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POTATO PHYTOPATOGENS OF GENUS *Dickeya* — A MINI REVIEW OF SYSTEMATICS AND ETIOLOGY OF DISEASES

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Abstract

In recent years, plant growers in Russian Federation have met significant changes in species of bacterial pathogens causing economically harmful diseases of potatoes that is associated with the import of infected planting material, recent climatic changes favorable for bacterial disease development, over-wintering of the pathogens and their vectors (insects, mites and nematodes), and with lack of bactericidal pesticides for integrated plant protection. Damage of potato plants (*Solanum tuberosum* L.) by *Enterobacteriaceae* family is one of the greatest problems in production of seed and food potatoes. The bacteria cause a black leg, wet rotting of the stem in the field, and soft rot of potato tubers in storage. In temperate climate, the bacterial diseases of potatoes was usually caused by two species of genus *Pectobacterium*, *Pectobacterium atrosepticum* as a pathogen of black leg of potato, and *Pectobacterium carotovorum* causing a soft rot of potato and different vegetable crops (A.N. Ignatov et al., 2015). However, recently, many countries have faced the spreading on potato fields of new enterobacteria of genus *Dickeya*, which has been normally considered as pathogen of ornamentals and vegetables, particularly in countries of tropical and subtropical climate. A detailed study of genus *Dickeya* has shown that this diverse group of bacteria affects a number of plant species, including many economically important crops (I.K. Toth et al., 2011). The strains differed in attacked host plants, and phenotypic properties. It was found that strains isolated from European potato fields in years 1979-1994 were mainly related to *D. dianthicola*, the species well-adapted to temperate climatic regions. However, since 2005, the variants of *Dickeya*'s biotype III, referred to the new species *D. solani* were detected on potato in Europe, and soon became one of the most aggressive pathogens of this crop. Clarification of the taxonomic position and diversity within species of the genus *Dickeya* (*D. chrysanthemi*, *D. dadantii*, *D. dianthicola*, *D. dieffenbachiae*, *D. paradisiaca*, *D. zaeae*, *D. solani*) gives a chance for development of new methods of diagnostics and control measures against these pathogens (L. Tsror et al., 2011). Except for *D. dieffenbachiae*, all the species of this genus can affect potatoes. Infection of *D. dianthicola* and *D. solani* has been already reported in some regions of the European part of the Russian Federation (A.N. Karlov et al., 2010, 2011; A.M. Lazarev, 2013), and genome sequencing of the isolated bacteria showed their identity with strains of this genus isolated in Western Europe and Latin America (S.V. Vinogradova et al., 2014). The spreading of these pathogens abroad and in Russia, data on taxonomic position and description of their biological properties, and sources of infection, created ground for development of control measures against them. It is believed that *D. dianthicola* and *D. solani* have aroused as potato pathogens moving from vegetable crops in the early 1990s. Now they are striking plants in European countries, USA, South America, Africa and Asia. *D. dianthicola* and *D. solani*, first described at the territory of the Russian Federation in 2009, cause serious potato losses in Russia in recent years. In 2009-2013, the annual two-fold increase of contamination of seed potatoes by these pathogens was documented. Thus, in just 4

years, the prevalence of pathogens of the genus *Dickeya* in potato seed lots in Russia increased from 3 % to 26-28 % (A.N. Ignatov et al., 2015). Control of these pathogens on potato is based on the rejection of contaminated material and prevention of contamination at all stages of the technological cycle of seed potatoes. Potato varieties resistant to these pathogens have not been yet discovered.

Keywords: potatoes, bacterial diseases, blackleg, soft rot, *Pectobacterium*, *Dickeya*

In recent years, in the Russian Federation significant changes in species of bacterial pathogens and their enhanced harmfulness have been noted. Primarily, it is associated with the import of infected seeds and planting materials, secondarily with climatic changes favorable for bacterial disease development, over-wintering of the pathogens and their vectors (insects, mites and nematodes), and thirdly with lack of the chemicals with high bactericidal effect [1].

Lack of information about pathogens diversity makes it impossible to assess potential losses from disease and to choose the correct strategy for selection of protective measures.

We analyzed available information about spreading, harmfulness and genetic diversity of new potato pathogens from genus *Dickeya* causing bacteriosis which are of interest in developing diagnostics methods and phytopathogen control.

