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THE “POTATO ROAD” AND BIOGEOGRAPHIC HISTORY OF POTATO CYST NEMATODE POPULATIONS FROM DIFFERENT CONTINENTS

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The general opinion about the introduction of potato in Europe is the one regarding the direction from South America to Spain and subsequent distribution to other continents. Some historical data point out an alternative road. The potato spread from its place of origin to other continents in the light of parasite-host relationship, relying on nematode molecular data, is discussed in the present work. Biogeographic history of potato cyst nematode populations from different continents is in congruence with historical records.

Key words: biogeography, potato, potato cyst nematodes

INTRODUCTION

The potato originated in the highlands of Peru particularly the region around Lake Titicaca. Potatoes were first domesticated at least 7 000 years ago. The food security provided by potato and maize allowed the development of civilizations such as the Huari and Inca. The Spanish conquest of South America began in 1532, bringing to an end the Inca Empire. As the Spanish extended their control of this vast new land they recorded the manner and customs of the native population. Pedro de Cieza Leon, a Spanish soldier was the first European to record the existence of the potato, in 1538, in the Upper Cauca valley in what is now Colombia (CHOISEUL *et al.*, 2008).

From the area of origin, the potato spread all over the world. Historical data suggest that there were two main “potato roads” to Europe in the past. The one was leading directly from Latin America to Spain and the other one was the introduction of the potato from North America to England.

From Spain the potato found its way to Italy and then it went to Vienna through the Governor of Mons in Hainhault (Belgium) who sent some to Clusius in 1598. To England the

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potato found its way from North America, being brought from Virginia by the colonists sent out by Sir Walter Raleigh in 1584. He was the first who planted the potato on his estate of Youghal, near Cork and soon it was carried into Lancashire. The use of potatoes became more and more known after the middle of the 18th century and has greatly increased in all parts of Britain. It is also very general in Holland and many parts of France and Germany and is increasing rapidly in Russia. In Spain and the East and West Indies they are not much cultivated, owing to the heat of the climate; but in all the temperate parts of North America, Australasia and South America they are grown by the colonists (SANDERS, 1905).

Introducing the potato to Europe they brought along its parasites – potato cyst nematodes (PCN): *Globodera pallida* (Stone) Behrens and *G. rostochiensis* (Wollenweber) Behrens. It took four centuries, from the 16th century when potato was first introduced to Europe to the second half of the 20th century, for *Globodera* parasites to be described. Nowadays they are present in all European potato growing regions, especially on the Balkan peninsula, either PCN or both are reported (ORO, 2011).

MATERIALS AND METHODS

For phylogenetic analyses the ITS1-5.8S-ITS2 region of PCN is used for this study. The comparison was made with sequences of PCN populations from different continents via NCBI GenBank database and scientific literature presented in Table 1. Serbian PCN populations, previously morphologically and molecularly characterized (ORO *et al.*, 2010; ORO and ORO RADOVANOVIĆ, 2012; ORO *et al.*, 2012) are also included.

Table 1 List of species used for phylogenetic analyses with locality and GenBank accession numbers

No.	Species	Acc. No.	Literature	Locality-Country
1.	<i>G. pallida</i>	DQ097514	-	Argentina
2.	<i>G. pallida</i>	GU084817	-	Porvenir-Peru
3.	<i>G. pallida</i>	GU084802	-	Apurimac-Peru
4.	<i>G. pallida</i>	EU006704	-	Huancabamba-Peru
5.	<i>G. pallida</i>	AF016867	-	Tiabaya-Peru
6.	<i>G. pallida</i>	AF016868	-	Santa Ana-Junin-Peru
7.	<i>G. pallida</i>	GU084818	-	La Libertad-Peru
8.	<i>G. pallida</i>	GU084804	-	Cusco-Peru
9.	<i>G. pallida</i>	EU006705	-	Amantani-Peru
10.	<i>G. pallida</i>	GU084805	-	Puno-Peru
11.	<i>G. pallida</i>	GU084798	-	Taquile-Peru
12.	<i>G. pallida</i>	AF016865	-	Pilayo-Peru
13.	<i>G. pallida</i>	HQ260427	-	Otuzco-Peru
14.	<i>G. pallida</i>	HQ260426	-	Capachica-Peru
15.	<i>G. pallida</i>	HQ260428	-	Huamachuco-Peru
16.	<i>G. pallida</i>	AF016866	-	Peru-Bolivia border
17.	<i>G. pallida</i>	GU084815	-	Filipic-Chile
18.	<i>G. pallida</i>	GU084814	-	Cassola-Chile
19.	<i>G. pallida</i>	GU084801	-	Terre de Feu-Chile
20.	<i>G. pallida</i>	EF153838	-	York-UK

