

REVISION OF THE PLANT NEMATODES OF THE FAMILY HETERODERIDAE  
ON THE BASIS OF THE TROPHIC SPECIALIZATION OF THESE PARASITES  
AND THEIR CO-EVOLUTION WITH THEIR HOST PLANTS

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Partial translation of pages 43-54:

COMPARATIVE ECOLOGICAL ANALYSIS AND EVOLUTION OF THE HETERODERIDS

According to Paramonov (1967), the study of phylogenetic relationships between individual groups in many cases requires a special ecological analysis of the phylogeny. It seems to us, therefore, that the comparative ecological approach must be viewed as the primary way in the tracing of the phylogeny of species in the Heteroderid family. In connection with this we tried to summarize the existing data on the trophic specialization of Heteroderids and to shed some light on some questions of their evolution (especially the collective genus Heterodera) on the basis of analyzing the interrelation of these parasites with their host plants and on the basis of current concepts on the phylogenetic development of flowering plants (Grossgeim, 1945; Takhtadzhyan, 1970).

The evolution of Angiospermae, according to A. A. Grossgeim (1945) can be viewed in three stages of development. The study of the trophic specialization of parasites gave rise to a hypothesis that the species of Heterodera which are parasites of flowering plants or Angiospermae and which are found at lower levels of phylogenetic development are characterized by a wider spectrum of plant hosts and a lower degree of trophic adaptability as compared to species which are parasites of plants found at a higher stage of phylogenetic development. The parasites of the latter have a high level of trophic adaptability which is expressed by the nematodes taking to one or a few related plant species (Krall', 1971; E. Krall' & Kh. Krall', 1970, 1973).

It became apparent that neither on what is assumed to be the primitive groups of Angiospermae (according to A. A. Grossgeim (1945) first stage of Protanthophyta with orders Magnoliales, Ranunculales and others), nor on Gymnospermae were found any certain specimen of species of the Heteroderid family.

The members of the second so called complex stage of development of flowering plants (according to Grossgeim (1945) Mesanthophyta with the large orders Caryophyllales, Fabales, Polygonales, Scrophulariales and Rhodales) are characterized by Heteroderid species with a wide spectrum of host plants. Only at this stage do we find Heteroderids which are capable to be parasites of plant groups very distant in taxonomical respects. Heteroderids of this group often have a wide ecological

plasticity; they adapt beautifully to the changing environment of their habitat. Thus, the host plants of Heterodera schachtii consist of 23 families (14 orders), the hosts of H. trifolii and H. glycines consist of 10 and 9 families (8 and 6 orders), and the hosts of H. galeopsidis and H. rosii consist of 6 and 4 families (5 and 4 orders).

Plants at the third, highest, that is most specialized, stage of development (Hypsanthophyta), host Heteroderid species which have a narrow spectrum of hosts. Heteroderids feeding in plants found at this stage are adapted to a most constant [and] narrowly specific habitat environment. Often they are found as parasites of only one species, genus, or family. On the basis of existing data we can assume that such Heteroderids are no longer capable of feeding on plants belonging to other phylogenetic stages. As an example we point out the group of Heteroderid which feed on cereals, sedge, Compositae, and umbellate plants. The finding on these plant groups of new, undescribed species of Heteroderid would lead to the conclusion with a rather high degree of probability that they are specialized to a high degree. On the other hand, the appearance of Heterodera on plants which are at the second (complex) stage of phylogenetic development would cause us to assume that they have a wide ecological plasticity even in cases when according to prior preliminary data they are considered to be "highly specialized."

Consequently, the evolution of Heteroderids generally coincides with the evolution of their hosts—flowering plants. Our hypothesis fully corresponds to the theory of the conjugate evolution of the host plant and the parasite (Vavilov, 1964; Zhukovskii, 1971; Leppik, 1970).

N. I. Vavilov (1964) in his theory of gene centers of the origin of cultivated plants stated the idea that one should look for disease-resistant species and varieties of plants in their original geographic native location. This was supported by the works of P. M. Zhukovskii (1971), according to whom the natural immunity to diseases and pests appears in the mutual native location of the host and the parasite, where their side-by-side evolution takes place and where a permanent infection background exists. The host plant shows an exclusive variability in its native location. As a result of divergence it continuously forms new varieties and forms (among them also disease resistant ones), and the parasite forms new and more aggressive races. A so called complementarity of genetic systems is formed in two systematic groups of organisms distant in phylogenetic relationships.

Ambiguity and sharp delineation of boundaries of the host spectrum, two extremes between which there is a whole row of transitions, are well-established for many groups of parasitic organisms (Goïman, 1954). As we see it, there is a direct interdependence between the character of the host spectrum (homo- or heteroxen) and their position in the system of flowering plants, or in other words, their phylogenetic relationships which without doubt most similarly reflect also the phylogeny of their particular parasites. It is understood that with different species of Heteroderid one can find many instances of contact between host spectra. But all the known cases of contact of spectra established from trustworthy

material, have a logical explanation from the point of view of phylogenetic relationships of hosts--they operate according to the natural rules that result from prolonged side-by-side evolution (coevolution) of parasites and their hosts.