Black leg and wet rotting pathogens belong to the group of pectolytic enterobacteria including species of the genus *Pectobacterium* (earlier *Erwinia*). The complex of *P. carotovorum* species includes subspecies *P. carotovorum* subsp. *actinidiae*, *P. carotovorum* subsp. *brasiliense*, *P. carotovorum* subsp. *carotovorum* and *P. carotovorum* subsp. *odoriferum*. *P. atrosepticum*, *P. betavasculorum* and *P. wasabiae* are grouped apart from *P. carotovorum*. Several new species (*P. aroidearum*, *P. cacticida*, *P. parmentieri*) were described for certain host plants [2, 3]. Polymorphous species of phytopathogenic bacteria *P. chrysanthemi* [4] which previously was a member of the genus *Pectobacterium*, in 2005 was defined as a separate genus *Dickeya* [5] based on the complex of phenotypic traits and genetic analysis data.

In Russia, the prevalence of *Dickeya dianthicola* and *D. solani* causing significant yield losses of potato was first described in 2009 [6]. To date, pathogens of the genus *Dickeya* have been found in all Russian regions [1, 6-8]. In 2009-2013, the infestation increased 2-fold each subsequent year. In just 4 years, the prevalence of the genus *Dickeya* in seed potatoes increased from 3% to 26-28% [1].

Whole genome sequencing of two strains *D. solani* D12 and Dfil, isolated in Russia in 2009 [9], showed that they have almost complete homology with strain IP2222 (T) detected in the Netherlands [10]. So, the most probable cause of *D. solani* penetration to the Russian Federation is import of the seed potato from countries of Western Europe, where in 2007 an extensive black potato leg epiphytosity on seed fields was noted [11]. Russian strains of *D. dianthicola* also had high genetic homogeneity and proximity to typical culture isolated earlier in Latin America and Europe [3].

Original name of *P. (Erwinia) chrysanthemi* is due to the fact that the pathogen was first described as a causative agent of the bacteriosis in chrysanthemums [4]. Further it has been shown that these microorganisms cause plant diseases in plant of at least 16 dicotyledonous and 10 monocotyledonous families [5, 12, 13]. R.A. Lelliott and R.S. Dickey [13] divided *P. chrysanthemi* species into 6 pathovars based on their host specificity: *chrysanthemi*, *dianthicola*, *dieffenbachiae*, *paradisiaca*, *parthenii* and *zeae*.

DNA hybridization and biochemical characterization of pectinolytic bacteria had led to the separation of *P. chrysanthemi* species from the genus *Pectobacterium* into a new genus named *Dickeya* in honor of the outstanding microbiologist R.S. Dickey [5] who had devoted many years to this bacterium research [13,

14]. To date, according to the official microbiological LPSN (List of prokaryotic names with standing in nomenclature) [15], the genus *Dickeya* is clearly differentiate in the following species: *D. aquatica*, *D. chrysanthemi*, *D. dadantii*, *D. dadantii* subsp. *dadantii*, *D. dadantii* subsp. *dieffenbachiae*, *D. dianthicola*, *D. fangzhongdai*, *D. paradisiaca*, *D. solani*, *D. zaeae*. All *Dickeya* spp. members, except for *D. paradisiaca*, are isolates from the cultivated and ornamental plants, including those imported to Russia from different countries [16].

The table shows host plants the most frequently affected by *Dickeya* spp. species, with synonyms.

Bacteria host plants of the genus *Dickeya* [11, 12, 14]

