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Morphological and electrophoretic studies on populations of the *Heterodera avenae* complex from the former USSR

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Summary. Isoelectric focusing of protein extracts of ten *Heterodera 'avenae'* populations from Russia, Ukraine and Tadzhikistan revealed a uniform protein pattern for all populations, except for one population from Putilovo, Leningrad region. A comparison with populations of *H. avenae, H. mani* and an obviously undescribed species of the *H. avenae* group from Germany showed that the population group from the former USSR is distinct from *H. avenae* and the other populations included in the study. Only the Putilovo population showed a protein pattern similar to the populations of the undescribed species. Morphological and morphometrical studies on the populations from the former USSR supported the results of the electrophoretic studies and the distinction of all populations from the *H. avenae* populations from Germany. The population from Tadzhikistan closely agrees with the original description of *H. filipjevi* and all populations from the former USSR are considered as representatives of this species, except the Putilovo population which proved to represent another species within the *H. avenae* (*s. str.*) complex.

Key words: *Heterodera avenae, H. filipjevi,* electrophoresis, morphology, measurements, distribution, Russia, Ukraine, Tadzhikistan, Germany.

The cereal cyst nematode *Heterodera avenae* Wollenweber, 1924 is widely distributed in Europe. It has been recorded also for Africa, several countries in Asia and America and for Australia and New Zealand. Early evidence that *H. avenae* appears to represent a group of species (Andersson, 1973, 1976; Cook, 1975; Sturhan, 1976; Stone, 1978; Stone & Hill, 1982) is confirmed by more recent results from morphological and electrophoretic studies on populations of different origin (Dalmasso *et al.*, 1982; Rumpenhorst, 1985; Ferris *et al.*, 1989, 1994; Valdeolivas & Romero, 1990).

Among the ten described species which are presently placed in the *H. avenae* group and considered as valid, *H. avenae, H. aucklandica* Wouts & Sturhan, 1995, *H. mani* Mathews, 1971, *H. iri* Mathews, 1971, *H. filipjevi* (Madzhidov, 1981) Stelter, 1984, represent a restricted complex of obviously closely related species. *H. ustinovi* Kirjanova, 1969 and *H. arenaria* Cooper, 1955 are generally considered *species inquirendae* (Wouts & Sturhan, 1995).

H. avenae has been recorded also for many regions of the former Soviet Union; other species of the *H. avenae* group reported for the USSR are *H. arenaria, H. bifenestra, H. filipjevi, H. latipons, H. hordecalis, H. turcomanica* and *H. ustinovi* (Kirjanova & Krall, 1971; Tikhonova, 1978; Nikitin, 1979). *H. filipjevi* had been described as *Bidera filipjevi* from Tadzhikistan (Madzhidov, 1981) and later transferred to the genus *Heterodera* (Stelter, 1984). With the exception of this species, the morphological characters of the other species of the *H. avenae* group have not been studied in much detail and no populations were used in electrophoretic studies. As mentioned by Krall (1977) for the former Soviet Union "the oat cyst nematode (*H. avenae*) complex is widespread, but further investigations are urgently needed to clarify the taxonomic position of the species involved."

In the present study morphological, morphometric and biochemical characters of several populations of the *H. avenae* group from the former USSR are compared with populations of *H. avenae* and an obviously undescribed species of the *H. avenae* group from Germany.

MATERIAL AND METHODS

Populations of the *Heterodera 'avenae'* group from the following localities in the former Soviet Union were available for the present study (Fig. 1):
Russia:
- Putilovo, Leningrad region, borders of an oat field with false wheat, *Elytrigia repens* L.;
- Pushkin, Leningrad region, field of the All-Russian Institute of Plant Protection, false wheat;
- Gorodets, Nizhni Novgorod region, oat fields (two populations);
- Vad, Nizhni Novgorod region, oat field;
- Baimak, Bashkiria, wheat field;
- Saratov, Saratov region, wheat field of the South-East Institute of Horticulture.

Ukraine:
- Chabany, Kiev region, rye field with false wheat of the Ukrainian Institute of Horticulture;
- Chernobyl region, small wheat plot of the Ukrainian Institute of Horticulture.

Tadzhikistan:
- near Dushanbe, wheat field (population considered as *H. filipjevi* by Madzhidov, pers. comm).

For comparison the following two populations from Germany, which are 'characteristic' representatives of *H. avenae,* were included:
- Taaken near Rothenburg, Lower Saxony;
- Rinkam near Straubing, Bavaria.

In addition, a *H. mani* population from Northrhine-Westphalia, Germany and two German populations of an obviously undescribed species of the *H. avenae* group, originating from grassland in Schleswig-Holstein and Bavaria, were used for comparison in the electrophoretic studies.

Groups of four cysts were placed in a microhomogenizer and crushed and homogenised in 15 ml extraction medium (0.2 N acetic acid with 1% CHAPS). The proteins from the homogenates were separated by isoelectric focusing in thin layer (300 µm) polyacrylamide gel with 1% CHAPS and a pH range 3 - 10 (Servalyt 3-10 Iso-Dalt). 10 µl of the homogenates were placed per slot of the applicator strip. The Desatronic 2000/300 power supply (DESAGA) was set to 2000 V, max. 10 mA, max. 7 W and 2500 Vh, the temperature was held at 5° C. The gels were fixed with 20% trichloroacetic acid followed by 50% methanol and stained with silver following the procedure of Ohms and Heinicke (1983).