As is generally known, the current systematics of animals and plants has for goal to reflect their phylogenetic ties. Still, as is justly emphasized by E. Mayr, E. Linsli, and R. Yuzinger (1956), many of our recent systems are pragmatic and based on the degree of similarity independent of the question of showing relationships or not. Systematics must often go to compromises in order to combine the practicality of the classification with its phylogenetic basis. On the other hand, in far from all cases is it successfully possible to reflect the phylogeny in the system, even if it is well enough known. For example, among the Heteroderids the genus Globodera includes species which are highly specialized in parasitism on Solanaceae, Compositae, and Rosaceae plants. Phylogenetic ties between these 3 groups of plants must still be considered as not elucidated. In spite of that [and] for the sake of convenience in classification it is advisable to consider the parasites of these plant groups as belonging to one genus, Globodera. The species Heterodera humuli is parasitic of plants which are found at the second (complex) stage of phylogenetic development. Because of the existence of cysts of the bifenestrate type this species reminds us of representatives of a new proposed genus Bidera. However, the analysis of the degree of trophic adaptation and the morphological characteristics of this species still do not allow us to draw conclusions about relationship ties of these two branches of Heteroderids. The origin of these branches from the common stem is possible but it is also possible to consider the theory of the existence of some convergent morphological characteristics. The animal kingdom is full of convergences when the similar demands of the environment call forth a similar phenotypical reaction in nonrelated or at least not closely related organisms (Mayr, 1968).

We come to the conclusion that today it is still too early to create a final scheme of phylogeny in Heteroderids, for the simple reason that far from all species of this group are known to science, and the proposed descriptions of many new species are completely inadequate, not to mention the great gaps in our knowledge of the bioecology of Heteroderids. The study on today's standards of additional materials of the group we are examining should bring correctives and supplements to the scheme proposed below.

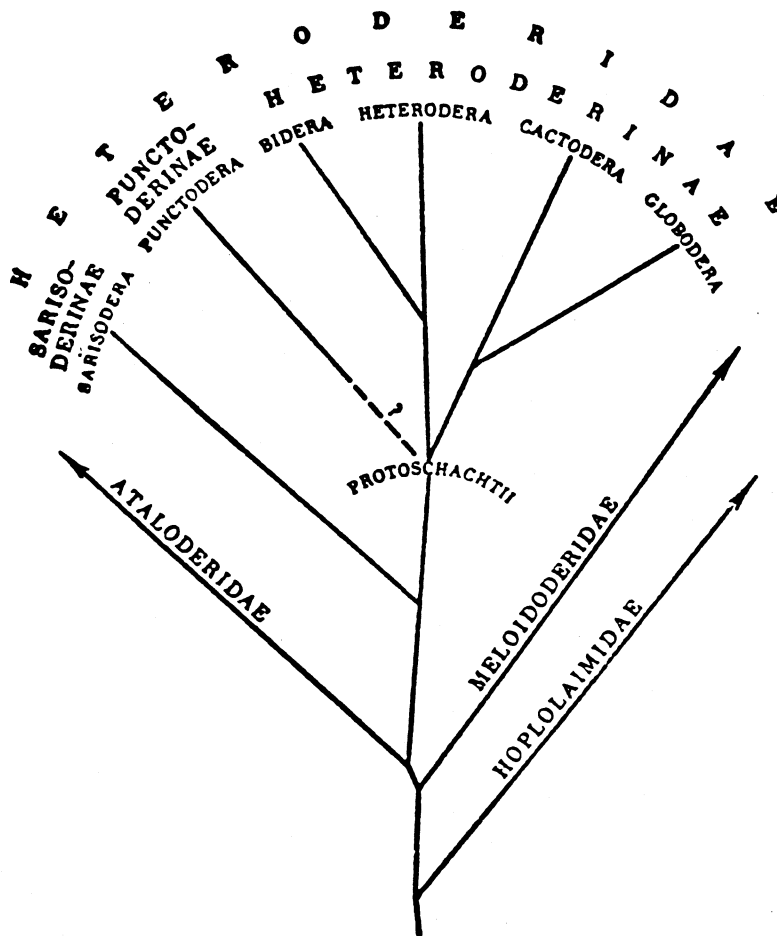
According to our concept, from ancient hypothetical ancestors of modern Heteroderids (group - "Protoschachtii"), which stemmed in all probability from the group reminding us of the modern Hoplolaimids, branch out different branches of phylogenetic development leading to the modern groups and species of Heteroderids. It seems that this ancient initial group was characterized by the existence of a lemon-like shape of the body and an anal-vulval plate of the ambifenestrate type. The strongest and most numerous line of development (genus Heterodera as we see it) is represented by lemon-like shapes of the ambifenestrate type and today includes 37 species with hetero- and homogenous spectra of host plants. A typical representative of this genus, the species H. schachtii, because of its morphophysiological characteristics, especially the level of the

trophic morphophysiological characteristics, especially the level of the trophic specialization, can generally be regarded as one of the oldest representatives of Heteroderidae. A special and quite ancient branch, the group of bifenestrate species (genus Bidera), was isolated from the common stem "Protoschachtii."

