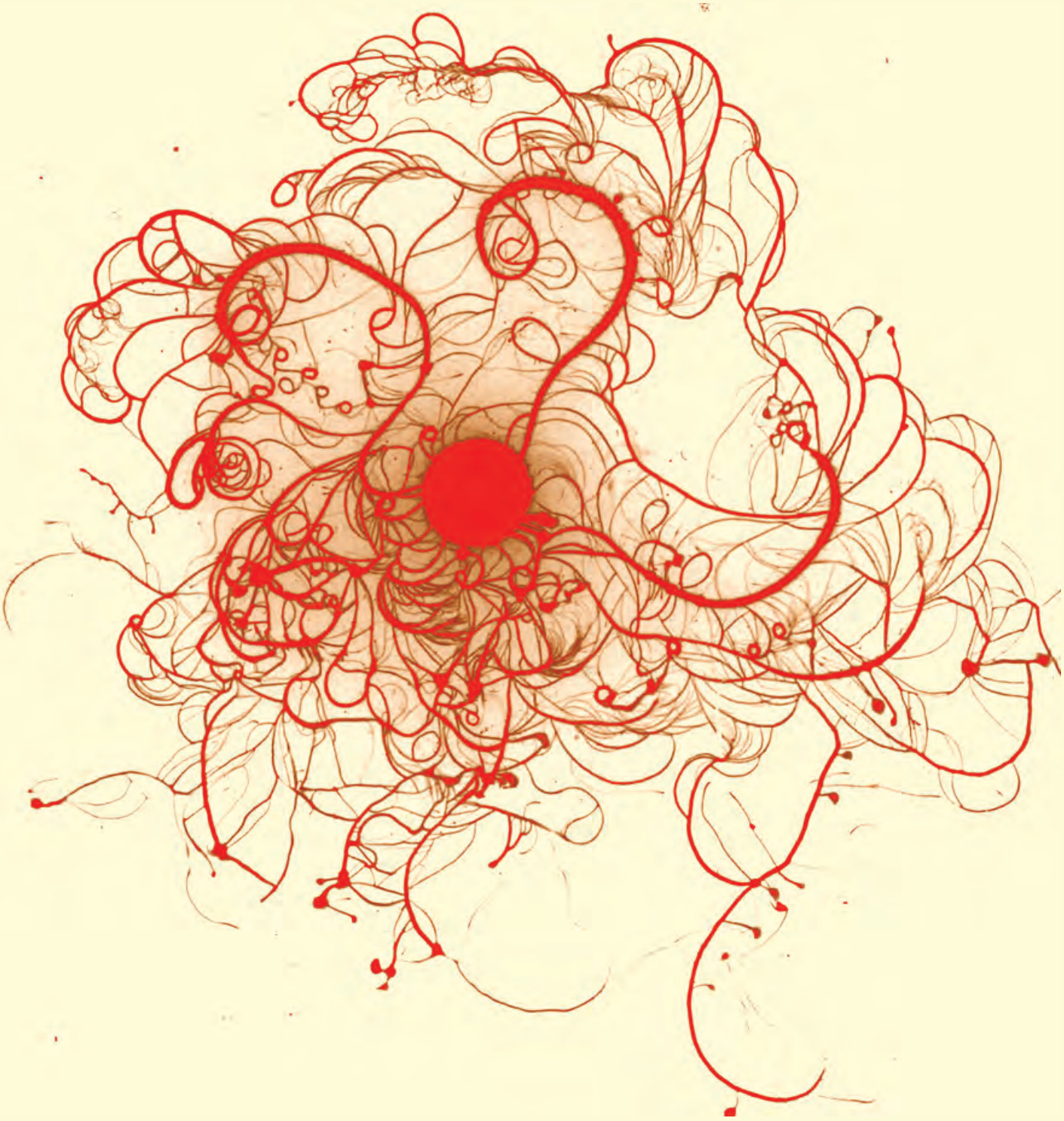

The Family Paenibacillaceae

Strain Catalog and Reference • BGSC • Daniel R. Zeigler, Director

The Family Paenibacillaceae

Bacillus Genetic Stock Center Catalog of Strains
Part 5

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Cover: *Paenibacillus dendritiformus* colony pattern formation. Color added for effect. Image courtesy of Eshel Ben Jacob.

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WELCOME TO THE BACILLUS GENETIC STOCK CENTER

WHAT IS THE BACILLUS GENETIC STOCK CENTER?

The primary mission of the Bacillus Genetic Stock Center (BGSC) is to maintain genetically characterized strains, cloning vectors, and bacteriophage for the genus Bacillus and related organisms and to distribute these materials without prejudice to qualified scientists and educators throughout the world. Since 1978, the National Science Foundation has funded the activities of the BGSC. The Department of Microbiology in the College of Biological Sciences at the Ohio State University provides facilities and administrative support. The Director of the BGSC, Dr. Daniel R. Zeigler, is assisted by a technician and a data entry specialist.

WHAT KINDS OF CULTURES ARE AVAILABLE FROM THE BGSC?

As of September 2013, the BGSC contains the following strains and plasmids:

Classification	Accessions	Classification	Accessions
B. subtilis 168 mutants	1310	*Brevibacillus* sp.	18
sporulation, germination	*162*	*Geobacillus* sp.	173
plasmid-bearing	*71*	*Jeogtibacillus* sp.	1
Other *B. subtilis*	55	*Lysinibacillus* sp.	153
B. thuringiensis	194	*Paenibacillus* sp.	25
B. cereus species cluster	106	*Rummelibacillus* sp.	5
B. megaterium	244	*Sporosarcina* sp	1
B. licheniformis	41	*Virgibacillus* sp.	1
B. pumilus	11	Other *Bacillus* sp.	47
B. atrophaeus	8	Plasmid tools	275
Aneurinibacillus sp.	2	Bacillus phages	5

In addition, the BGSC maintains a warehouse containing the *Bacillus* strain collections of Joshua Lederberg, Eugene Nester, Bernard Reilly, Patricia Vary, Allan Yousten, Stanley Zahler, and the late Ernst W. Freese. Please inquire about any of these strains that might be of interest to you. Note that we do not have—nor do we ever intend to obtain—any strains of *Bacillus anthracis,* even attenuated strains. Life is a little simpler for us that way.

WHAT YOU CAN DO TO HELP THE BGSC

Our NSF grant currently subsidizes some of the services we offer. There are some additional ways, however, that members of the *Bacillus* research community can give back to the BGSC. We would especially appreciate the following kinds of help:

- *Service Plan Purchases:* The BGSC has resisted mandatory payment of user fees for academic scientists. We are in the same position, and we understand how difficult it can be to make funding stretch to cover all needed materials. However, it is essential that most academic users voluntarily support our continued existence by paying the invoices that we send with each order. The One-Year Service Plan provides a convenient way to purchase a subscription to BGSC strains. Details are below. Please help us with our cost recovery efforts if you are able!
- *Strain contributions:* Although we have obtained a few cultures from other strain repositories, the vast majority of our holdings were contributed by individual researchers. Please take a moment to look over our collection and consider: are there strains, vectors, phage, or clones that you have developed or

acquired that we do not have? Would these materials be of some potential use to others in the research community? If so, please take the time to deposit the material in the BGSC. There is no charge whatsoever to you. There is also no compensation--except for the knowledge that you have made the fruits of your labor more accessible for the benefit of others. Generally, all we would require would be a culture (or lysate) with appropriate reprints or other helpful information. Please contact us (see below) if you have any questions.