The morphological and morphometrical studies were conducted with cysts extracted from soil samples and second-stage juveniles squashed from cysts, killed by gentle heat, fixed in TAF and embedded in glycerol on permanent slides following Seinhorst's method. Cyst vulval cones prepared from brown cysts were mounted in glycerine-gelatine. The specimens were examined with the light microscopes JENAVAL and LEITZ Dialux equipped with Nomarski optics. Cluster analysis was conducted using SYSTAT 5.0 programme.

RESULTS

The results of our polyacrylamide gel-electrophoretic study of water-soluble proteins from cysts, which are presented in Fig. 2, allow the distinction of three groups of populations: (1) the *H. avenae* populations Rinkam and Taaken (Nos. 1 and 2), (2) the Chabany, Chernobyl, Pushkin, Gorodets, Vad and Baimak populations, which show a close agreement in their protein band patterns (Nos. 3 - 5, 7 - 10) and (3) the Putilovo population, which is distinct from the other groups of populations (No. 6). Fig. 3 shows that also the Dushanbe (No. 5) and Saratov (No. 8) populations can be classed into group 2, whereas the Putilovo population (No. 3) closely agrees with the two grassland populations from Germany (Nos. 1 and 2).

The results of the morphological studies support the distinction of three groups of populations. According to the measurements presented in Table 1, the cysts in the group 2 populations studied are slightly bigger than those of the Putilovo and Taaken/Rinkam populations and the fenestrae are larger. The measurements of the 2nd stage juveniles in Table 2 show lowest average body length for the Putilovo population, longest stylets for the German *H. avenae* populations and shortest tail and hyaline tail portions in the group 2 populations.

The comparative study of other morphological characters revealed that the stylet knobs in the 2nd stage juveniles from Putilovo are generally flattened anteriorly, whereas they are projecting in the *H. avenae* populations and, in particular, the group 2 populations (Fig. 4, A-C). The tail end is more slender in the Putilovo population (Fig. 4, D-F). In cyst characters the latter population is distinguished from *H. avenae* by slightly less 'massive' bullae which are usually not located directly under the fenestrae. The cysts of the group 2 populations distinctly differ from the *H. avenae* and Putilovo populations by the presence of a long and weak but distinct underbridge, which is located well below the vulval bridge. The bullae are generally grouped in the vulval cone at some distance from the fenestrae (Fig. 5).

The cluster analysis using the single linkage method (nearest neighbour) with 21 morphometric characters of the 2nd stage juveniles and the cone top structures of the cysts distinctly differentiates the

Table 1. Morphometrics (in µm) of cysts of populations of the *Heterodera avenae* complex.

Population	Putilovo Russia	Pushkin Russia	Baimak Russia	Gorodets Russia	Chabany Ukraine	Dushanbe Tadzhikistan	*H. filipjevi* (Madzhidov,1981)	Taaken Germany	Rinkam Germany
Cysts									
n	30	18	30	34	35	32	25	30	30
Length excluding neck	757±19.2 (480-960)	852±32.8 (672-1080)	928±20.0 (712-1192)	762±14.4 (624-936)	858±16.8 (600-1040)	801±25.8 (544-1040)	690 (490-830)	709±19.3 (488-896)	696±15.1 (552-880)
Width	565±15.2 (400-704)	585±28.0 (384-816)	685±16.8 (384-792)	530±12.0 (368-680)	623±14.4 (464-832)	578±20.1 (360-816)	490 (340-620)	490±13.7 (360-584)	470±12.8 (360-584)
Length/width	1.4±0.02 (1.2-1.6)	1.5±0.01 (1.1-2.0)	1.4±0.02 (1.1-1.9)	1.4±0.01 (1.3-1.7)	1.4±0.02 (1.2-1.7)	1.4±0.02 (1.3-1.8)	- -	1.5±0.02 (1.3-1.7)	1.5±0.02 (1.3-1.8)
Vulval areas									
n	13	6	18	15	21	16	25	20	20
Fenestra length	42.7±0.7 (37.5-47.5)	51.6±1.8 (45.0-57.5)	53.3±0.9 (47.5-60.0)	50.7±0.9 (45.0-57.5)	54.5±0.9 (47.5-62.5)	53.6±1.1 (49.5-61.4)	51.5 (41-64)	47.8±0.7 (42.5-52.5)	47.5±1.1 (40.0-55.0)
Vulval slit length	10.6±0.4 (8.8-12.5)	14.0±0.6 (12.5-15.0)	10.9±0.4 (7.5-15.0)	10.3±0.3 (9.3-12.5)	11.9±0.3 (9.5-14.3)	10.9±0.6 (7.9-15.8)	7.1 -	10.1±0.3 (8.0-12.5)	8.9±0.3 (6.3-10.8)
Mean semifenestral width	23.1±0.8 (17.5-27.5)	27.0±1.6 (20.0-30.0)	30.4±0.8 (27.5-37.5)	28.3±0.6 (25.0-32.5)	28.7±0.6 (25.0-32.5)	28.2±0.8 (23.8-31.7)	27.5 (21-33)	24.8±0.6 (20.0-30.0)	23.2±0.5 (17.5-26.5)
Vulval bridge width	7.0±0.5 (5.0-10.0)	7.9±0.8 (5.0-10.0)	8.1±0.4 (5.0-10.0)	9.4±0.4 (7.5-11.3)	10.5±0.3 (7.5-12.5)	8.8±0.4 (6.9-10.9)	7.7 (6.3-9.4)	7.3±0.2 (6.3-7.5)	7.1±0.4 (5.0-10.8)
Underbridge length	absent	59.4; 83.2	92±3.5 (83-99)	weak	90±2.8 (75-99)	88±2.5 (75-98)	82 (72-108)	absent	absent