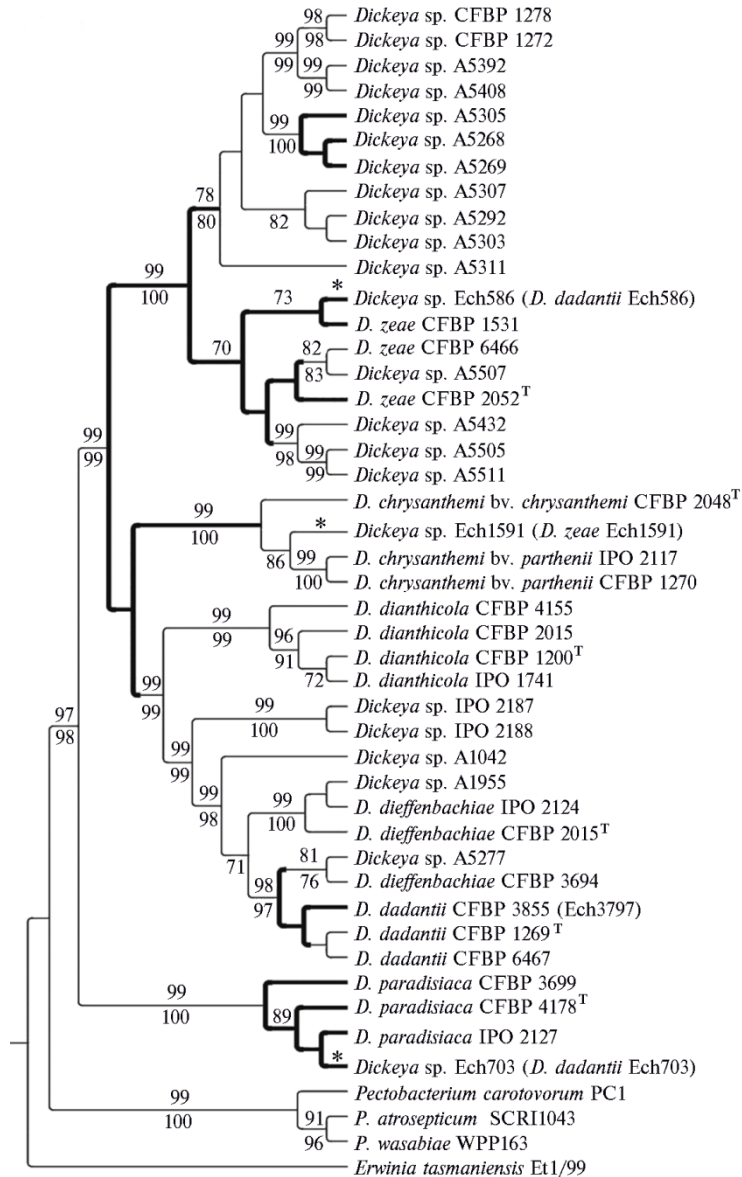
Species	Host plants
<i>Dickeya dianthicola</i> [syn.: <i>Pectobacterium</i> (<i>Erwinia</i>) <i>chrysanthemi</i> , biobars I, VII, IX; <i>E. chrysanthemi</i> pv. <i>dianthicola</i>]	Carnation Chinese, potatoes, tomato, chicory, artichoke, dahlia, hyacinth, iris, kalanchoe
<i>D. dadantii</i> [syn.: <i>P. (E.) chrysanthemi</i> , biobars III and VIII]	Pelargonium, potato, Chinese yam, pineapple, banana, carnation species, euphorbia, senpolia, maize, philodendron, scindapus (divel's ivy), ragwort, eryngium (sea holly), arrowhead vine
<i>D. zaeae</i> [syn.: <i>P. (E.) chrysanthemi</i> , biobars III and VIII]	Maize, potato, pineapple, banana, tobacco, rice, Para grass, chrysanthemum, wheat, carnation species, cantante, ahmeya (ehmeya), scindapus, cabbage, difffenbachia
<i>D. chrysanthemi</i> bv. <i>chrysanthemi</i> [syn.: <i>P. (E.) chrysanthemi</i> , biobar V; <i>P. (E.) chrysanthemi</i> pv. <i>chrysanthemi</i>]	Chrysanthemum, chicory, tomato, sunflower, potato, carrot, patrenium (wild quinine), euphorbia
<i>D. paradisiaca</i> [syn.: <i>P. (E.) chrysanthemi</i> , IV биовар; <i>P. (E.) chrysanthemi</i> pv. <i>paradisiaca</i> ; <i>E. aradisiaca</i> ; <i>Brenneria paradisiaca</i>]	Banana
<i>D. dieffenbachiae</i> [syn.: <i>E. chrysanthemi</i> , biobar II; <i>P. (E.) chrysanthemi</i> pv. <i>dieffenbachiae</i>]	Dieffenbachia, tomato
<i>D. fangzhongdai</i>	Pear
<i>D. aquatic</i>	The host plant was not identified

Evolutionarily, genus *Dickeya* is monophyletic and represents a sister clade for the genus *Pectobacterium* (Fig.), and they differ substantially from other phytopathogenic and non-symbiotic enterobacteria [17]. In addition to species similar to the previously described *P. chrysanthemi* pathovars (*D. chrysanthemi*, *dadantii*, *dieffenbachiae*, *dianthicola*, *paradisiaca*, *zaeae*), several European researchers defined strains of so-called biovar III, causing a new potato disease in Western Europe, as a new species *D. solani* [18]. *D. solani* is highly aggressive and causes typical symptoms of the potato disease (watery stem rot). Lately, the species *D. aquatic* which is often isolated from river water but still not detected in plants were identified [19], and the last of known species of the genus *Dickeya*, *D. fangzhongdai* causing pear disease, has been described recently [20].