- *Financial Contributions:* The BGSC relies on corporate strain sales and contributions to purchase equipment and undertake special projects not covered by the NSF grant. The Ohio State University Development Fund has a separate account for the BGSC. Contributions are tax deductible to the full extent of the law. Please contact us if you wish to make such a contribution.

HOW TO ORDER CULTURES

There are several ways to place orders with or request information from the BGSC:

- E-mail: zeigler.1@osu.edu
- Web: www.bgsc.org
- Phone: (+1) 614-292-5550
- FAX: (+1) 614-292-3206
- Mail: Daniel R. Zeigler, Ph.D.
  Department of Microbiology
  The Ohio State University
  484 West Twelfth Avenue
  Columbus, OH 43210 (USA)

Please provide with your order the names of the strains you wish to obtain along with your full shipping address and contact information. Non-profit users should indicate whether they intend to pay the subscription price or some portion of it. From any user, we can accept a purchase order or payment in the form of credit card, wire transfer, or bank check. All payments must be in US currency. Shipping is by US mail. For profit users will receive automatic upgrade to UPS express shipment, provided that certain conditions are met (see below). Non-profit users can expedite their order by providing a FedEx or UPS account number for us to charge or by providing a prepaid label.

PRICING INFORMATION (EFFECTIVE JULY 1, 2013)

ACADEMIC, GOVERNMENT, AND NON-PROFIT USERS—

Not-for-profit users are requested to pay a $195 yearly subscription fee. This subscription entitles the user to receive up to 20 strains over a twelve-month period. Alternatively, strains may be purchased individually for $35 each. If you lack grant support, please contact us to discuss your situation.

FOR-PROFIT CORPORATE USERS—

Users may purchase cultures as needed for a $135 per culture charge. For UPS shipping, a $75 charge on overseas orders under $270 will apply. Alternatively, users may pay a $1950 fee, entitling them to up to 50 cultures within the next twelve calendar months at no additional cost. Express delivery service is provided at no extra charge (to a maximum of three express deliveries per year on overseas shipments).

IMPORTANT NOTICE

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INTRODUCTION TO THE FAMILY PAENIBACILLACEAE

During the century following the isolation of *Bacillus subtilis* from hay infusions (Cohn 1872), any bacterium was classified as belonging to the genus *Bacillus* if it had a few basic characteristics in common with Cohn's isolate: a rod-like shape, an aerobic or facultatively anaerobic metabolism, and an ability to form endospores. What could not have been understood at the time was how ancient this "Bacillus lifestyle" actually is. Recent studies suggest that the ability to form endospores has appeared only once in the tree of life, and that was near the very base of the bacterial phylum Firmicutes (Abecasis, Serrano et al. 2013). The criterion of endosporulation, then, is far too broad for the purpose of gathering up species into a single genus. The development of 16S rRNA sequencing during the 1980s finally provided a tool that could organize both higher and lower order taxonomic groupings among morphologically similar bacterial isolates (Woese 1987). In a 1991 study, scientists at the BBSRC Institute of Food Research determined 16S rRNA gene sequences for standard strains of 51 species then defined as *Bacillus* and reported that the sequences segregated into several distinct phylogenetic clusters (Ash, Farrow et al. 1991). Two of these clusters formed nuclei for the description of the novel genera *Paenibacillus* (Ash, Priest et al. 1993) and *Brevibacillus* (Shida, Takagi et al. 1996). These two genera, along others that have been more recently described, are now recognized to comprise a separate bacterial family, Paenibacillaceae (De Vos, Ludwig et al. 2009).

Although this family is circumscribed by 16S rRNA gene sequence similarity, there are at least a few phenotypes that are common among its members. They are usually small to medium straight or curved rods, about 0.5-1.0 x 2-6 µm, with a typical Gram-positive wall structure. Their endospores frequently swell the sporangium. Beyond that basic description, there is much diversity. Isolates can be psychrophilic, mesophilic, or thermophilic; they can be neutrophiles or alkaliphiles, aerobes or anaerobes. The G+C content of their genomes can range from 36-59%. The name Paenibacillaceae (like that of its type genus, *Paenibacillus*) is derived from the Latin *paene* and the Greek *Bacillus:* "almost" or "nearly" a *Bacillus.* The name is meant to indicate a similarity between these organisms and *Bacillus sensu stricto.* But this is something of a misnomer. These bacteria are not "almost" significant. We are in fact learning that they are a rich and varied group with a high level of importance in many environments (Table 1).

Table 1. Recent microbial ecology studies detecting Paenibacillaceae in natural microbial communities

Environmental Source	Location	Cultured	Method	Reference
Deep-sea sediment	Tyrrhenian Sea	Y	25°C marine agar	(Ettoumi, Guesmi et al. 2013)
Desert brines, soils	Tunisia	Y		(Guesmi, Ettoumi et al. 2013)
Compost	California	Y	60°C switchgrass broth	(D'Haeseleer, Gladden et al. 2013)
Banana roots	Brazil	Y	25°C complete agar	(Souza, Xavier et al. 2013)
Hot spring, cold deserts	India	Y	various conditions	(Pandey, Singh et al. 2013)
Grassland soil, subarctic	Alaska	Y	15°C humic acid	(Park and Kim 2013)
Coffee cherries	Brazil	N	16S rRNA gene	(Oliveira, Santos et al. 2013)
Orchid meristem	Brazil	Y	28°C MS medium	(Faria, Dias et al. 2013)
Sugarcane roots	Cuba	Y	30°C N-free solid	(de Los Milagros Orbera Raton, Yano et al. 2012)
Ice cores	Antarctica	Y	4°C or 20°C various	(Antony, Krishnan et al. 2012)
Snow surface	Antarctica	Y	4°C TSB	(Van Houdt, Deghorain et al. 2013)
Wild legume roots	China	Y	30°C various	(Li, Sinkko et al. 2012)
Sandstone biofilm	Cambodia	N	16S rRNA gene	(Gaylarde, Rodriguez et al. 2012)
Styrian pumpkins	Austria	Y	20°C R2A agar	(Furnkranz, Lukesch et al. 2012)
Maize, teosinte seed	North America	Y	20°C various	(Johnston-Monje and Raizada 2011)
Wild legume roots	Sweden	Y	25°C YMA agar	(Ampomah and Huss-Danell 2011)
Agronomic plant roots	Japan	Y	25°C chitin	(Someya, Ikeda et al. 2011)
Wild legume roots, desert	Tunisia	Y	28°C YMA agar	(Fterich, Mahdhi et al. 2011)
Forest soil	Brazil	Y	23°C various	(Bruce, Martinez et al. 2010)
Brain coral reef	Brazil	N	16S rRNA gene	(de Castro, Araujo et al. 2010)

The depth and complexity of Paenibacillaceae is evident from a phylogram constructed from the 16S rRNA gene sequences of the type strains from the 195 species described for this family as of August 2013 (see Figure 1 on next page). At a glance one can see that there is still work to be done in sorting out the taxonomy of this group. While most of the nine genera are composed of closely related species, the genus *Paenibacillus* will doubtless require significant subdivision in the future. In addition, a few species—for example, *Cohnella thailandensis* and *C. terrae*—seem to have been placed in the wrong genus altogether. Other genera, such as *Ammoniphilus* and *Oxalophagus,* should perhaps be combined. The work of bacterial taxonomy is something of an acquired taste, but every microbiologist benefits from its fruit. Perhaps Figure 1 will impress the reader with the enormous gains in this important field during the current generation while encouraging the rising generation of microbiologists to make their own contributions.