Table 2. Morphometrics (in µm) of 2nd stage juveniles of populations of the *Heterodera avenae* complex.

Population	Putilovo Russia	Pushkin Russia	Baimak Russia	Gorodets Russia	Chabany Ukraine	Dushanbe Tadzhikistan	*H. filipjevi* (Madzhidov, 1981)	Taaken Germany	Rinkam Germany
n	20	15	20	20	20	16	45	20	20
Body length (L)	504±4.5	539±4.5	552±3.7	526±4.9	520±7.1	519±4.7	506	566±4.8	557±5.6
	(471-532)	(504-568)	(514-573)	(485-570)	(478-577)	(494-537)	(431-581)	(522-598)	(491-595)
a	24.5±0.3	26.7±0.5	25.2±0.3	24.9±0.4	23.1±1.2	23.0±0.3	23.6	26.3±0.3	26.5±0.3
	(22.0-26.8)	(23.5-30.1)	(23.9-27.2)	(21.6-28.3)	(22.5-26.9)	(21.2-26.9)	(21-25)	(23.3-29.3)	(23.5-29.1)
b	4.5±0.1	4.6±0.1	4.5±0.1	4.3±0.04	4.2±0.1	4.7±0.1	3.8	4.4±0.05	4.6±0.1
	(4.0-5.5)	(4.2-5.1)	(4.1-5.0)	(3.9-4.5)	(3.8-4.6)	(4.1-5.6)	(3.3-4.4)	(3.7-4.8)	(4.1-4.9)
c	7.8±0.1	9.0±0.1	9.2±0.1	9.5±0.1	9.5±0.1	9.4±0.1	9.1	8.3±0.07	8.1±0.1
	(7.3-8.5)	(8.5-9.5)	(8.6-10.2)	(8.7-10.2)	(8.5-10.7)	(8.8-9.8)	(6.8-10.7)	(7.5-8.8)	(7.6-8.8)
Stylet length	24.9±0.2	25.2±0.2	25.4±0.2	24.5±0.1	24.9±0.2	24.8±0.2	26.5	26.8±0.1	26.6±0.1
	(22.4-26.0)	(24.5-26.0)	(23.5-26.5)	(23.9-25.5)	(23.5-26.0)	(23.2-25.6)	(21.7-30.8)	(25.5-27.5)	(25.0-27.5)
Lip region height	4.1±0.1	4.3±0.1	4.3±0.1	4.1±0.1	4.3±0.1	3.9±0.03	3.7	4.3±0.1	4.4±0.1
	(4.0-4.3)	(4.1-4.6)	(3.9-5.1)	(3.9-4.4)	(3.9-5.1)	(3.8-4.0)	(3.5-4.2)	(4.1-5.1)	(4.1-5.1)
Lip region width	9.5±0.1	10.1±0.1	10.1±0.1	9.8±0.1	10.0±0.1	9.8±0.1	9.9	9.6±0.1	9.7±0.1
	(9.7-10.2)	(9.8-10.2)	(9.4-10.3)	(9.2-10.2)	(9.4-10.3)	(9.2-10.4)	(9.8-10.5)	(9.2-10.2)	(9.2-10.2)
DGO	6.0±0.2	6.5±0.2	6.2±0.2	6.2±0.1	5.9±0.1	5.9±0.3	5.3	5.5±0.2	5.7±0.1
	(5.7-7.1)	(5.6-7.1)	(5.1-7.9)	(5.2-7.1)	(5.1-6.1)	(4.0-6.4)	(4.2-6.3)	(4.9-7.1)	(5.3-6.1)
Anterior end to excretory pore	105±1.2	113±1.4	114±2.0	107±0.9	102±2.2	105±1.0	95	115±1.0	110±1.4