D. dianthicola (called *E. chrysanthemi*) was first reported in the Netherlands in the 1972 [11]. Then the pathogen was detected in Israel [21], Sweden [2], Switzerland [22], Spain [23], Finland [24], France and UK [25], Poland [26], Greece [27] and Japan [28]. There were reports about *Dickeya* spp. presence in Scotland, Denmark, Hungary, Germany, and Belgium [5]. Withal, in most European countries, the losses associated with *D. dianthicola* remained low, except for Switzerland where the potato damage from *Dickeya* spp. was predominant as early as in 1992 [22]. During field tests in Finland [29] in comparing direct losses from *D. dianthicola* and *D. solani*, significant differences of tubers damage (5-6%) were not identified, but significant damage of stems with the second pathogen (73% vs. 20%) was noted. By the report of R. Czajkowski et al. [30], during a three-year study the differences in frequency of potato disease caused by *D. solani* and *D. dianthicola* was not detected. However, in another paper it was noted, that the losses from *D. solani* exceeded the harm from *D. dianthicola*, *P. atrosepticum* and *P. carotovorum* subsp. *carotovorum* [5].

Signs of new potato bacteriosis are similar to the black leg of stem and

the tuber soft rot caused by *Pectobacterium*. Unlike them, *D. dianthicola* causes tubers soft rot at higher temperature (at 27 °C), and *D. solani* causes mainly the stems wilting (watery rot) and the destruction of the vascular ring in the tubers, which remind the development of ring (*Clavibacter michiganensis* subsp. *sepedonicus*) or brown (*Ralstonia solanacearum*) potato rot. Strains *Dickeya* spp. are able to cause plants damage with lower pathogen load than *Pectobacterium*, they have more possibilities to spread through the vascular tissue and are more aggressive.



Phylogenetic tree of bacteria genus *Dickeya* constructed using *dnaA*, *dnaJ*, *dnaX* and *recN* gene sequences [17]. Strains *Dickeya* marked with an asterisk were initially defined as *D. dadantii* (Ech586, Ech703) or *D. zeae* (Ech1591). T means typical species strains. Tree branches differed in construction by some genes and combined sequences are indicated in bold. Bootstrap values $\geq 70\%$ are shown above branches for tree constructed by maximum parsimony method, and below branches for maximum credibility method.

Pre-germination development of tuber infection or its early post-germination appearance usually is followed by the damage of the mother (seed) tuber and causes plant losses. At the optimum pathogen temperature, the plants are

stunted, their leaves show yellowing, become small, hard and fold along the middle vein. The springs are located at an acute angle to the stem and growth up, and its lower part shows up from yellow-brown to dark in a color. Infected plants are pulled from the soil easily. At low temperature, infected plants may keep pace in growth with healthy ones, but with warming, their stems get dark suddenly from the ground to the upper leaves, leaves droop and gradually fade without changing color. Bacteria enter the tubers through the stolons which partly rot. Like in bacterial wilting and ring rot, genus *Dickeya* pathogens stimulate growth of saprophytic and low pathogenic microorganisms on affected tubers. Usually infected tubers remain without symptoms until the spring, with hidden (latent) infection of stolons and the vascular ring until spring planting [2]. The quantity of young tubers with a latent infection depends on blackleg development on the plants during the growing season. In particular years up to 75% of the tubers of infected plants are carriers of phytopathogenic bacteria. Under unfavorable climatic conditions (dry cool weather), the disease does not develop, and bacteria from the planting tuber through the plant and stolons penetrate into the daughter tubers without visible signs [30].

J.K. Toth et al. [11] note the ability of *Dickeya* spp. species, unlike the cold-loving *P. atrosepticum*, to attack potato in subtropical regions (e.g., in North America, North Africa, Israel and southern Europe). It is suggested that global climatic changes (especially temperature rise in spring and autumn) can aggravate the problem of new species spreading, especially *D. solani*, which has caused the largest yield losses in potato during the last 5-6 years in Europe.