The role of Paenibacillaceae in the environment is an ongoing research focus. Spores are commonly found in soils of all types, as is also the case for the Bacillaceae. But it would be a mistake to think of these organisms as generic "soil bacteria." Their environmental roles may in fact be quite specialized. Certain species are obligate pathogens of honeybees (Genersch 2010) or scarab beetles (Pettersson, Rippere et al. 1999). Others may be adapted to colonize the vertebrate intestinal tract, including that of humans (Hoyles, Honda et al. 2012); see also Human Microbiome Project genome PRJNA54029. Perhaps the most frequently reported isolation of Paenibacillaceae, however, is from endophytic and other plant-associated communities. Isolates have been obtained from the interiors of surface-sterilized fruits, seeds, stems, and roots of a variety of wild plants and cultivated crops (see Table 1). Evidence strongly suggests that many of these isolates are actually plant-growth promoting bacteria, and that certain characteristics of these species—including antibiotic production and biofilm formation—play an essential role in this activity (Timmusk, Grantcharova et al. 2005); more on this below.

These environmental adaptations found among members of the Paenibacillaceae make them attractive candidates for many biotechnological applications. The plant-growth promoting traits of rhizobacteria and other endophytes make them promising candidates for **biocontrol** applications in agricultural and forest crops. The same traits of antibiotic production and biofilm formation, along with other adaptations to survival in the intestine, may soon allow other isolates to be developed into effective **probiotics** both for livestock and human use. Other plant-associated Paenibacillaceae bacteria, especially those that are thermophilic, are frequent members of compost microbial communities; it is conceivable that these isolates could be incorporated into schemes to produce **fuels from cellulosic biomass**. Finally, the pathogenicity of certain isolates to insects and other invertebrates make them potential **biopesticides**.

In summary, the bacteria that make up the family Paenibacillaceae are a diverse group that participates in important environmental functions that are only now being elucidated. They likely have significant biotechnological potential that remains to be exploited. Microbiologists of all specialties—taxonomists, environmental microbiologists, and biotechnology researchers—are invited to make use of the Bacillus Genetic Stock Center collection to pursue these and other goals.

The Family Paenibacillaceae

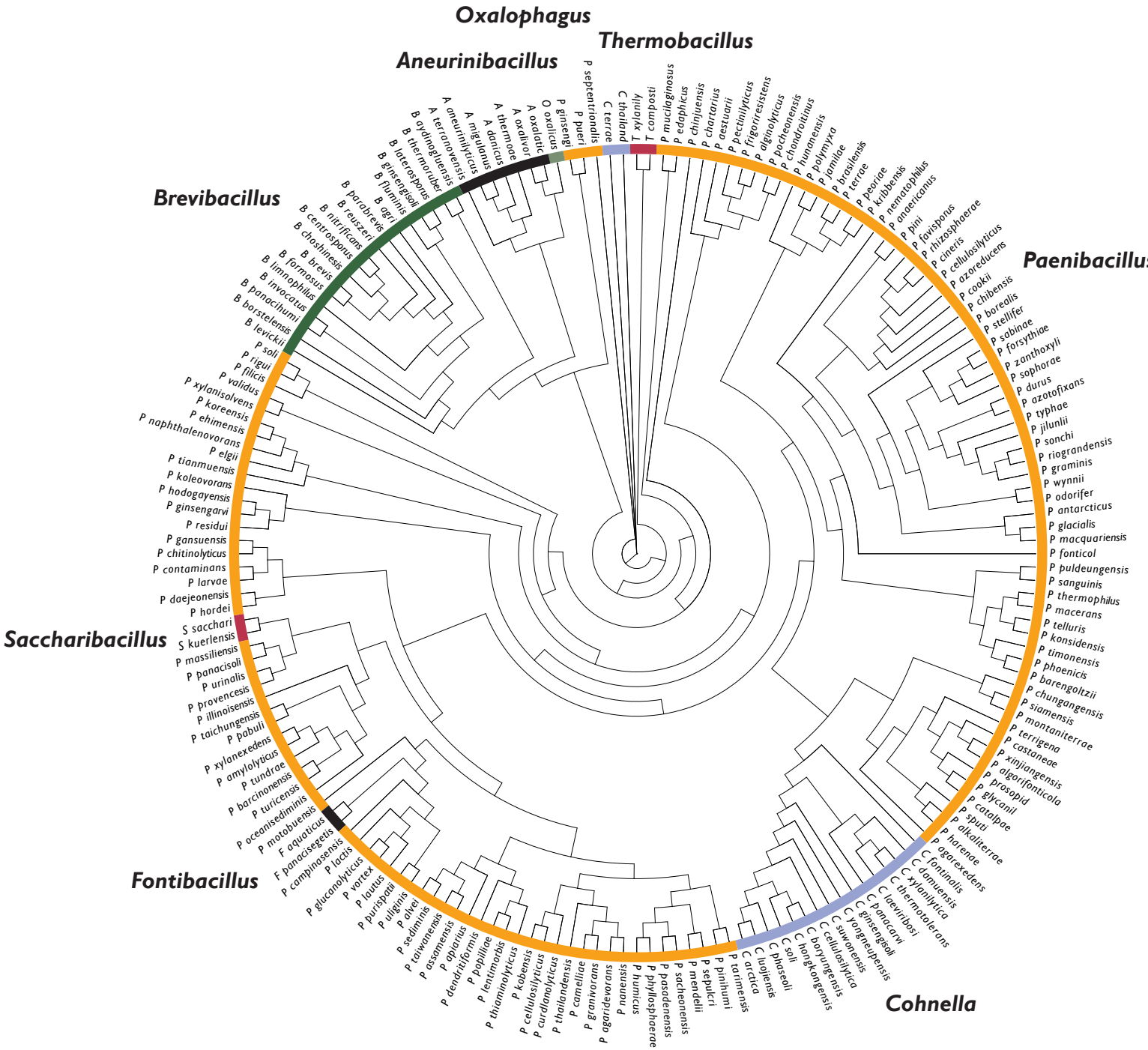

Figure 1. Phylogram of 16S rRNA gene sequences from the type strains of the 195 species belonging to the eight genera that comprise the family Paenibacillaceae. Species belonging to a genus are marked withi the same color. Sequence alignments generated by Clustal Omega (Seivers, Wilm et al 2011) were analyzed with PhyML 3.0 (Guindon, Dufayard et al 2010) to generate a maximum likelihood phylogeny, which was visualized as a circular phylogram with the Phylowidget application (Jordan, Piel 2008).