Botanists consider that representatives of families and genera of plants existing among the modern flora were already known in the lower Cretaceous age. There is all reason to assume that the areas of many taxa, found in the tropical regions of both the continents of the Old and New World, must have been formed around the middle of the Cretaceous period, before the final split of Gondwana.

The place of origin of a certain species or genus is usually the area where we find the most variety in its forms. Hence we consider the centers of origin and colonization of the genera Heterodera and Bidera (that is, ambifenestrate and bifenestrate Heteroderids) to be in the Old World, more precisely, Mediterranean, trans-Caucasian and some Middle Asiatic areas of Eurasia. The center of origin of the phylogenetic line Cactodera most likely lies in the New World. The genus Globodera, close to the Cactodera, that lies on a separate branch, is undoubtedly also of American origin. The evolution of the species that belongs here occurred in the mountainous regions of South America. In addition to the primary center of the formation of this genus, a secondary center of Globodera colonization appeared in Europe. The genus Cactodera is undoubtedly also of American origin. Both of these close groups evolved from the common stem "Protoschachtii." As far as the cyst forming genera Sarisodera and Punctodera are concerned, they quite strongly differ from the above mentioned groups of Heteroderids. The phylogeny of these groups is still insufficiently studied. Whereas Punctodera can be traced from the common stem "Protoschachtii" by a quite ancient independent line the morphological characteristics of Sarisodera, especially the lack of fenestration, point to an earlier origin of this genus. A very ancient origin can also be attributed to members of the family Ataloderidae and Meloidoderidae. (See chart.)

The known correlation of the level of trophic specialization of modern species and groups of Heteroderid with some morphological characteristics (form of the body, type of fenestration) supports the phylogenetic importance of the comparative ecological analysis conducted by us. The suggested new groups below were at first considered in our first publications on this subject as "phylogenetic lines" of Heteroderids (E. Krall', Kh. Krall', 1970, 1973). The analysis of new data of recent years supported the correctness of these ideas, in connection with which we give such phylogenetic lines the status of separate genera of the given family. The phylogenetic lines of Heteroderids Globodera and Punctodera were arranged into separate genera with full substantiation (Mulvey & Stone, 1976). In connection with this it is necessary to revise the family we are examining, which should include only cyst-forming species. The other groups, up to now attributed to Heteroderids by various authors, must be placed into separate families (see scheme). The Heteroderid family according to current concepts of its extent, really does split into three sub-families, among which two were first proposed by us. Let us examine a short characterization of the different groups of Heteroderids:



Scheme of the phylogenetic development of Heteroderids.

Key to classification of sub-family and genera of the family Heteroderidae.

1. (2) Vulva sunken inside the terminal cone, no fenestration.  
Males have no tail.  
..., sub-family Sarisoderinae subfam. n. (genus Sarisodera).
2. (1) Vulva not sunken inside terminal cone; fenestration exists.  
Males have tails.

3. (4) Anus in form of large fenestra, almost same size as fenestra around vulva.  
..., sub-family Punctoderinae subfam.n. (genus Punctodera).
4. (3) Anus much smaller than vulva, not in form of large fenestra.  
..., subfamily Heteroderinae.
5. (8) Structure of vulva area ambi - and bifenestrate.
6. (7) Vulval bridge narrow, vulval area ambifenestrate (H. humuli - bifenestrate); vulval slit is 30 - 70 um long, same as the width of fenestra or its length.  
..., Genus Heterodera.
7. (6) Vulval bridge wide (bifenestrate type of fenestration), vulval slit is less than 20 (25) um, shorter than the width of fenestra.  
..., Genus Bidera gen.n.
8. (5) Vulval area circumfenestrate type (with round fenestra).
- 9.(10) Cysts more or less lemon-shaped, vulval cone exists: short, stand out sharply or is blunted; sometimes the width of cyst is more than its length, but there are species with exclusively elongated cysts.  
..., Genus Cactodera gen. n.
10. (9) Cyst ball-shaped, pear shaped or egg-shaped without vulval cone; width of cyst not more than length.  
..., Genus Globodera.

FAMILY HETERODERIDAE FILIPJEV & SCHUURMANS  
STEKHOVEN, 1941

Diagnosis: Hoplolaimoidea. Females ball-shaped, pear-shaped or lemon-shaped always turn into cyst after death. Cuticle not annulated. Anus dorsal to vulva or on the inside the dorsal fold of vulva. Vulva terminal. Second stage larvae without labial disc. Oral cuticle of even width. Esophageal glands fill whole width of body. Males worm - shaped, up to 1.5mm long. Oral disc nonexistent or not sharply expressed. Tail short, blunt or practically nonexistent. Spicules longer than 30 um.

Type genus: Heterodera Schmidt, 1871

Subfamilies: Heteroderinae Skarbilovich, 1947.  
Sarisoderinae subfam.n.; Punctoderinae subfam n.