The blackleg and soft rot differ from others potato diseases visually. But in the hot and dry conditions bacteriosis symptoms caused by *D. dianthicola* or *D. solani* are easily confused with the disease caused by *Verticillium dahliae* or with accelerated plant ageing [21].

In plants attacked by *Dickeya* spp. pathogens, it is important to know the sources of infection to successfully restrict their further spread. There are two ways of spreading *D. dianthicola* and *D. solani* bacteria: i) transfer through the potato seed material and other host plants, and ii) transfer through rainwater, irrigation water and pest vectors. Due to a wide range of host plants (including ornamentals), *D. dianthicola* and *D. solani* can be further spread around the world not only in the seed trade and via food potatoes, but also through sale of flower crops [11]. Thus, there are reports of the *D. dianthicola* isolation from ornamental host plants in the USA, Colombia, Japan and New Zealand [11]. We are aware of the facts of *Dickeya* spp. survival in the bitter nightshade (*Solanum dulcamara*) in Sweden [31]. In Israel, asymptomatic plant samples of the local weed species were analyzed in details for the presence of *Dickeya* spp. and aisle-weed (*Cyperus rotundus*) plants infected at a frequency of 6.7 up to 14.3% was detected [32].

There are reports of potato diseases caused by different *Dickeya* ssp. species: *D. chrysanthemi* is isolated in the USA and Taiwan [25, 26], *D. dianthicola* in Brazil [26], Peru [25, 28] and Zimbabwe [34], *D. zae* in Australia and Papua New Guinea [25, 35]. Members of the *D. zae* species were isolated from river water in Scotland and England, but were not found on potatoes [11]. *Dickeya* sp. bacteria isolated from potato plants in the Krasnodar and Stavropol territories belongs to *D. dadantii* (A.N. Ignatov, unpublished data).

Numerous researches indicate that at least one species of the genus *Dickeya* (*D. dadantii*) is closely associated with phytophagous insects. This species can colonize pea aphid (*Acyrtosiphon pisum*) and is pathogenic for three other insect species (*Drosophila melanogaster*, *Sitophilus ozuzae* and *Spodoptera littoralis*) [36, 37]. Infection transmitted by insects is possible even in a short-term nutrition on plants.

Compared to *P. carotovorum*, *Dickeya* spp. is less sensitive to cold, but better survives in water [35].

At present, the reliable information on the resistance of potato varieties to *Dickeya* spp. are absent. I.K. Toth et al. [11] showed that all tested in the UK varieties were susceptible to *D. dianthicola*. It was identified that *D. solani* can colonize potato roots within a day, regardless of the lesion presence. The pathogen was detected in stolon and stems 15 days after the soil contamination. It was also reported that *Dickeya* spp. colonizes the vascular system of potato plants more actively than *P. atrosepticum* [11, 38].

It was suggested to compare aggressiveness of tested *D. solani* strains by measuring the weight of the infected tissue using tuberous bioprobe (with 48 hour incubation at 30 °C) [39]. Nevertheless, the questions still remain about the *Dickeya* spp. interaction with other phytopathogens, especially in the latent infection, which is extremely important for the development of plant protection measures and parameters of seed potato infection while introducing new standards for growing.

With the widespread of *D. dianthicola* and *D. solani* on potato in most areas of our country, it is impossible to exclude in the near future the transition of these pathogens to tomato and other plants in greenhouses [11, 12, 14]. The biological characterization of bacteria from this genus is rather complete and a collection of their Russian strains is created. However, the species composition of genus *Dickeya* on the territory of the Russian Federation has not been determined in detail. Russian quarantine services should pay special attention to these microorganisms in view of imported potatoes from states with significant spreading of species *Dickeya* sp. Unfortunately, neither previously used, nor recently adopted regulations for assessment of seed potato infection with black leg pathogens (RF State Standard GOST 33996-2016) have made no distinction between *Dickeya* sp. and *Pectobacterium* spp., which can lead to rapid spread of *Dickeya* sp. in Russia.

Thus, we have summarized the available information on the spreading, damage and genetic diversity of new potato bacteriosis pathogens from the genus *Dickeya*. This information is of interest for the development of diagnostic tests to control seed purity and potato diseases. At the high infection load of seed potato with bacterial pathogens, it is extremely important to increase attention to new harmful species that have a significant potential for spreading and adapting to local conditions, but are not subjected to control by international and national quarantine organizations.

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