PLANT GROWTH PROMOTION

The ability of certain soil bacteria to promote plant growth is a significant focus of environmental microbiology and agricultural biotechnology (Lugtenberg and Kamilova 2009). The population of bacteria in the layer of soil surrounding roots—the rhizosphere—differs from that of bulk soil. Roots exude certain nutrients, including amino acids, fatty acids, nucleotides, organic acids, phenolics, plant growth regulators, putrescine, sterols, sugars, and vitamins. The availability of these nutrients supports a higher bacterial population density than is typically found in soil. Some of these bacteria, termed Plant Growth Promoting Rhizobacteria (PGPR), are beneficial to the plant. Various mechanisms have been shown for plant growth promotion. **Biofertilizers** supply the plant with nutrients through nitrogen fixation or phosphate solubilization. **Rhizoremediators** degrade soil pollutants. **Phytostimulators** produce plant hormones or release beneficial volatiles, such as 2,3-butanediol and acetoin. **Stress controllers** can degrade the precursors of ethylene and mitigate plant stress responses to unfavorable conditions. Other bacteria also function to control **soilborne diseases** of plants. Mechanisms include **antibiosis,** the production of antibiotic compounds that kill pathogens; **predation and parasitism** of pathogenic fungi; **competition for ferric ions** in limited supply; **niche exclusion,** if populations of beneficial bacteria can become established on the root; and **induced systemic resistance,** in which PGPR stimulate the innate immunity of plants. Members of the family Paenibacillaceae, especially *P. polymyxa,* have been well studied in this regard, and many of these mechanisms have been proposed for them (see Table 2 and references therein). As members of the spore-forming Firmicutes,

Table 2. Studies documenting Plant Growth Promotion by Paenibacillaceae isolates

Bacterium	Plant	Stress	Proposed Mechanism	Reference
P. polymyxa		*Leptosphaeria maculans*	Fusaricidin-like cyclic depsipeptides	(Beatty and Jensen 2002)
Brevibacillus	Sugarcane	*Curvularia* and *Fusarium*		(de Los Milagros Orbera Raton, Yano et al. 2012)
P. polymyxa		*Fusarium oxyporum*	Direct interaction	(Dijksterhuis, Sanders et al. 1999)
P. polymyxa	Peanut	*Aspergillus niger*	Biofilm formation, niche exclusion	(Haggag and Timmusk 2008)
P. polymyxa	Wheat	*Fusarium graminearum*	Enzymatic or antibiotic activity	(He, Boland et al. 2009)
P. polymyxa	Wheatgrass, clover		IAA production	(Holl, Chanway et al. 1988)
P. polymyxa	Wheat		Cytokinin production	(Timmusk, Nicander et al. 1999)
P. polymyxa	Tomato	Root-knot nematode		(Khan, Kim et al. 2008)
P. polymyxa	Tomato	*Phytophthora infestans*		(Lamsal, Kim et al. 2013)
P. polymyxa	Arabidopsis	*Pseudomonas syringae*	Volatile compounds	(Lee, Farag et al. 2012)
P. polymyxa		*Xanthomonas campestris*	1.3 kDa lipopeptide	(Mageshwaran, Walia et al. 2012)
P. polymyxa	Wheat	*Erwinia* spp.	Polymyxin P	(Niu, Vater et al. 2013)
P. polymyxa	Pepper	*Xanthomonas campestris*	Volatile compounds	(Phi, Park et al. 2010)
Paenibacillus sp.	Soybean	*Rhizoctonia bataticola*		(Senthilkumar, Swarnalakshmi et al. 2009)
P. polymxya, P. lentimorbus	Tomato	root-knot nematode and *Fusarium*		(Son, Khan et al. 2009)
P. polymyxa	Arabidopsis	*Erwinia,* drought	Induction of plant stress genes	(Timmusk, Grantcharova et al. 2005)
P. polymyxa	Arabidopsis	*Phytophthora palmivora, Pythium aphanidermatum*	Biofilm formation, niche exclusion	(Timmusk, van West et al. 2009)
Brevibacillus sp.	White clover	Zn-toxicity	Zn accumulation; IAA stimulation	(Vivas, Biro et al. 2006)
Paenibacillus sp.	Locust	*Penicillium expansum*	Heat stable 4.5 kDa protein	(Zhou, Huang et al. 2008)
P. polymyxa	Sesame	Nine fungal pathogens		(Ryu, Kim et al. 2006)

Paenibacillaceae have significant potential for practical application in agriculture. Even in the rhizosphere, starvation conditions are the norm. Spore-formers are therefore likely to have superior persistence than Gram-negative bacteria under real-world field conditions (Francis, Holsters et al. 2010).

The available genome sequences for *P. polymyxa* and its relatives suggest some of the underlying mechanisms of plant growth promotion for these isolates. *P. polymyxa* E681, isolated from the wheat rhizosphere, has the genomic capacity to synthesize and export the antibiotic polymyxin, the nonribosomally synthesized antifungal peptide fusaricidin, a novel lantibiotic, a polyketide, and at least two other potential peptide antibiotics. Biosynthesis of plant hormones through the indole-3-pyruvic acid pathway may also be possible (Kim, Jeong et al. 2010). Similar genetic potential has been reported for the pepper rhizosphere isolate *P. polymyxa* SC2, which can also apparently synthesize the antibiotics bacitracin and iturin A (Ma, Wang et al. 2011), and also for the type strain of *P. polymyxa,* ATCC 842^{T} (Jeong, Park et al. 2011). The genome of *P. polymyxa* M1, another wheat root isolate, devotes about 4.5% of its content to encoding nine nonribosomal peptide antibiotics (Niu, Rueckert et al. 2011). A genomic basis for antibiosis has also been reported for a strain of *P. peoriae* (Jeong, Choi et al. 2012).

The potential of Paenibacillaceae family members for exploitation in "green" agricultural applications is only beginning to be explored. One hopes that more researchers will be attracted to this quickly developing field.

PESTICIDAL ISOLATES

Certain Paenibacillaceae species are known to be specialized insect pathogens, such as *Paenibacillus lentimorbus* and *P. popilliae,* the causative agents of milky disease in scarab beetle grubs, and *P. larvae*, the causative agent of American foulbrood in honeybees. In nature these species appear to be obligate parasites in insects. They are rather fastidious in their growth requirements and difficult to maintain in laboratory culture. Yet there are many other members of the Paenibacillaceae, isolated from soil or the rhizosphere, that display a low to moderate level of toxicity to a wider range of invertebrates, including larval and adult insects, nematodes, and molluscs. Although this activity is lower than what has been measured for the Cry toxins and Vip proteins produced by *Bacillus thuringiensis* (Bt), it is nevertheless intriguing. The evidence is certainly preliminary, but it may be that the toxic factors produced by Paenibacillaceae are very different from Bt-encoded proteins in structure and mode of action. Perhaps there will be a role for these isolates in pest control and resistance management.