21.	<i>G. pallida</i>	GQ294522	-	Avondale-Canada
22.	<i>G. pallida</i>	EF153837	-	Idaho-USA
23.	<i>G. pallida</i>	AF016871	-	Spain
24.	<i>G. pallida</i>	DQ847109	-	Risby-UK
25.	<i>G. pallida</i>	AJ606687	-	Uzhorod-Ukraine
26.	<i>G. pallida</i>	EF622533	-	LI Pali-NZ
27.	<i>G. pallida</i>	AF016869	-	Northern_Ireland
28.	<i>G. pallida</i>	AF016870	-	Romania
29.	<i>G. pallida</i>	-	Blok <i>et al.</i> , 1998	The Netherlands
30.	<i>G. pallida</i>	EU855119	-	Poland
31.	<i>G. pallida</i>	HM159428	-	Kladnica-Serbia
32.	<i>G. rostochiensis</i>	GU084809	-	Laguna Pampa-Bolivia
33.	<i>G. rostochiensis</i>	GU084810	-	Tiraque-Bolivia
34.	<i>G. rostochiensis</i>	AF016872	-	Allpachaka-Peru
35.	<i>Globodera</i> sp.	GU084808	-	Antofagasta-Chile
36.	<i>G. rostochiensis</i>	AF016877	-	Cuapiaxtla-Mexico
37.	<i>G. rostochiensis</i>	DQ847117	-	Moscow-Russia
38.	<i>G. rostochiensis</i>	AB207271	-	Japan
39.	<i>G. rostochiensis</i>	EF622532	-	Victoria-Australia
40.	<i>G. rostochiensis</i>	AY700060	-	Libelice-Slovenia
41.	<i>G. rostochiensis</i>	DQ847118	-	Scarcliffe-UK
42.	<i>G. rostochiensis</i>	AF016876	-	Falkland_Islands
43.	<i>G. rostochiensis</i>	EF153840	-	York-UK
44.	<i>G. rostochiensis</i>	EF153839	-	New York-USA
45.	<i>G. rostochiensis</i>	GQ294521	-	British Columbia-Canada
46.	<i>G. rostochiensis</i>	FJ212164	-	Newfoundland-Canada
47.	<i>G. rostochiensis</i>	EU855120	-	Poland
48.	<i>G. rostochiensis</i>	DQ887562	-	South_Africa
49.	<i>G. rostochiensis</i>	AF016873	-	Peru
50.	<i>G. rostochiensis</i>	AF016874	-	Anta-Peru
51.	<i>G. rostochiensis</i>	HM159430	-	Milatovici-Serbia
52.	<i>G. rostochiensis</i>	KC508111	-	Gojna Gora-Serbia

The sequences were aligned by using ClustalW. The genetic distances among 52 PCN populations were calculated using pairwise distances of Mega 4 (TAMURA *et al.*, 2007). Phylogenetic trees were created using Phylml 2.4.4. (GUINDON and GASCUEL, 2003) and MrBayes 3.1.2. (HUELSENBECK and RONQUIST, 2005). The Phylml tree was obtained using model of GTR (TAVARE, 1986) + G as the model of nucleotide substitution. Evaluation of dendrogram reliability was calculated by the bootstrap test (FELSENSTEIN, 1985). The dendrogram obtained by Bayesian inference was created by 1 200 000 generations of MCMC (Markov Chain Monte Carlo), with the frequency of the sample of 100, and burnin function of

3 000. Nucleotide evolution model was GTR+I+G. Posterior probabilities are shown next to the node. Values less than 70% are omitted.

RESULTS

Pairwise distances were used as matrix for creating a 52X52 table that is not suitable for presentation so we created a chart (Fig. 1). Bar lengths represent genetic distances among all populations with each other, varying from 0.00 to 5.59. Shorter bars show distances within species while longer bars represent distances between two PCN species. The rows with the same motif and length indicate same sequences such as populations: 4-7, 20-22, 44-45 etc.