	(94-113)	(101-117)	(105-125)	(99-114)	(90-116)	(100-113)	(77-109)	(106-121)	(102-114)
Anterior end to valve of median bulb (MB)	76±0.8	80±0.5	78±0.9	74±1.0	72±1.5	73±0.9	69.6	77±1.0	73±1.4
	(68-81)	(76-84)	(71-86)	(65-79)	(63-84)	(69-79)	(57-84)	(67-84)	(64-84)
Oesophagus length	114±1.9	118±1.6	122±1.4	122±0.8	123±1.5	112±3.1	132	130±1.4	122±1.8
	(92-128)	(105-128)	(115-133)	(117-128)	(107-133)	(94-128)	(115-158)	(120-143)	(112-133)
Body width at:									
mid-body	20.6±0.2	20.1±0.3	21.8±0.2	21.2±0.2	21.4±0.1	22.5±0.2	22.9	21.5±0.2	21.0±0.1
	(19.4-21.9)	(17.3-22.4)	(20.4-23.5)	(19.4-22.4)	(20.4-22.4)	(21.2-23.2)	(21-24.5)	(20.4-23.5)	(20.4-21.9)
anus (BWA)	15.1±0.1	15.9±0.2	15.4±0.1	15.5±0.1	15.6±0.1	15.7±0.2	-	16.3±0.08	15.6±0.1
	(14.3-15.3)	(15.3-17.3)	(14.3-16.3)	(14.9-16.3)	(14.8-16.3)	(14.4-16.6)	-	(15.8-17.3)	(14.3-16.8)
Hyaline part of tail length (H)	41.9±0.7	37.0±0.7	38.9±0.6	32.8±0.7	34.6±0.5	31.1±0.6	35	44.8±0.6	44.1±0.7
	(38.8-44.9)	(33.7-40.8)	(35.7-44.9)	(27.5-37.7)	(30.6-38.8)	(28.8-36.0)	(31-39)	(39.8-49.0)	(38.8-50.0)
Tail length	65.0±0.9	59.9±0.6	60.2±0.9	55.2±0.9	54.4±0.9	54.9±0.6	57	68.7±1.0	68.6±0.9
	(59.2-69.4)	(56.1-62.2)	(55.1-67.3)	(50.0-62.2)	(50.0-60.2)	(52.0-59.2)	(49-63)	(59.2-79.6)	(61.2-75.5)
Tail length/BWA	4.3±0.1	3.8±0.1	3.9±0.1	3.6±0.1	3.5±0.1	3.5±0.05	-	4.2±0.1	4.4±1.0
	(4.1-4.9)	(3.6-4.2)	(3.5-4.4)	(3.4-3.9)	(3.2-4.0)	(3.2-3.9)	-	(3.5-4.6)	(4.0-4.7)
H/stylet length	1.8±0.01	1.5±0.03	1.5±0.02	1.3±0.01	1.4±0.02	1.3±0.02	1.3	1.7±0.02	1.7±0.02
	(1.2-1.9)	(1.3-1.6)	(1.4-1.7)	(1.1-1.5)	(1.2-1.6)	(1.2-1.4)	(1.0-1.6)	(1.5-1.8)	(1.5-1.8)
L/MB	6.7±0.1	6.7±0.1	7.1±0.1	7.2±0.1	7.2±0.1	7.1±0.1	-	7.3±0.1	7.7±0.1
	(6.2-7.2)	(6.5-7.2)	(6.6-8.0)	(6.7-8.6)	(6.8-7.8)	(6.6-7.8)	-	(6.7-8.1)	(7.0-9.0)