Isolates of *Brevibacillus laterosporus* are easily recognized during stationary phase by the presence of a canoe-shaped inclusion cradling a firmly attached endospore (Hannay 1957, Fitz-James and Young 1958). Over the past several decades there have been numerous reports that certain strains of *B. laterosporus* can kill a wide range of invertebrate pests. Favret and Yousten showed that over half of the strains in their *B. laterosporus* collection could kill larvae of the mosquito *Culex quinquefasciatus,* although these strains were 100-1000 times less toxic than Bt subsp. *israelensis* (Favret and Yousten 1985). Rivers et al. followed up on these observations by assaying a similar collection for toxicity against various insect larvae from the orders Diptera, Lepidoptera, and Coleoptera. Over half the isolates tested showed measurable activity against neonates of the mosquito *Aedes aegypti.* Preliminary bioassays with several isolates suggested significant toxicity towards larvae of the cigarette beetle, *Lasioderma serricorme,* and the Colorado potato beetle, *Leptinotarsa decemlineata* (Rivers, Vann et al. 1991). Soon afterwards, Singer reported that some *B. laterosporus* isolates are measurably toxic either to nematodes, such as *Heterodera glycines* and *Trichostrongylus colubriformis,* or to molluscs, such as *Biomphalaria glabrata* and *Dreissena polymorpha,* or simultaneously to both (Singer 1996). De Oliveira et al. subsequently confirmed that several *B. laterosporus* strains are significantly toxic to *B. glabrata* and measurably active against larvae of the boll weevil, *Anthonomus grandis,* and the velvetbean caterpillar, *Anticarsia gemmatalis* (de Oliveira, Rabinovitch et al. 2004). Finally, a series of reports from the Luca Ruiu lab have documented the efficacy of some *B. laterosporus* isolates

against both the larval and adult forms of the housefly *Musca domestica* (Ruiu, Delrio et al. 2006, Ruiu, Floris et al. 2007, Ruiu, Satta et al. 2008). Although rather high concentrations of *B. laterosporus* spores are required to control houseflies, these preparations nevertheless show a comparable level of efficacy with the biocontrol agent azadirachtin in field tests (Ruiu, Satta et al. 2011).

Exactly how *B. laterosporus* is killing these invertebrate targets remains an open question. A few natural isolates produce a parasporal crystal in addition to the canoe-shaped parasporal body. These crystals are similar to those observed in Bt both morphologically and in the timing of their formation during sporulation (Smirnova, Minenkova et al. 1996). It may be that the *B. laterosporus* crystals are indeed formed from Bt-like Cry proteins, for when they are purified, they show toxicity against larvae of the mosquitoes *Aedes aegypti* and *Anopheles stephensi* in the 3-5 ng/ml range, comparable for purified crystals from *B. thuringiensis* subsp. *israelensis* (Orlova, Smirnova et al. 1998). Most *B. laterosporus* isolates appear to lack such crystals, however. For these strains, the toxic factor(s) are produced during the early stationary phase, before any visible formation of forespores. Cell fractionation studies showed that mosquitocidal toxicity was associated with the cell pellet rather than the supernatant and the particulate rather than the soluble fraction (Favret and Yousten 1985). In contrast, a portion of the nematicidal activity may be due to secreted proteases (Huang, Tian et al. 2005). At least against houseflies and *A. aegypti*, the canoe-shaped inclusion itself is toxic, and this activity is associated with a 14-kDa protein that makes up this inclusion (Ruiu, Floris et al. 2007). Although any discussion of mechanism of action would be premature, a histopathological study of housefly larvae that ingested lethal doses of *B. laterosporus* showed disruption in their midgut architecture, similar to what has often been observed in other insects dosed with Bt Cry toxin action (Ruiu, Satta et al. 2012).

Toxicity to invertebrate pests has also been detected in other species of *Brevibacillus.* Singer and colleagues studied 40 isolates with measurable activity against the schistosomiasis snail vector *B. glabrata* (Singer, Bair et al. 1994). Three of these isolates were later deposited with the BGSC, where 16S rRNA gene sequences assigned them to *Brevibacillus formosus,* a close relative of *B. brevis* (Zeigler, unpublished). In contrast to what has been reported with *B. laterosporus,* the nematicidal activity of *B. formosus* accumulates during exponential growth, well before the onset of sporulation. The toxin is proteinaceous, heat stable, and associated with the cell-wall particulate fraction. Preliminary data suggest that it correlates with the presence of small proteins of 5.3 and 8.7 kDa (Singer, Bair et al. 1994). Some of these molluscicidal isolates also show toxicity against nematodes (Singer 1996).

Pesticidal activity has also been reported for *Paenibacillus* sp., although the available data are likewise quite limited. Four decades ago Singer studied 91 environmental isolates of *Bacillus sensu lato* that could kill larvae of the mosquito *Culex pipiens.* Although many were determined to be *Lysinibacillus sphaericus,* a known mosquitocidal species, 41 of the isolates were broadly identified as belonging to the *"B. alvei-circulans"* group. At least some of this latter group have since been assigned to *P. alvei* (Zeigler, unpublished). Follow up studies with one of these isolates, BGSC accession 33A2, established that it also displayed moderate molluscicidal activity against *B. glabrata* and *D. polymorpha* and strong nemacticidal activity against *H. glycines*. The toxic factors remain to be identified, although the mosquito toxin was shown to be synthesized in stationary phase (Singer 1996).

In summary, the family Paenibacillaceae appears to be a reservoir of potential weapons against invertebrate pests. Activity in natural isolates is only low to moderate, but the possibility of increasing these levels through overexpression has yet to be explored. The possibility of nematode control is especially intriguing, although largely unexploited. Most of these isolates have been studied little if at all since the mid-1990s. Many powerful technologies have been developed since then could elucidate the underlying mechanisms of these pesticidal properties so that they could be better evaluated for applications in biocontrol. Perhaps this brief summary will inspire someone to reexamine these strains with new tools and a fresh set of eyes.

PATTERN FORMATION

One of the most fascinating features of certain Paenibacillaceae family members is their ability to form complex—and often quite beautiful—multicellular structures as they grow on agar surfaces (see Figure 2 below as well as the image on the cover). Patterns may be highly branched and bush-like, or may be intricately swirled and chiral. Like the patterns themselves, the study of their formation is complex, and I will not attempt to review it here in any great detail. Still, a brief summary may suffice to direct the interested reader into the research literature.