SUBFAMILY HETERODERINAE SKARBILOVICH, 1947

Diagnosis: Heteroderidae. Females ball-shaped, pear shaped or lemon shaped with very prominent fenestration of ambi-, bi-, or

circumfenestrate type. Anus small in size, often hard to distinguish, lying dorsally to vulva (large vulval fenestra nonexistent).

Type genus: Heterodera Schmidt, 1871

Other genera: Globodera Mulvey & Stone, 1976; Bidera gen.n.;  
Cactodera gen.n.

Genus Heterodera Schmidt, 1871

Cysts lemon-shaped with vulval cone, structure of vulva area of ambifenestrate type, that is the outline of fenestra looks like thickened number "8" or bifenestrate type (H. humuli). Vulval slit long (30-70 um). Egg matrix usually exists. Bullae exist or not.

Type species: \*Heterodera schachtii, 1871

Species:

- |   |   |
|---|---|
| <u>H. amygdali</u> Kir'yanova & Ivanova, 1975               | <u>H. medicaginis</u> Kir'yanova in Kir'yanova & Krall', 1971 |
| <u>H. cajani</u> Koshy, 1967                                | <u>H. methwoldensis</u> Cooper, 1955                          |
| <u>H. cardiolata</u> Kir'yanova et Ivanova, 1969            | <u>H. mothi</u> Khan & Husain, 1965                           |
| <u>H. carotae</u> Jones, 1950                               | <u>H. oryzae</u> Luc & Berdon - Brizuela, 1961                |
| * <u>H. cruciferae</u> Franklin, 1945                       | <u>H. oxiana</u> Kir'yanova, 1962                             |
| <u>H. cyperi</u> Golden, Rau & Cobb, 1962                   | <u>H. para trifolli</u> Kir'yanova, 1963                      |
| <u>H. elachiata</u> Oshima, 1974                            | * <u>H. polygona</u> Cooper, 1955                             |
| <u>H. fici</u> Kir'yanova, 1954                             | * <u>H. rosii</u> Duggan & Brennan, 1966                      |
| * <u>H. galeopsidis</u> Goffart, 1936                       | <u>H. rumocis</u> Pogosyan, 1961                              |
| * <u>H. glycines</u> Ichinohe, 1952                         | <u>H. sacchari</u> Luc & Merny, 1963                          |
| <u>H. goettingiana</u> Liebscher, 1892                      | <u>H. salixophila</u> Kir'yanova, 1969                        |
| <u>H. graduni</u> Kir'yanova in Kir'yanova & Krall', (1971) | <u>H. scleranthii</u> Kaktyma, 1957                           |
| <u>H. graminis</u> Stynes, 1971                             | <u>H. sonchophila</u> Kir'yanova, Krall' & Krall', 1976       |
| <u>H. graminophila</u> Golden & Birchfield, 1972            | <u>H. tadshikistanica</u> Kir'yanova & Ivanova, 1966          |
| * <u>H. humili</u> Filip'ev, 1934                           | * <u>H. trifolli</u> Goffart, 1932                            |
| <u>H. lespedezae</u> Golden et Cobb, 1963                   | <u>H. urticae</u> (Cooper, 1955) Mulvey, 1974                 |
| <u>H. leuceilyma</u> Di Edwardo & Perry, 1964               | <u>H. vigni</u> Edward & Misra, 1968                          |
| <u>H. limonii</u> Copper, 1955                              | <u>H. zaeae</u> Koshy, Swarup & Sethi, 1971                   |
| <u>H. longicolla</u> Golden & Dickerson, 1973               |   |

\*Species with wide heterogenic spectrum of host plants are marked with stars.

The oldest representatives of the phylogenetic line of the genus Heterodora may be the amphimixic diploid species, such as H. schachtii, H. glycines, maybe also H. salixophila. More recent are the poliploid species, propagating by parthenogenesis (H. trifolii, H. galeopsidis, H. lespedezae, maybe also H. rosii and H. polygoni). A special branch of this line is morphologically characterized by cysts with undeveloped bullae and according to existing data include only diploid amphimixic species, such as H. goettingiana, H. carotae, and H. cruciferae. Bullae are protective devices in cysts; the high variability of this characteristic does not allow us to give it special significance in the phylogeny of nematodes.

Some representatives of both branches of Heterodera have reached high levels of specialization which indicates a narrow adaptation in the area of the given phylogenetic line. A number of other species are heuristically characterized partly because of a greater knowledge of primary pests in agricultural cultures. In fact, relatively resistant plant species belong not frequently to the list of hosts of Heterodera - On these species, the spreading of the parasites occurs only exceptionally, and remains at insignificant levels. According to terminology used in phytopathology, such hosts are called collateral (opposite of basic) uncongenial, chance, experimental and even "resistant" (Goiman, 1954). For instance, all basic natural hosts of sugarbeet nematodes belong to the families of goosefoot and Cruciferae and to a lesser extent to carnations and buckwheat plants. The members of all the other rather numerous families of plants are collateral or chance hosts of this species or are known to be such only in special experimental conditions (experimental hosts). The basic natural hosts of the soybean nematode are in the families of bean plants; of the clover nematode in families of beans, goosefoot, cruciferae, carnations and buckwheat; of the pickle nematode in families of Labiatae, beans, carnations and buckwheat; of the Irish or British mustard nematode in the buckwheat family.