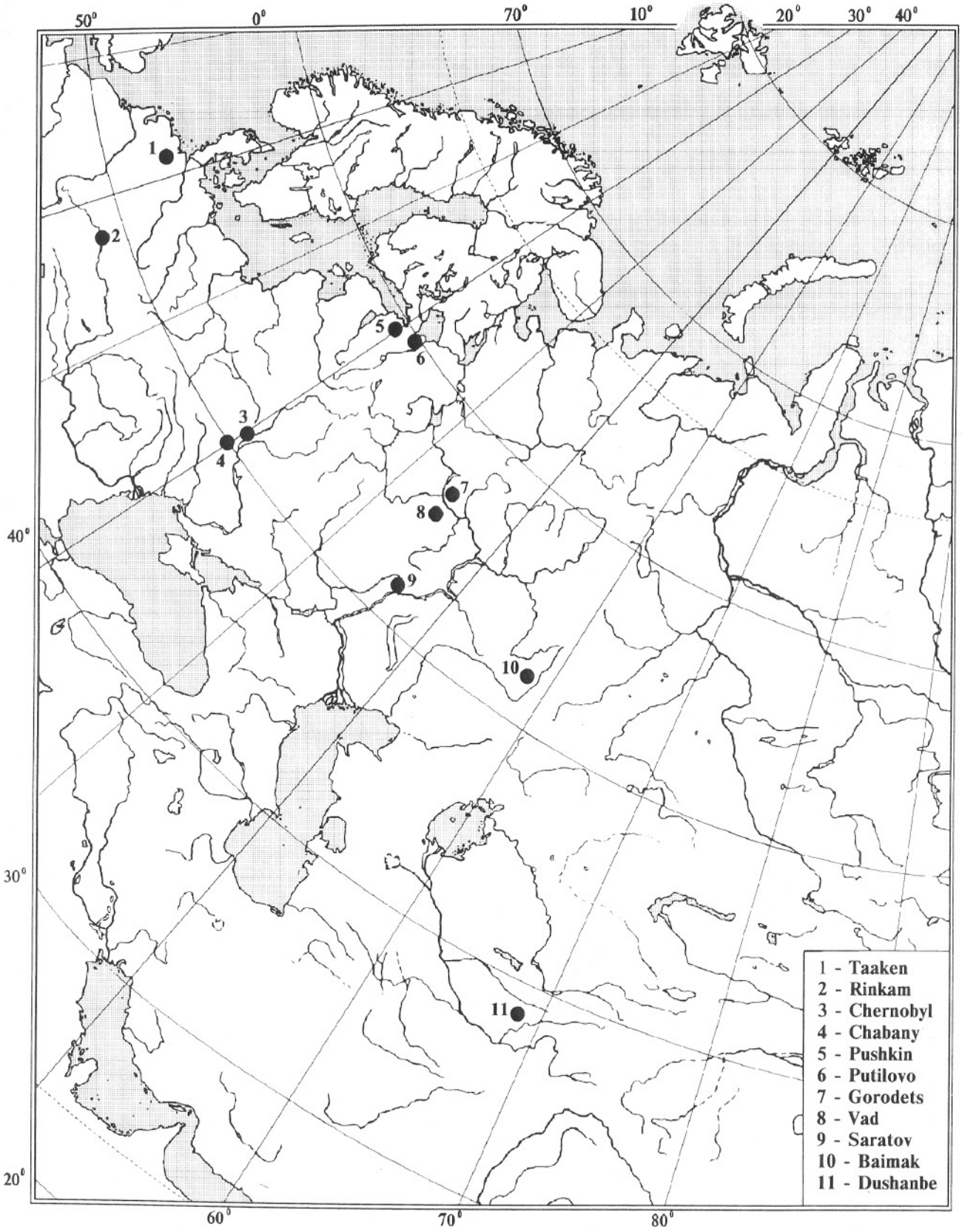

Fig. 1. Geographical origin of the *Heterodera 'avenae'* populations studied.

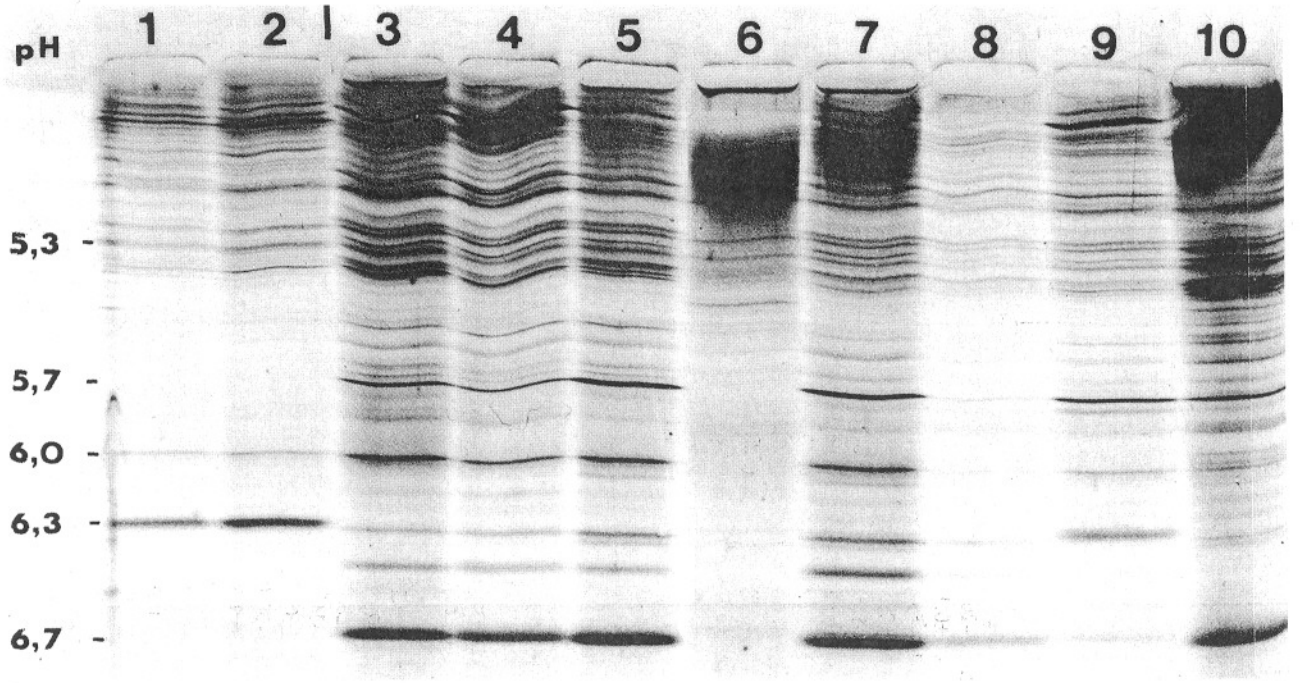

Fig. 2. IEF protein patterns of *Heterodera avenae*, populations Rinkam, Taaken (lanes 1,2); *Heterodera 'avenae'*, populations Chabany (3), Chernobyl (4), Pushkin (5), Gorodets I (7), Gorodets II (8), Vad (9), Baimak (10); *Heterodera* spec., population Putilovo (6).