Pattern formation is driven by the phenomenon of swarming motility, a flagellum-powered group movement of bacteria across a solid surface (Kearns 2010, Partridge and Harshey 2013). In some *Paenibacillus* isolates, such as *P. vortex,* swarming behavior is strikingly cooperative. On low concentration agar, *P. vortex* cells join in "snakelike" structures that can extend as rapidly as a centimeter per hour, avoiding contact with other "snakes" formed by the macrocolony. On high agar concentrations, hundreds or thousands of bacteria can adhere into rafts, forming spinning microcolonies capable of rotating once every few seconds. These rotating rafts produce whirlpool and streaming patterns within the mass. Rotation, as opposed to straight-line motility, may be related to the intrinsically curved shape of *P. vortex,* at least when grown on laboratory media (Ingham and Ben Jacob 2008).

In contrast to the rotating patterns observed with *P. vortex, P. dendritiformis* morphotype T forms bush-like patterns on solid surfaces (Tcherpakov, Ben-Jacob et al. 1999). The macrocolony extends by growing at the tips of the "branches"; bacteria further from the tips do not move at all, but serve as the sites of spore formation (Be'er, Smith et al. 2009). The rate of tip growth appears to be controlled primarily by the presence of a surfactant that decreases surface tension rather than by the speed of individual bacteria (Kozlovsky, Cohen et al. 1999, Be'er, Smith et al. 2009). The *P dendritiformis* C morphotype forms a chiral, rather than tip-splitting, pattern. Colonies form by sending out thin tendrils that curl with a predictable handedness (see the cover photograph). In contrast to type T, this morphotype is composed of long, rigid hyperflagellated cells that move in straight-line jets rather than swirls. At intervals of about 20 s, individual cells within a jet abruptly reverse directions. Remarkably, environmental conditions had little effect on the periodicity of these reversals, suggesting the presence of a robust biological clock (Be'er, Strain et al. 2013).

An interesting feature of *P. dendritiformis* is the production of a bacteriocin-like "sibling lethal factor" (Be'er, Zhang et al. 2009, Be'er, Ariel et al. 2010). This factor is produced by the proteolytic action of subtilisin on a pre-protein. In low concentrations, subtilisin actually stimulates colony growth, but at very high concentrations, such as at the interface between two sibling colonies, subtilisin activates the lethal factor, killing cells at the interface. This system gives *P. dendritiformis* colonies the ability to self-regulate growth. In particular, it could prevent neighboring colonies form invading each other's space (Be'er, Ariel et al. 2010).

The collective swarming behavior of *Paenibacillus* may have some surprising real-world applications. Computer simulations based on a few simple principles derived from the study of these bacteria—show that adaptable interactions between members of a group of moving objects, modifying movement based on peer influence and on navigation in a beneficial direction, gives superior performance compare to models based on static interactions of repulsion and orientation only. Bacteria-inspired principles may one day be applied to deployment of swarming robots in difficult terrain (Shklarsh, Ariel et al. 2011). Imagine, perhaps, the exploration of a planet's surface by a swarm of autonomous robots. The artificial intelligence of these explorers might be based in part on the simple "intelligence" of Paenibacillaceae and other bacteria.

Figure 2. *Paenibacillus vortex* colony pattern formation on agar plates, colorized for effect. (Image courtesy of Eshel Ben Jacob)

PAENIBACILLACEAE GENOMES

As of August 2013, over 30 complete or scaffold genome sequences were publicly available. A *Bacillus* geneticist is immediately struck by the large sizes of these genomes. While members of the *B. subtilis* species complex have genomes of around 4 Mb, the mean size of the currently sequenced Paenibacillaceae genomes exceeds 6 Mb (Table 3). Interestingly—and probably significantly—the smallest of these genomes all belong to the dedicated insect pathogens, *Paenibacillus popilliae* (3.83 Mb), *P. lentimorbus* (3.91 Mb), and *P. larvae* (4.03-4.35 Mb). As mentioned above, isolates from these species are fastidious in their habits and difficult to maintain on laboratory media; their genomes most likely have been streamlined as they have adapted to rapid growth in the insect hemolymph. Paenibacillaceae isolates from other environments can have much more complex genomes. Examples are *Paenibacillus* sp. JDR-2 (7.18 Mb), a xylanolytic strain isolated from decaying hardwood (Chow, Nong et al. 2012); *P. elgii* B69 (7.96 Mb), a soil isolate encoding a battery of antibiotics and other antimicrobial compounds (Wu, Shen et al. 2010, Ding, Li et al. 2011); and *P. mucilaginosus* (8.66-8.82 Mb), a rhizosphere isolate widely used in China for its plant growth promotion properties (Ma, Wang et al. 2012). It may be that the large genome size in many isolates enables them to compete effectively in very complex environments inhabited by diverse microbial communities. One example is afforded by the genome of the type strain of *P. polymyxa,* which is equivalent to BGSC 25A2^{T}. It includes large gene clusters encoding the antibiotics tridecaptin, fusaricidin, any polymyxin, as well as a lantibiotic and a battery of secreted carbohydrolases (Jeong, Park et al. 2011). Another is the genome of *Paenibacillus* sp. Y412MC10 (BGSC 36A2). Although it was isolated from a hot spring in Yellowstone Park, it is a thermophile with strong similarities to known intestinal isolates of *Paenibacillus*. It encodes an array of enzymes allowing utilization of biomass that is poorly digested by ruminants (Mead, Lucas et al. 2012). The growing availability of genome sequences should foster the exploitation of these bacteria in biotechnology and agriculture.