Among the remaining species with a narrow but heterogeneous (of different genera) spectrum of plant hosts there is the cabbage nematode (H. cruciferae) - parasite of Cruciferae and in isolated cases of Labiatae plants. The narrow spectrum in this case results from a long-term specialization, therefore, H. cruciferae cannot be considered as a phylogenetically older species compared to H. schachtii and related forms.

Many species of Heterodera have a narrow and homogenous (of one genus) spectrum of hosts (within one family, genus or even one species of a plant) in moderate climates and subtropical and tropical climates. To these belong H. goettingiana on bean plants, H. carotae on umbellate plants, H. urticae on nettle plants. Among the southern species H. mothi and H. cyperi feed only on sedge plants, H. zaeae on corn and barley in India, H. oryzae on rice in African countries and possibly in Japan, H. sacchari on sugar cane and rice in African and Indian countries, H. leuceilyma on stenotafrum in Florida, H. cardiolata and H. graminis on wire grass (dog's tooth) [ = Cynodon dactylon or bermuda grass] in Central Asia and Australia respectively, H. graminophila on some cereals in U.S.



It is interesting to note that host plants of Heterodera species are represented by lines which were initially developed in the tropics, such as suborder Oryzoidea, Eragrostoidea, and Panicoidea. Contrary to this all the species of the suggested new genus Bidera relate to parasites of plants in the sub-order Festucoidea, which developed in temperate latitudes. It is obvious that this fact witnesses the totally different origin of Heterodera as compared to Bidera.

Unfortunately, data on the ecology of many species ascribed to Heterodera is still very scanty. Thus, some species, especially parasites of bean, carnation and buckwheat plants can actually have a wider and heterogenous spectrum of hosts (since they feed on plants found at the second phylogenetic stage of development), although today they are known to feed on only one or a few closely related species of plants.

A typical representative of the genus Heterodera, the sugar beet nematode, today belongs to the group of Heterodera species scattered throughout the world. The primary center (epicenter, involving the evolution of the sugar beet nematode and apparently a number of other species of this line) of their hosts is also found in the Mediterranean countries; such an epicenter coincides with the Mediterranean origin of cultivated plants. One may believe that primarily H. schachtii resided on wild species of the sugar beet and cabbage, the primary areas of which spread from the Mediterranean Coast to the Asiatic steppe. Consequently, the sugar beet nematode migrated from wild goosefoot and cruciferae to the fields and became a pest of the sugar beet as well as many other kinds and varieties of beets. The origin from areas with moist marine climates left a mark on some of the morphophysiological characteristics of this species. To these belongs the relatively long vulval slit, deposition of eggs in special egg matrix which are discharged during a ripening period and finally, the lack of a rest period, since during the vegetative season there can be formed several generations of the parasite. The number of the latter in the Ukraine 5-6, in Lithuania 2-3, Kirghizia more than 3, and in W. Europe 1-2 per year. (Kir'yanova & Krall', 1969-1971).

Genus Bidera gen. n.

Synonym: Bidera Krall' & Krall', 1973 (nomen nudum).

Heteroderinae. Cysts lemon-shaped, less frequently egg-shaped, usually with well-formed vulval cone (the latter sometimes can be absent in rounder specimen even within the species). Structure of vulval area of bifenestrate type, i.e., the shape of fenestra resembles a lengthened figure "8". The vulval slit usually between 10-14  $\mu$ m, seldom up to 20 (25)  $\mu$ m, always less than width of fenestra. Eggs not deposited in egg matrix, which is in most typical cases completely absent or is only of an insignificant size.

Type species: Bidera avenae (Wollenweber, 1924) comb. n.

Species:

- |  |  |
|--|--|
| <u>B. arenaria</u> (Cooper, 1955) comb. n.         | <u>B. longicaudata</u> (Seidel, 1972)<br>comb. n.                |
| <u>B. bifenestra</u> (Cooper, 1955)<br>comb. n.    | <u>B. mani</u> (Mathews, 1971) comb. n.                          |
| <u>B. hordecalis</u> (Andersson, 1975)<br>comb. n. | <u>B. turcomanica</u> (Kir'yanova &<br>Shagalina, 1965) comb. n. |
| <u>B. iri</u> (Mathews, 1971) comb. n.             | <u>B. ustinovi</u> (Kir'yanova, 1969)<br>comb. n.                |
| <u>B. latipons</u> , (Franklin, 1969)<br>comb. n.  |  |

Species of the genus Bidera typically have special protective morpho-physiological devices to survive in unfavorable surroundings. These have only one generation per year and a long period of rest. The activation of larvae in cysts becomes possible after they remain a relatively long time at low temperatures.