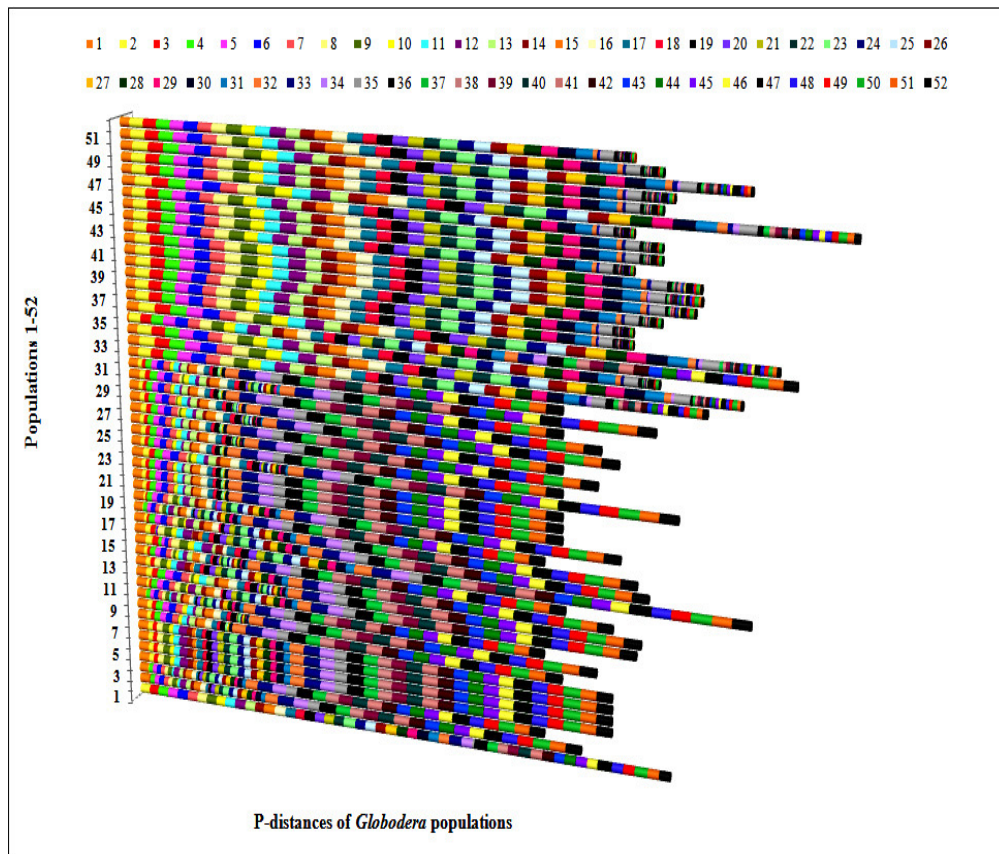


Fig.1 Pairwise distances of PCN populations presented in Table 1

Generally, both dendrograms employing Maximum Likelihood and Bayesian inference (Fig. 2 and Fig. 3, respectively) are in agreement.