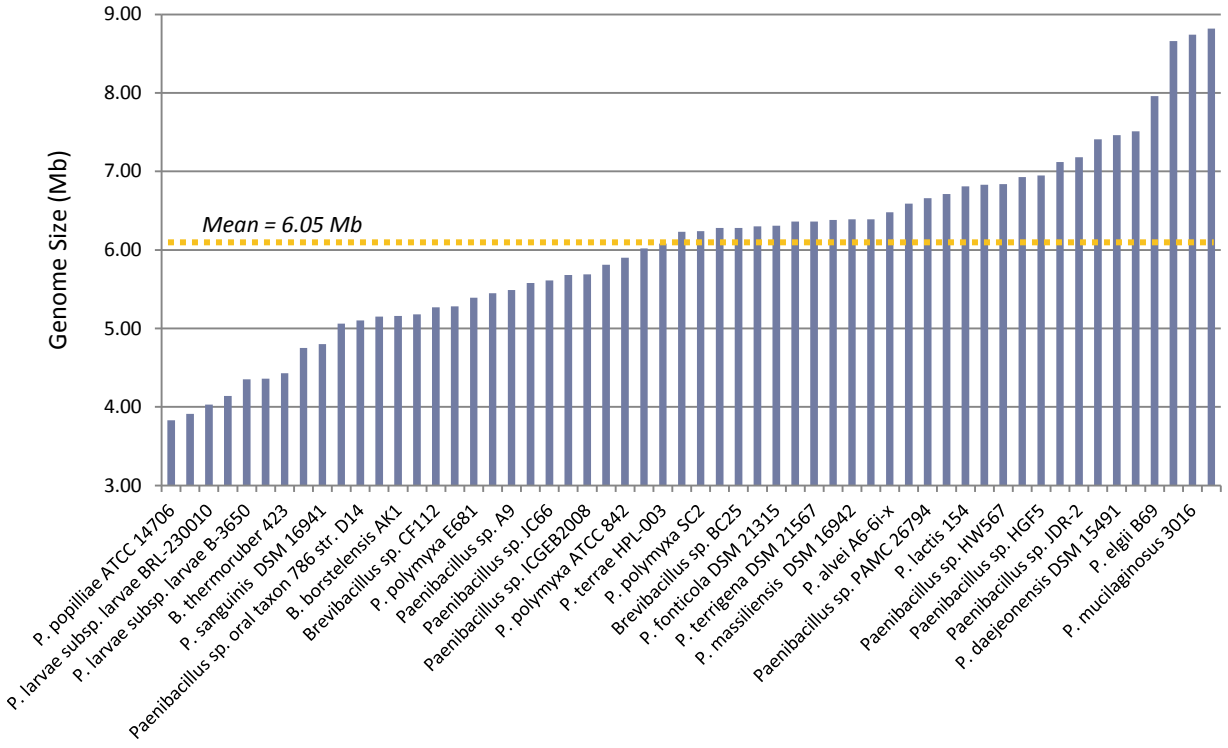

Figure 3. Sequenced genomes of the family Paenibacillaceae.. (Some names are omitted for clarity.)

GENETIC SYSTEMS

As we have seen, the members of the Gram-positive family Paenibacillaceae have considerable potential in the development of tools for promoting plant growth, controlling insects and other invertebrate pests, processing lignocellulosic biomass into useful products, untangling complex bacterial community interactions, and addressing a variety of other research questions. Now that an increasing number of Paenibacillaceae genome sequences have become available, one key limiting factor has been the lack of genetic tools for these organisms. Now that need is beginning to be addressed. A survey of published work underscores three important points. First, it seems that some protocols developed for the genus *Bacillus* can be adapted and optimized for Paenibacillaceae as well. Second, replicative plasmids that function in *Bacillus* can be used for experiments with Paenibacillaceae. Published examples include pNW33N, a general purpose shuttle vector from BGSC strain ECE136, and pAD43-25, a GFP-expressing plasmid from BGSC strain ECE166 (Zarschler, Janesch et al. 2009, Poppinga and Genersch 2012). Third, it is possible to use integrative vectors successfully, at least with *P. polymyxa,* if the transforming DNA is denatured with alkali or is pretreated with UV irradiation (Kim and Timmusk 2013). Utilization of these tools and optimization of these protocols could facilitate many investigations into the basic and applied biology of the Paenibacillaceae.

Table 1. Comparison of electroporation conditions developed for Paenibacillaceae isolates

	(Huang, Tian et al. 2010)	(Zarschler, Janesch et al. 2009)	(Poppinga and Genersch 2012)	(Kim and Timmusk 2013)
Species	*B. laterosporus*	*P. alvei*	*P. larvae*	*P. polymyxa*
Growth medium	LB with sorbitol, 0.5 M	Not specified	MYPGP broth	BHI with sucrose 10% (w/v)
Growth OD_{600}	0.85-0.95	0.2-0.3	0.3	0.5
Ice water bath	10 min	-	-	10 min
Electroporation buffer	Sucrose, 250 mM $MgCl_2$, 1 mM HEPES, 1 mM Glycerol, 10% (v/v)	Sucrose, 250 mM $MgCl_2$, 1 mM HEPES, 1 mM Glycerol, 10% (v/v)	Sucrose, 0.625 M	Sucrose 10% (w/v), $MgCl_2$, 1 mM
Washes	4 x	5 x	3 x	2 x
Final suspension	1.0 – 1.3 x 10^{10} cfu/ml	1/500 culture volume	1/500 culture volume	Not specified
Transformation mix	60 µl cells, 50 ng plasmid	50 µl cells, 500 ng plasmid	40 µl cells, 500 ng plasmid	Unspecified volume; denatured DNA
Cuvette gap	1 mm	1 mm	1 mm	2 mm
Field parameters	1.6 kV/25 µF/200 Ω	1.75 kV/25 µF/100 Ω	0.9 – 1.0 kV	12.5 kV/25 µF/200 Ω
Recovery medium	LB with sorbitol, 0.5 M mannitol, 0.38 M	CASO broth (Sigma) with sucrose, 250 mM, $MgCl_2$, 5 mM $MgSO_4$, 5 mM	MYPGP broth	BHI with sucrose 10% (w/v)
Recovery time	3 h at 37°C	2 h at 37°C	16 h at 37°C	
Expected yield	Not reported	~10^3 cfu/µg	4 x 10^4 – 2 x 10^6 cfu/µg	20 – 100 cfu/µg; 10-60% integrants

LIST OF STRAINS

ANEURINIBACILLUS ANEURINILYTICUS

BGSC 80A1^{T}

Original Code:	*Aneurinibacillus aneurinilyticus* NRS-1589^{T}
History:	BGSC ← NRRL ← Smith NR
16S rRNA gene:	X94194
Genome sequence:	not available
Growth conditions:	LB, TBAB, Nutrient Agar, or other rich medium at 26°C
Why study it?	Strain 80A1^{T} is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work.
Reference(s):	Shida O, Takagi H, Kadowaki K, Komagata K. Int J Syst Bacteriol. 1996 Oct;46(4):939-46 (PMID: 8863420)

ANEURINIBACILLUS MIGULANUS

BGSC 81A1^{T}

Original Code:	*Aneurinibacillus migulanus* NRS-1589^{T} (= NRS-1137^{T}) (= ATCC 9999^{T}) (= NCTC 7096^{T})
History:	BGSC ← NRRL ← ATCC ← NCTC ← Gause GF
16S rRNA gene:	X94195
Genome sequence:	not available
Growth conditions:	LB, TBAB, Nutrient Agar, or other rich medium at 30°C
Why study it?	Strain 81A1^{T} is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work.
Reference(s):	Shida O, Takagi H, Kadowaki K, Komagata K. Int J Syst Bacteriol. 1996 Oct;46(4):939-46 (PMID: 8863420)

BREVIBACILLUS AYDINOGLUENSIS

BGSC 43A1

Original Code:	*Brevibacillus aydinogluensis* OH3-1
Reference(s):	Zeigler DR (unpublished)
History:	BGSC ← Zeigler DR
16S rRNA gene:	KF597239
Genome sequence:	not available
Growth conditions:	TBAB at 55°C
Why study it?	43A1 is a wild **thermophilic** strain isolated from landscape soil at Ohio Stadium on The Ohio State University campus, Columbus, OH USA. It forms a spreading, confluent lawn on TBAB plates at 63°C. Cells are medium rods with subterminal ovoid endospores that do not swell the sporangium. *B. aydinogluensis* is closely related to *B. thermoruber.*

BGSC 43A2

Original Code:	*Brevibacillus aydinogluensis* OH11-3
History:	BGSC ← Zeigler DR
16S rRNA gene:	KF597240
Genome sequence:	not available