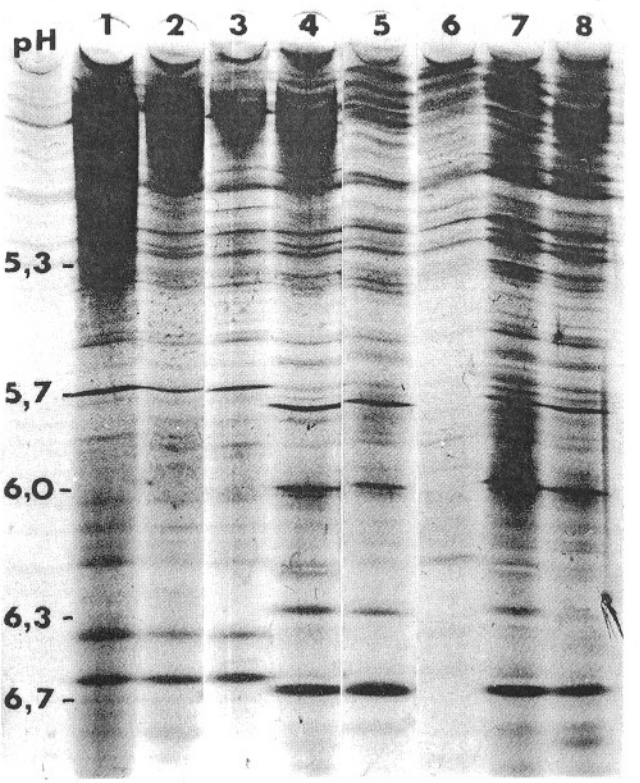

Fig. 3. IEF protein patterns of *Heterodera* spec., populations Schleswig-Holstein (1), Bavaria (2), Putilovo (3); *Heterodera filipjevi*, population Dushanbe (5); *Heterodera mani* (6); *Heterodera 'avenae'*, population Pushkin (4), Chernobyl (7), Saratov (8).

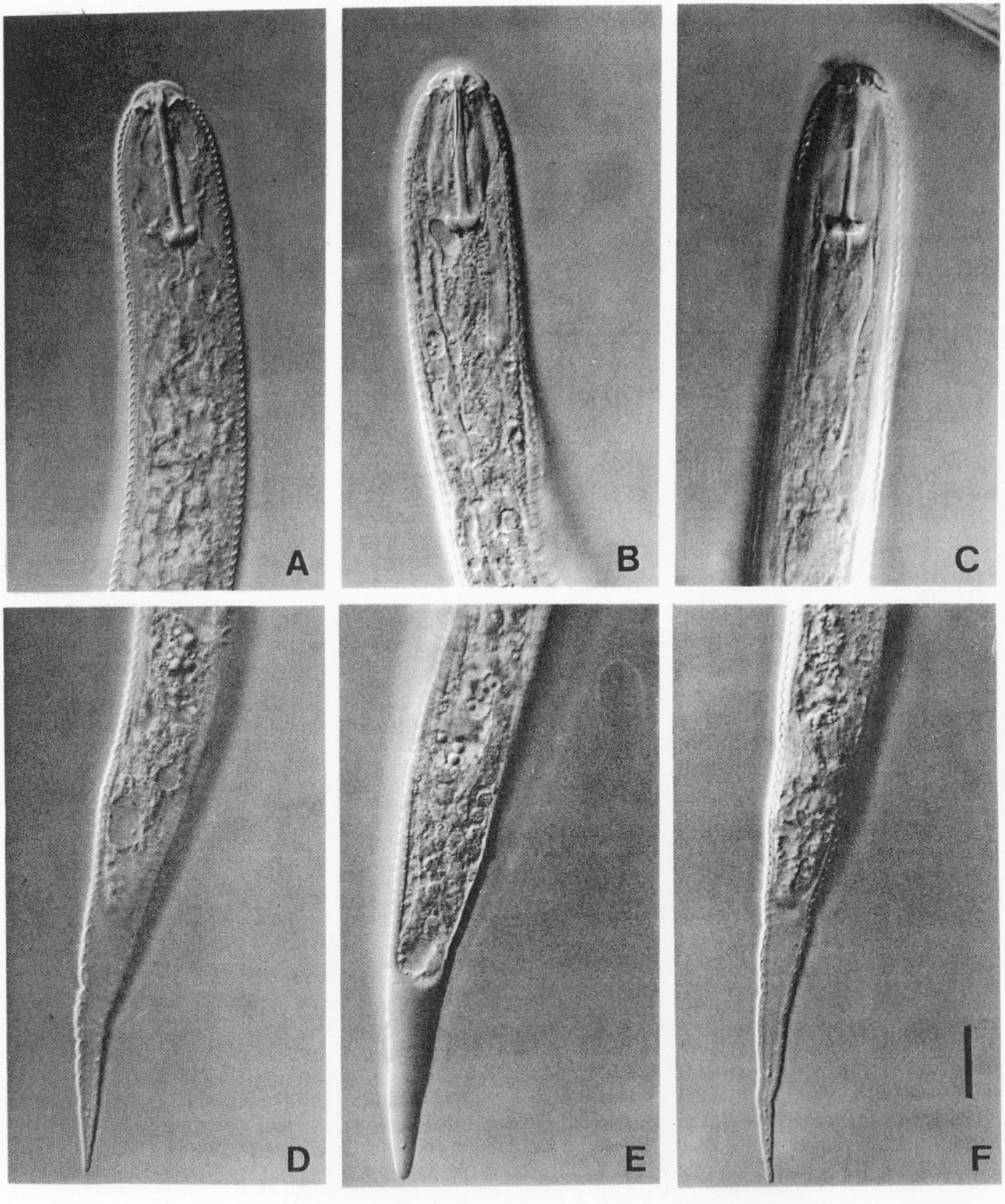

Fig. 4. Anterior end and tail of 2nd stage juveniles of *Heterodera avenae*, Taaken population (A, D); *H. filipjevi*, Dushanbe population (B, E) and *Heterodera* sp., Putilovo population (C, F). Scare bar: 10 μm.