The species of the genus Bidera are distinguished by a narrow homogenous spectrum of plant hosts and are specific parasites on cereals (a plant host has not been established for B. turcomanica). Representatives of the genus Bidera (especially oat nematode) are now widespread in the world. It may be assumed that the possible primary center of differentiation of species relevant here is the native land of their host plants (Zhukovskii, 1971; Leppik, 1970). In this area, finds of special interest are oat nematodes in Israel, Morocco, Tunis, and in the USSR in Tadzhikistan (Kir'yanova & Krall', 1969-1971). Recently three more species of Bidera were described.

We are convinced that special research in the areas of Transcaucasus, Central Asia, and surrounding territories can bring forth new discoveries, leading to a more detailed understanding of the phylogeny of bifenestrata species of Heteroderidae. From a practical point of view it is in these areas that we must look for species and varieties of plants resistant to numerous biotypes of the oat nematode.

The evolution of species of the genus Bidera went in the direction of adaptation to the constantly increasing conditions of aridization in continental regions of Eurasia. For this fact account special types of fenestration, but above all a very short vulval slit, a wide and long vulval bridge (especially in the case of B. latipons and B. turcomanica), a complete absence of, or the presence of a very small egg matrix, etc. These initial characteristics of adaptation were preserved in the oat nematode even after the cereals and their particular parasites were transferred to many different geographic places strange to them. In new regions appear secondary adaptations. The optimal temperature for the emergence of larvae of oat nematodes in Canada is 10-15°C, in Southern Australia it is around 20°C (Banyer & Fisher, 1971; Fushtey & Johnson, 1966). The most recent research did not support the aboriginal character of the population of oat nematodes in Australia (Meagher, 1972), the parasite was obviously brought there, just as to North America, from Europe.

Phylogenetically very interesting is the recently described Swedish species B. hordecalis (Andersson, 1975). Among the characteristics, undoubtedly typical to the genus Bidera, such as bifenestrate type of anal-vulval disc, spectrum of plant hosts, wide vulval bridge etc., it has a relatively long vulval slit 17-25 (20)  $\mu$ m. These characteristics not usual for Bidera may be connected with the adaptation of this species to the regions with moister climates. It is fully possible that B. hordecalis represents an intermediate form, originating from the divergence of Heteroderinae to Heterodera. Such an intermediate form could have been preserved only in conditions of moist coastal climates, where its further evolution took place. We cannot assume that from Bidera specialized to arid climates there could have stemmed secondary similar but less specialized forms. The long vulval slit must be characteristic to species of the genus Heterodera, from which later sprung another phylogenetic branch, leading to the modern species of the genus Bidera, losing this characteristic in the process of specialization to adapt to continental climates.

Genus Cactodera gen. n.

Synonym: Cactodera Krall' & Krall', 1973 (nomen nudum).

Heteroderinae. Cysts are lemon-shaped, egg-shaped or almost ball-shaped, with a vulval cone which may stand out sharply or may be blunted. Sometimes the width of cysts is greater than the length, or the body is significantly lengthened. The structure of vulval area is circumfenestrate (with round fenestra). Vulval slit less than 30  $\mu$ m. Anus smaller than vulva. Bullae exist or not. Vulval brige narrow, easily destroyed at maturation of females.

Type species: Cactodera cacti (Filipjev & Schuurmans Stekhoven, 1941) comb. n.

Species:

- |   |   |
|---|---|
| <u>C. amaranthi</u> (Stoyanov, 1972),<br>comb. n.         | <u>C. estonica</u> (Kir'yanova & Krall',<br>1963), comb. n. |
| <u>C. aquatica</u> (Kir'yanova, 1971),<br>comb. n.        | <u>C. weissi</u> (Steiner, 1949), comb. n.                  |
| <u>C. betulae</u> (Hirschmann & Riggs,<br>1969), comb. n. |   |

Plant hosts of species in genus Cactodera are in the second stage of phylogenetic development.

The species C. cacti and C. betulae have heterogenous spectra of host plants, the species C. amaranthi, C. estonica and C. weissi have narrow homogenous spectra of hosts according to existing data. A plant-host has not been established for C. aquatica.

We consider the ancient area and primary centers of origin of species in the genus Cactodera to be in the New World. The native land of C. cacti is considered to be Mexico (Kir'yanova & Krall', 1969-1971). The plant

hosts of the cactus nematode are spread out primarily in Central America, in southern regions of North America and in arid areas of northern and central parts of South America. Along with its host, C. cacti has been brought to many countries in the world where several generations of this species develop annually in hot houses. We know that at temperatures of 18-26°C, C. cacti needs only 29-34 days to develop one generation. Birch cyst forming nematode C. betulae has a not yet stabilized caryotype, it reproduces by meiotic partenogenesis and apparently stems from a diploid amphimictic ancestor, possibly from C. cacti (Triantaphyllou, 1970). Among the 80 species of plants examined from 20 families, good hosts for the birch cyst-forming nematode were only different species of birches; but we found this species also on alder trees and one species in the family of capers (Riggs et al., 1969). Our most recent research has confirmed that the host plant of the species C. estonica is knotgrass [P. aviculare] in the buckwheat family. At the same time the estonian cyst-forming nematode was found to be a tropical amphimictic species.

