WOUTS, W.M. 1973. A revision of the family Heteroderidae (Nematoda: Tylenchoidea). II. The subfamily Meloidoderinae. *Nematologica* 19: 218-235.
- WOUTS, W.M. 1985. Phylogenetic classification of the family Heteroderidae (Nematoda: Tylenchida). *Systematic Parasitology* 7: 295-328.
- WOUTS, W.M. & SHER, S.A. 1971. The genera of the subfamily Heteroderinae (Nematoda: Tylenchoidea) with a description of two new genera. *Journal of Nematology* 3: 129-144.
- WOUTS, W.M. & WEISCHER, B. 1977. Eine Klassifizierung von fünfzehn in Westeuropa häufigen Arten der Heteroderinae auf Grund von Larvenmerkmalen. *Nematologica* 23: 289-310.
- WOUTS, W.M. & STURHAN, D. 1995. *Heterodera aucklandica* sp. n. (Nematoda: Heteroderidae) from a New Zealand native grass, with notes on the species of the *H. avenae* group. *New Zealand Journal of Zoology* 22: 199-207.
- WOUTS, W.M. & STURHAN, D. 1996. *Heterodera litoralis* sp. n. (Nematoda: Heteroderidae) from

- austral glasswort, *Sarcocornia quinqueflora*, in New Zealand. *Nematologica* 42: 62-70.
- WOUTS, W.M., SCHOEMAKER, A., STURHAN, D. & BURROWS, P.R. 1995. *Heterodera spinicauda* sp. n. (Nematoda: Heteroderidae) from mud flats in the Netherlands, with a key to the species of the *H. avenae* group. *Nematologica* 41: 575-583.
- ZHUO, K., WANG, H., YE, W., PENG, D. & LIAO, J. 2013. *Heterodera hainanensis* n. sp. (Nematoda: Heteroderinae) from bamboo in Hainan Province, China – a new cyst nematode in the *Afenestrata* group. *Nematology* 15: 303-314.
- ZHUO, K., WANG, H.H., YE, W., PENG, D.L. & LIAO, J.L. 2014a. *Cryphodera sinensis* n. sp. (Nematoda: Heteroderidae), a non-cyst-forming parasitic nematode from the roots of ramie *Boehmeria nivea* in China. *Journal of Helminthology* 88: 468-480.
- ZHUO, K., WANG, H., ZHANG, H. & LIAO, J. 2014b. *Heterodera guangdongensis* n. sp. (Nematoda: Heteroderinae) from bamboo in Guangdong Province, China – a new cyst nematode in the *Cyperi* group. *Zootaxa* 3881: 488-500.

D. Sturhan. Диагностическая и филогенетическая значимость линий латерального поля, фазмид и других морфологических признаков личинок второй стадии и самцов Heteroderidae (Nematoda, Tylenchida) с замечаниями по их хозяевам и филогеографии.

Резюме. Проведен анализ современных представлений о числе линий латерального поля, форме фазмид и кончика спикул у 158 валидных видов, относящихся к 19 родам семейства Heteroderidae. Все эти признаки обладают диагностическим значением для разграничения родов и внутриродовых групп видов, но требуется дополнительное их изучение. Различия в числе линий латерального поля или в размере фазмид среди видов *Cryphodera*, *Meloidodera* и *Atalodera* рассматриваются как признаки, указывающие на парафилетическое происхождение этих родов. В полном соответствии с молекулярными данными предложены три дополнительных группы (*Cardiolata*, *Koreana* и *Orientalis*) для видов рода *Heterodera*, у которых хозяевами служат растения порядка Мятликоцветных (Poales). Предложено разделить род *Globodera* на три группы видов *Rostochiensis*, *Millefolii* и *Zelandica*. Информация о группах растений-хозяев и особенностях реакции хозяина на заражение нематодами рассматриваются как важная составляющая для понимания филогенетических связей и оценки эволюционного «возраста» таксонов. Изучение биогеографических данных с выявлением именно «естественного» распространения нематод, с привлечением данных по геологическим и палеоклиматическим изменениям также важны для понимания предполагаемых мест появления отдельных групп паразитических нематод растений и становления отдельных таксонов. Даны краткие описания нескольких популяций гетеродерид из Африки, предварительно идентифицированных как представители родов *Meloidodera*, *Hylonema*, а также гетеродерид из Вьетнама, предварительно определенных как представители рода *Sarisodera*. Другие неопределенные до вида или представляющие собой новые роды представители этого семейства описаны с Калимантана, Канарских островов, Доминиканской республики, Новой Зеландии, Таиланда, Туниса и Вьетнама.