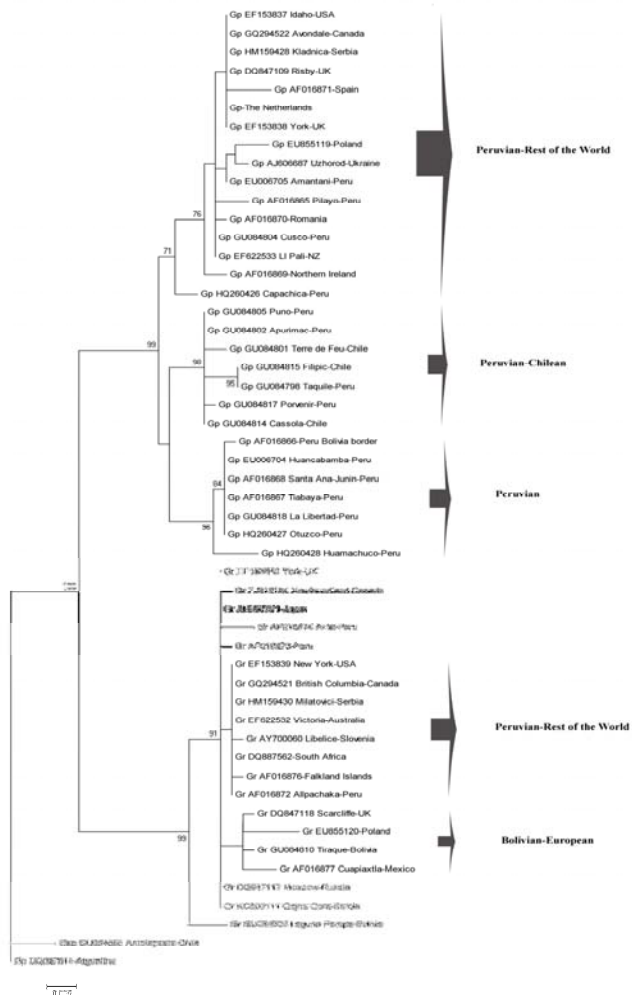


Fig. 2 Dendrogram of PCN populations derived from Maximum Likelihood based on ITS1-5.8S-ITS2 rRna sequences

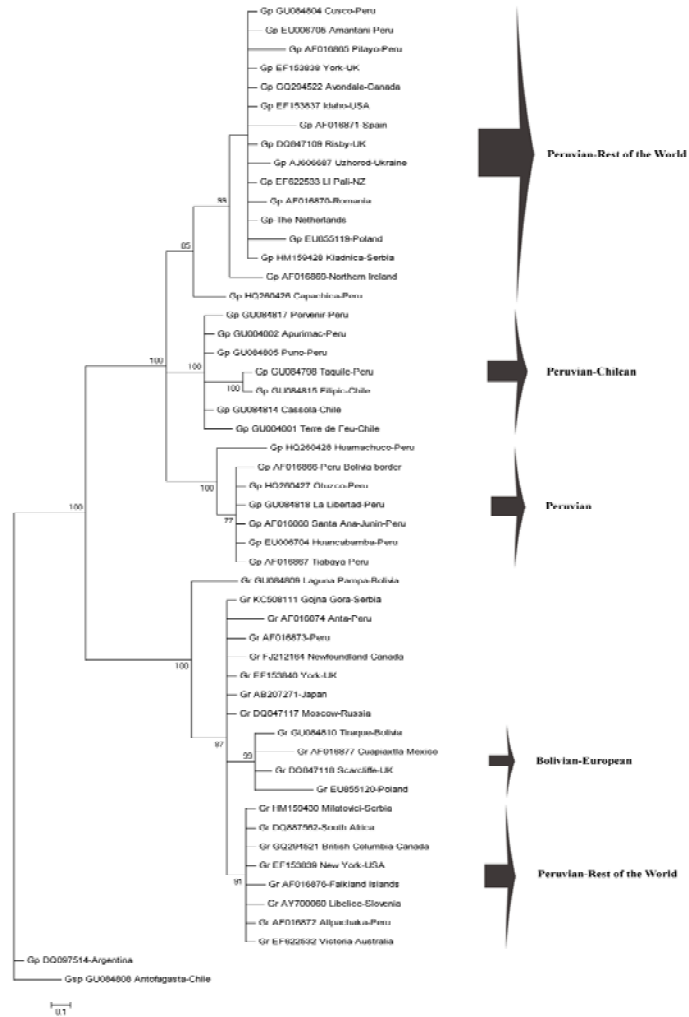


Fig. 3 Dendrogram of PCN populations derived from Bayesian inference based on ITS1-5.8S-ITS2 rRna sequences

Regarding *G. pallida* populations, dendrograms show three clusters. The first one, Peruvian-rest of the world with the following localities: Cusco, Amantani, Pilayo and Capachica from Peru, York (UK), Avondale (Canada), Idaho (USA), Spain, Risby (UK), Uzhorod (Ukraine), Li Pali (New Zealand), Romania, The Netherlands, Poland, Kladnica (Serbia), Northern Ireland. The next cluster is Peruvian-Chilean with Peruvian populations (Porvenir, Apurimac, Puno, Taquile) and Filipic, Cassola and Terre de Feu from Chile. The third cluster is a strictly Peruvian representing populations only from Peru and located mainly in the central part, north of Titicaca, comprising: Huancabamba, Tiabaya, Santa Ana-Junin, La Libertad, Otuzco, Huamachuco and a population from border to Bolivia.