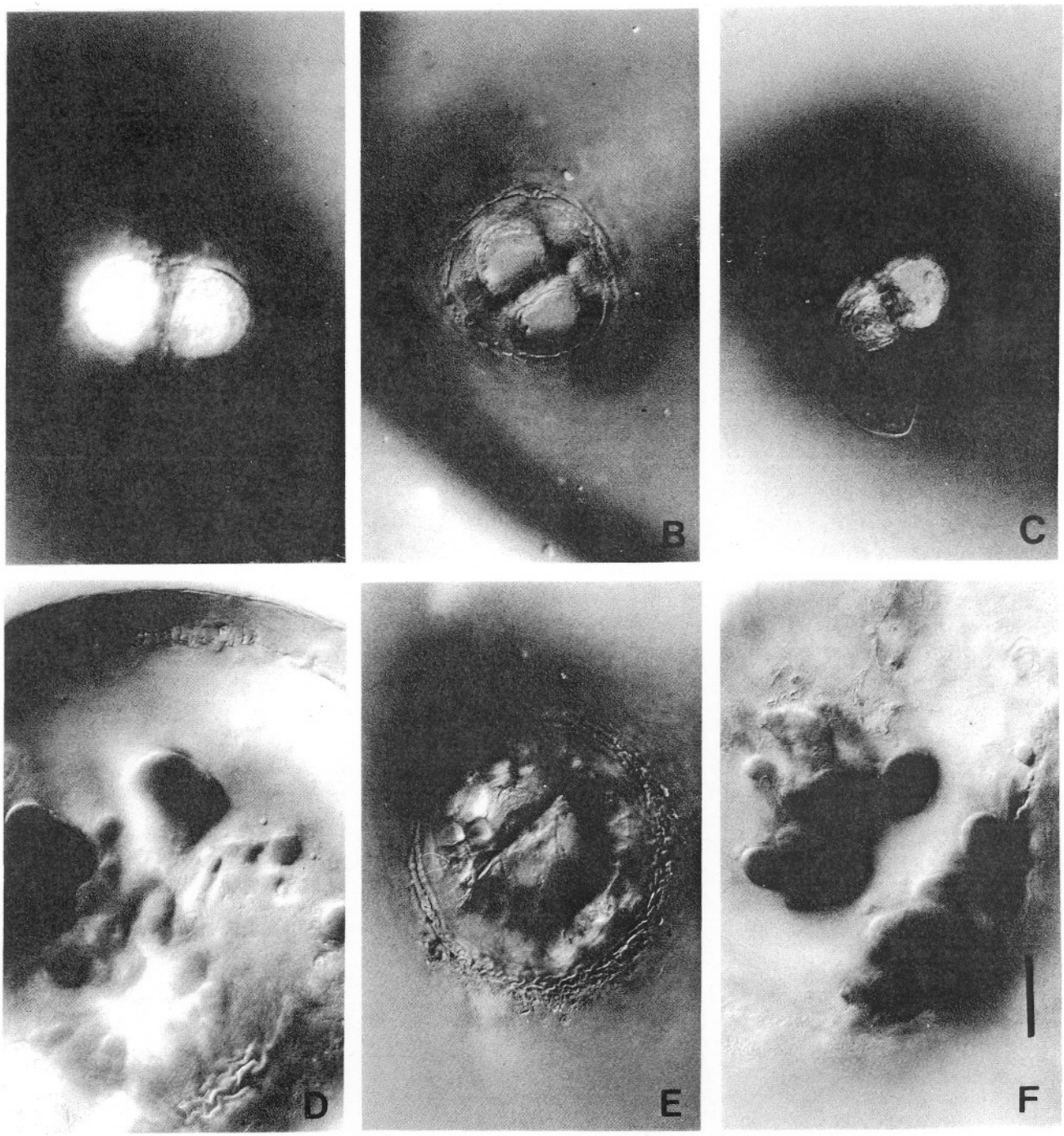

Fig. 5. Fenestration pattern and bullae region in cyst cones of *Heterodera avenae,* Taaken population (A, D); *H. filipjevi*, Dushanbe population (B, E) and *Heterodera* sp., Putilovo population (C, F). Scale bar: 20 μm.

Putilovo population from the other populations (Fig. 6A). Use of the 1-Pearson correlation coefficient (average linkage method) with the same characters resulted in clear distinction of the Taaken, Rinkam and Putilovo populations from the other populations studied morphometrically (Fig. 6B).