Genus Globodera (Skarbilovich, 1959) Mulvey & Stone, 1976

Synonym: Heterodera (Globodera) Skarbilovich, 1959

Heteroderinae. Cysts ball-shaped, almost ball-shaped, pear-shaped, or egg-shaped with round or sometimes uneven hind end, but always without a vulval cone. Structure of vulval area circumfenestrate. Vulval slit short, less than 20 um long. Anus smaller than vulva. Egg matrix absent.

Type species: Globodera rostochiensis (Wollenweber, 1923) Mulvey & Stone, 1976

Species:

- |   |   |
|---|---|
| <u>G. achilliae</u> (Golden & Klindic, 1973), Mulvey & Stone, 1976        | <u>G. mirabile</u> (Kir'yanova, 1971), Mulvey & Stone, 1976           |
| <u>G. artemisiae</u> (Eroshenko & Kasachenko, 1972), Mulvey & Stone, 1976 | <u>G. pallida</u> (Stone, 1973), Mulvey & Stone, 1976                 |
| <u>G. chaubattia</u> (Gupta & Edward, 1973), n. comb.                     | <u>G. pseudorstochiensis</u> (Kir'yanova, 1963), Mulvey & Stone, 1976 |
| <u>G. leptonepia</u> (Cobb & Taylor, 1953), Mulvey & Stone, 1976          | <u>G. solanacearum</u> (Miller & Cray, 1972), Mulvey & Stone, 1976    |
| <u>G. mali</u> (Kir'yanova & Borisenko, 1975), Mulvey & Stone, 1976       | <u>G. tabacum</u> (Lownsbery & Lownsbery, 1954), Mulvey & Stone, 1976 |
| <u>G. millefolii</u> (Kir'yanova & Krall', 1965), Mulvey & Stone, 1976    | <u>G. virginiae</u> (Miller & Jgay, 1968) Mulvey & Stone, 1976        |

The species of the genus Globodera have a narrow or a wide, but always homogenous, spectra of host plants in three families of Dicotyledons.

1. Specific parasites of Solanaceae: G. rostochiensis, G. pallida, G. pseudorstochiensis, G. solanacearum, G. tabacum, G. leptonepia, G. virginiae.

2. Specific parasites of Compositae: G. achilleae, G. artemisiae, G. millefolli.

3. Parasites of Rosaceae: G. chaubattia, G. mali.

A host plant has not been established for the species G. mirabile.

We find a great interspecific diversity among the Globodera species feeding on the potato and other Solanaceae. The species G. rostochiensis and G. pallida include pathotypes, whose number and characteristics require a more accurate definition. The epicenter of this branch of phylogenetic development is found in South America. A comparatively low temperature optimum (15-20°C) and the length of development of one generation (Kampfe, 1962) correlate well with the climate conditions of mountainous regions of the Andes, where the evolution of the primary species of Globodera on wild Solanaceae took place. The majority of the species of this branch have partially touching spectra of plant hosts, but each of them also has one or several specific hosts, so called host-differentials. The spectra of host plants of the Globodera parasites on Compositae and Rosaceae are still not researched adequately. Nevertheless, for the species G. millefolli, 13 species of host plants have already been established, in 8 genera of the Compositae family. It is possible to assume that other species of this group also have a larger number of hosts than is known at this time. Of special interest is the study of trophic relationships of the Globodera parasites of Rosaceae (G. chaubattia, G. mali). Rosaceae are considered to be a rather ancient branch in the general evolution of flowering plants, leading to the emergence of Solanaceae. In connection with this, one can consider the Globodera which feed on Rosaceae to be more ancient in their appearance than Globodera which feed on Solanaceae. Of course, both groups could have appeared independently of each other as a result of convergent development -- the acquisition of some morphological characteristics on different groups of plant hosts. The origin of Globodera, feeding on Compositae, cannot be considered elucidated at the present time.

#### SUBFAMILY PUNCTODERINAE SUBFAM. N.

Heteroderidae. Cysts without vulval cone, ball-shaped, egg-shaped, or pear-shaped. Cuticle meshed, subcuticle with dot-like structures. Vulval slit very short, underbridge absent. Bullae present or absent. Perineal tubercles absent. Fenestration of the circumfenestrate type. Anus also surrounded by a fenestra of circumfenestrate type of the same size, anus lying near the ventral edge of the anal fenestra. Larva spear less than 30  $\mu$ m. Esophageal glands fill up the width of the body. Phasmids without lens-shaped structures. Males up to 1.5 mm long with weakly expressed lip disc (cap). Length of tail not more than half of body diameter.

Type genus: Punctodera Mulvey & Stone, 1976

Synonym: Punctodera Krall' & Krall', 1973 (nomen nudum).

Type species: P. punctata (Thorne, 1928) Mulvey & Stone, 1976.

Species: P. matadorensis Mulvey & Stone, 1976.