Phylogenetic relationships of *G. rostochiensis* populations depict two main groups: Peruvian-rest of the world and Bolivian-European as a second one. There is a group of unresolved populations from Peru, Europe and Asia. The Peruvian-rest of the world group represents Allpachaka population from Peru with Victoria (Australia), Libelice (Slovenia), Falkland Islands, New York (USA), British Columbia (Canada), South Africa and Milatovici (Serbia). The second Bolivian-European group clustered populations: Tiraque (Bolivia), Cuapiaxtla (Mexico) with Scarcliffe (UK) and a population from Poland.

DISCUSSION

Based on distribution of species EVANS *et al.*, (1975) reported that *G. pallida* was dominant north of Lake Titicaca in Peru, Ecuador and Colombia. *Globodera rostochiensis* was dominant south of the lake (parts of Peru and Bolivia). In the southern parts of Peru, both species were present around the lake.

The Western European populations of *G. pallida* are derived from a single restricted area in the extreme south of Peru, located between the north shore of the Lake Titicaca and Cusco (PLANTARD *et al.*, 2008), data based on cytochrome b and microsatellite sequences. Phylogenetic data of the Peruvian-rest of the world clade confirm not only origin of European populations in area of Cusco but the same origin of *G. pallida* populations from USA, Canada and New Zealand as well.

According to MADANI *et al.*, (2010) Canadian *G. pallida* is almost identical to European and USA populations and formed a large clade with all these populations on the phylogenetic trees. The same study also supports a previously proposed hypothesis regarding introduction of *G. pallida* from a restricted area in Peru, firstly into Europe with subsequent spread to other continents including North America. However, SANDERS (1905) described that the potato's alternative road of introduction to Europe (Ireland, England) was from North America. Molecular data point out equality of sequences from York (UK) and Idaho (USA) but do not resolve the direction of PCN introduction.

The next Peruvian-Chilean cluster from the dendrograms suggests the possible origin of Chilean *G. pallida* populations from area located on the west of Titicaca (Puno-Porvenir-Apurimac) in Peru. The third Peruvian cluster represents populations only from Peru which are located mainly on Central Cordillera, north of the lake.

The biogeographic history of European populations of *G. rostochiensis* inferred from the dendrograms suggest multiple entries of the golden nematode. The Peruvian-rest of the world group represents populations from South Africa, Australia, North America (USA and Canada), Europe and Peru with Allpachaka locality as a possible site of origin of most world populations. The other Bolivian-European cluster suggesting Bolivia as another possible site of origin. There

is also a population from Mexico, somewhat different, in the same subclade. In both clusters there are European populations of *G. rostochiensis* originating from different sites indicating its multiple introduction.

According to PICARD *et al.*, (2008), the Peruvian populations of *G. pallida* exhibit a clear evolutionary pattern with deeper more ancient lineages occurring in the Andean southern Peru and shallower, younger lineages occurring progressively northwards, demonstrating that altitude in the Peruvian Andes was acquired longitudinally from south to north i.e. in the direction of decreasing orogenic volume. GRENIER *et al.*, 2010 argued that the uplift of the Andes Mountains has triggered a variety of adaptive biotic radiations for Solanaceous plant-parasitic nematodes and has represented a key factor for the evolution and specialisation of *Globodera* species.

The great Inca civilization and Empire before them left Inca road system linked together about 40 000 kilometers. Placed along the road were small villages which provided lodging and food (VOLPE MARTINCUS *et al.*, 2012). As one of main agriculture crops Incas grew potato. The great genetic diversity of South American PCN populations, as indicated in PLANTARD *et al.*, (2008), may be the result of constant mix of populations since the people transported and grew potato all the time along the Inca road which generally coincide with PCNs occurrence and has longitudinal south-north or north-south direction. Thus, the «Great Inca road» became «PCN road» since potato was followed by its parasites during centuries.

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**“PUT KROMPIRA” I BIOGEOGRAFSKA ISTORIJA POPULACIJA CISTOLIKIH
NEMATODA KROMPIRA SA RAZLIČITIH KONTINENATA**

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Izvod

Generalno mišljenje o introdukciji krompira u Evropu je pravac iz Južne Amerike do Španije i naknadna distribucija na druge kontinente. Neki istorijski podaci ukazuju i na alternativni put. U radu je diskutovano širenje krompira od mesta porekla do drugih kontinenata u svetlu odnosa parazit-domaćin, bazirajući se na molekularne podatke nematoda. Biogeografska istorija cistolikih nematoda krompira sa drugih kontinenata je u saglasnosti sa istorijskim podacima.

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