DISCUSSION

Isoelectric focusing of the protein extracts proved to be a useful method for grouping populations in the *H. avenae* complex used in the present study. The results were supported by certain morphological

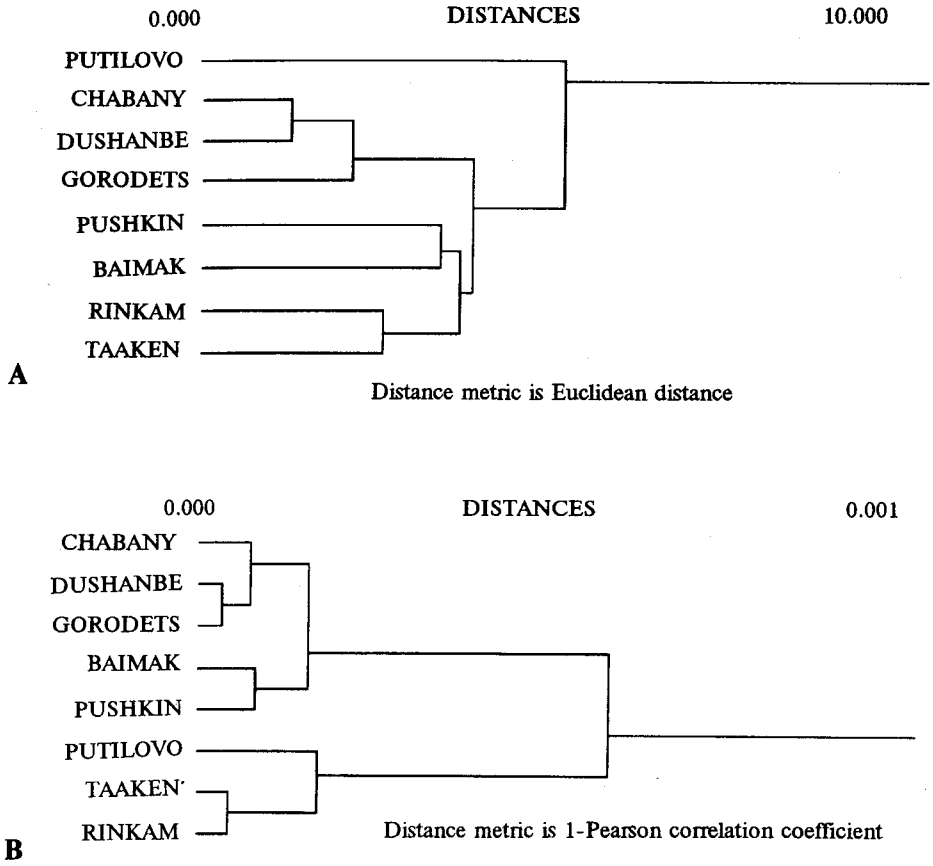

Fig. 6. Tree diagrams illustrating cluster analysis of eight cyst nematode populations of the *H. avenae* group, based upon morphometric characters of second stage juveniles and cyst vulval cones. A) Single linkage method; B) Average linkage method.

characters of the cysts and the 2nd stage juveniles.

The most remarkable observation is that among the ten populations of the *H. avenae* group from the former USSR studied by us not a single population of *H. avenae* (*s. str.*) could be found. Whereas one population (Putilovo) can be grouped with the two German populations of an apparently undescribed species belonging to the *H. avenae* group, the remaining nine populations form a rather uniform group, which is well distinguished from *H. avenae*.

The Dushanbe population used in this study was collected by A.R. Madzhidov from a wheat field near Dushanbe (Tadzhikistan) and considered by him as a representative of the species *H. filipjevi*, which he had originally described from Tadzhikistan. The present study confirmed close agreement of the newly collected Tadzhik material with the original description of the species (Tables 1 and 2). Because of close agreement in biochemical and morphological characters of the cysts and the 2nd stage juveniles to the Dushanbe population, all the other populations in group 2 are considered as conspecific. As a result *H. filipjevi* comes out to be a cyst-forming species widely distributed in the former USSR with a range of occurrence from as far north as theLeningrad region to Tadzhikistan in the south and to the Kiev area in the west. Madzhidov (1991) reported the presence of *H. filipjevi* from many parts of Tadzhikistan.

The results of our studies support evidence for a (western) European origin of *H. avenae sensu stricto* as suggested by Meagher (1977), rather than an origin in the arid continental Euroasiatic region as assumed by Krall & Krall (1978) for the *H. avenae* group.

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Субботин С.А., Румпенхорст Г.Е., Штурхан Д. Морфологическое и электрофоретическое изучение популяций комплекса *Heterodera avenae* из бывшего СССР.

Резюме. Изоэлектрическое фокусирование протеинов цист десяти популяций '*Heterodera avenae*' из России, Украины и Таджикистана показало сходную картину распределения белков для всех исследованных популяций за исключением одной из Путилово, Ленинградская область. Сравнение с популяциями *H. avenae, H. mani* и нового неописанного вида из группы *H. avenae* из Германии показало, что популяции из бывшего СССР отличаются от *H. avenae* и от других популяций, включенных в исследование. Только популяция из Путилово имела сходную картину белков с популяциями нового неописанного вида. Морфологическое и морфометрическое изучение популяций из бывшего СССР подтвердило результаты электрофоретических исследований. Популяция из Таджикистана, сходная по описанию с *H. filipjevi*, и все популяции из бывшего СССР рассматриваются как представители одного вида, за исключением популяции из Путилово, принадлежащей к другому неописанному виду комплекса *H. avenae*.