Despite the almost worldwide distribution of this genus, its discovery on corn in Central America (Sosa Moss, 1968), the cultivation of which is known from early times in the New World, is of special interest, from the point of view of the phylogeny of this genus. A high degree of specialization of plant hosts (found at the third level of phylogenetic development) correlates well with the absence of the vulval cone in the parasite. These characteristics, so typical of Punctodera, support the concept of an ancient origin of the genus, possibly from the common stem of the ancestral group "Protoschachtii." This is supported also by the parasite Punctodera feeding on two lines of development of cereals -- Panicoideae and Festucoideae considered to be independent.

Only one generation of Punctodera occurs during vegetation. Nevertheless, in Mexico it was found that some eggs of Punctodera were capable of hatching without a previous period of rest (development at 20° takes 45 days) and there is the opinion that in nature there exists a second generation of the parasite (Sosa Moss, 1968).

Among all the Heteroderidae groups, Punctodera appears furthest north, as indicated by its presence in North America (Canada) and Europe (Iceland, USSR). The fact that with cereals of the order Festucoideae in northern regions there appear only Punctodera and not the usual numerous members of Heterodera and Bidera found on the same cereals further south, speaks for the adaptation of the studied group to severe climates. Morphologically this is expressed by the presence in Punctodera of the smallest vulval slit (only 4  $\mu$ m in P. matadorensis) of all Heteroderidae. In respect to this character, Punctodera apparently went through a convergent evolution with Bidera. The appearance of the large anal fenestra in Punctodera also may be explained as an adaptation of this group to the surroundings of the North. The presence of 2 large fenestra allows a fast emergence of larvae from the cysts after they hatch at the onset of a short vegetative period.

#### SUBFAMILY SARISODERINAE SUBFAM. N.

Heteroderidae. Females with mesh ornamentation on cuticle. Vulval slit sunken inside terminal cone which is formed by hypertrophied vulval lips. No fenestration around vulva. In males, the lip area is not offset from the contours of the body; basal annule without longitudinal lines. Spicules almost straight, narrowing in the distal direction. Cloaca placed subterminally. No tail.

Type genus: Sarisodera Wouts & Sher, 1971.

Type species: S. hydrophila Wouts & Sher, 1971.

Species: S. africana Luc, Germani & Netscher, 1973.

The absence of fenestration and the sunken vulva do not allow us to take this group from the common stem "Protoschachtii"; it undoubtedly has an earlier origin. The two species included in this phylogenetically sharply isolated group are parasites of willows and cereals (Luc et al., 1973; Wouts & Sher, 1971). Phylogenetic relationship of this group are not resolved.

In connection with the creation of two new families in the Heteroderidae [from taxa] considered by various authors (Golden, 1971; Wouts, 1972) as subfamilies of this group, we note their brief characteristics.

FAMILY ATALODERIDAE WOUTS, 1973, GRAD. N.

Hoplolaimoidea. Cuticle in females not annulated. Cyst stage absent. Anus and vulva placed terminally on projection of body. No fenestration. Eggs remain inside body. Larvae of second stage with undefined labial disc. Esophageal glands fill less than half of body in width. Males up to 1.5 mm long, with well expressed labial disc. Tail is either present or absent.

Type genus: Atalodera Wouts & Sher, 1971

Genus: Sherodera Wouts, 1973.

The type species of genus Atalodera (A. ucri) is a parasite on the roots of Compositae. The type species of genus Sherodera (S. lonicerae) on the roots of honeysuckle. Undescribed species of this genus were found on the roots or in soil around the roots of Labiatae, Cruciferae, and other plants. They all belong in Southern California. The family has an ancient origin, but the phylogenetic relationships of this group cannot be considered cleared up.

FAMILY MELOIDODERIDAE GOLDEN, 1971, GRAD. N.

Hoplolaimoidea. Females with annulated cuticle, without cyst stage. Anus placed terminally or dorso-subterminally. Vulva equatorial or terminal. Larvae of second stage with labial disc. Width of esophageal glands equal to body diameter. Males have labial disc, they are less than 1 mm long. Tail present. Spicules less than 30 um.

Type genus: Meloidodera Chitwood, Hannon & Esser, 1956.

Genera: Cryphodera Colbran, 1966; Zelandodera, Wouts, 1973.

The degree of its trophic specialization speaks also in favor of the hypothesis of an exclusively ancient origin of this morphologically very unique group. Feeding of the species Meloidodera floridensis on several species of pine, i.e. on representatives of Gymnospermae (bare seeds) is not recorded in a single modern species of the family Heteroderidae. The only known species of the genus Cryphodera - C. eucalypti - is a parasite on eucalyptus in Australia. These facts speak for the separation of this group from Heteroderids and the establishment of an independent family. Phylogenetical relationships within the group must be considered unclear.

\* \* \*

Thus, thanks to the definition of exact reciprocity between the range of the spectra of host plants and the morphology of representatives of separate phylogenetic lines of Heteroderids, we may today be able to prognose the degree of tropical specialization of many not well-known parasites. In this fashion the solution of deeply theoretical problems, for example, the elucidation of phylogenetic relationships between phytonematodes, will have a paramount significance for a better understanding of many actual problems (tasks) standing before the practice of agriculture.

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