Growth conditions:	TBAB at 55°C
Why study it?	43A2 is a wild **thermophilic** strain isolated from landscape soil near Cunz Hall on The Ohio State University campus, Columbus, OH USA. It forms round, flat, shiny colonies with a diameter of ~3 mm on TBAB plates at 63°C. Cells are medium rods with subterminal ovoid endospores that do not swell the sporangium. *B. aydinogluensis* is closely related to *B. thermoruber.*
Reference(s):	Zeigler DR (unpublished)

BREVIBACILLUS BORSTELENSIS

BGSC 41A1^{T}

Original Code:	*Brevibacillus borstelensis* NRS-818^{T} (= Porter strain B4)
History:	BGSC ← NRRL
16S rRNA gene:	KF597237
Genome sequence:	not available
Growth conditions:	LB, TBAB, or Nutrient Agar at 30°C
Why study it?	Strain 41A1^{T} is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work.
Reference(s):	Shida O, Takagi H, Kadowaki K, Komagata K. Int J Syst Bacteriol. 1996 Oct;46(4):939-46 (PMID: 8863420)

BREVIBACILLUS CENTROSPORUS

BGSC 42A1^{T}

Original Code:	*Brevibacillus centrosporus* NRS-664^{T}
History:	BGSC ← Nakamura LK
16S rRNA gene:	KF597238
Genome sequence:	not available
Growth conditions:	LB, TBAB, or Nutrient Agar at 30°C
Why study it?	Strain 42A1^{T} is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work.
Reference(s):	Shida O, Takagi H, Kadowaki K, Komagata K. Int J Syst Bacteriol. 1996 Oct;46(4):939-46 (PMID: 8863420)

BREVIBACILLUS FORMOSUS

BGSC 26A2

Original Code:	*Brevibacillus formosus* SS 86-3
History:	BGSC ← Singer S ← Ofori J
16S rRNA gene:	KF597215
Genome sequence:	not available
Growth conditions:	NYSM agar at 30°C
Why study it?	Strain 26A2 has demonstrated **molluscicidal activity** against the schistosomiasis vector *Biomphalaria glabrata.* (Note: This strain was received as *B. brevis* but is reclassified here based on 16S rRNA sequence.)
Reference(s):	Singer S, Bair TB, Hammill TB, Berte AM, Correa-Ochoa MM, Stambaugh AD. J Ind Microbiol. 1994 Mar;13(2):112-9 (PMID: 7764671)

BGSC 26A3

Original Code:	*Brevibacillus formosus* SS 86-4
History:	BGSC ← Singer S ← Ofori J
16S rRNA gene:	KF597216
Genome sequence:	not available
Growth conditions:	NYSM agar at 30°C
Why study it?	Strain 26A3 has demonstrated **molluscicidal activity** against the schistosomiasis vector *Biomphalaria glabrata.* (Note: This strain was received as *B. brevis* but is reclassified here based on 16S rRNA sequence.)
Reference(s):	Singer S, Bair TB, Hammill TB, Berte AM, Correa-Ochoa MM, Stambaugh AD. J Ind Microbiol. 1994 Mar;13(2):112-9 (PMID: 7764671); Singer S. Adv Appl Microbiol. 1996;42:219-61 (PMID: 8865586)

BGSC 26A4

Original Code:	*Brevibacillus formosus* SS 86-5
History:	BGSC ← Singer S ← Ofori J
16S rRNA gene:	KF597217
Genome sequence:	not available
Why study it?	Strain 26A4 has demonstrated **molluscicidal activity** against the schistosomiasis vector *Biomphalaria glabrata.* (Note: This strain was received as *B. brevis* but is reclassified here based on 16S rRNA sequence.)
Reference(s):	Singer S, Bair TB, Hammill TB, Berte AM, Correa-Ochoa MM, Stambaugh AD. J Ind Microbiol. 1994 Mar;13(2):112-9 (PMID: 7764671)

BREVIBACILLUS LATEROSPORUS

BGSC 40A1

Original Code:	*Brevibacillus laterosporus* ATCC 9141
History:	BGSC ← Rivers D
16S rRNA gene:	KF597228
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A1 has demonstrated **mosquitocidal activity** against *Culex quinequefasciatus* and *Aedes aegypti.*
Reference(s):	Rivers DB, Vann CN, Zimmack HL, Dean DH. J Invertebr Pathol. 1991 Nov;58(3):444-7 (PMID: 1787329)

BGSC 40A2

Original Code:	*Brevibacillus laterosporus* ATCC 6457
History:	BGSC ← Rivers D
16S rRNA gene:	KF597229
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A2 has demonstrated **mosquitocidal activity** against *Culex quinequefasciatus* and *Aedes aegypti* and **anti-coleopteran activity** against larvae of *Leptinotarsa decemlineata* and *Lasioderma serricorne*
Reference(s):	Rivers DB, Vann CN, Zimmack HL, Dean DH. J Invertebr Pathol. 1991 Nov;58(3):444-7 (PMID: 1787329)

BGSC 40A3

Original Code:	*Brevibacillus laterosporus* ATCC 31932
History:	BGSC ← Rivers D
16S rRNA gene:	KF597230
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A3 was the subject of patents, now expired, dealing with **antibiotic production**
Reference(s):	Rivers DB, Vann CN, Zimmack HL, Dean DH. J Invertebr Pathol. 1991 Nov;58(3):444-7 (PMID: 1787329); Umezawa H, Takeuchi T, Naganawa H, Iinuma H, Kunimoto S. November 1983. US patent 4,416,899; Umezawa H, Takeuchi T, Naganawa H, Iinuma H, Kunimoto S. October 1984. US patent 4,474,880

BGSC 40A4

Original Code:	*Brevibacillus laterosporus* ATCC 53694
History:	BGSC ← Rivers D
16S rRNA gene:	KF597231
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A4 produces a **parasporal crystal** morphologically similar to those produced in *Bacillus thuringiensis.* It was the subject of a patent, now expired, dealing with the control of corn rootworm; activity against this pest was only marginal, however.
Reference(s):	Aronson AI, Dunn PE. March 1991. US patent 5,055,293

BGSC 40A5

Original Code:	*Brevibacillus laterosporus* ATCC 6456
History:	BGSC ← Rivers D
16S rRNA gene:	KF597232
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A5 does not show toxicity against the mosquito *Aedes aegypti,* but its pesticidal activity has yet to be fully investigated.
Reference(s):	Rivers DB, Vann CN, Zimmack HL, Dean DH. J Invertebr Pathol. 1991 Nov;58(3):444-7 (PMID: 1787329)

BGSC 40A6

Original Code:	*Brevibacillus laterosporus* NRRL B-4189
History:	BGSC ← Rivers D
16S rRNA gene:	KF597233
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A6 has a demonstrated **mosquitocidal activity** against *Aedes aegypti.*
Reference(s):	Rivers DB, Vann CN, Zimmack HL, Dean DH. J Invertebr Pathol. 1991 Nov;58(3):444-7 (PMID: 1787329)

BGSC 40A8

Original Code:	*Brevibacillus laterosporus* NRS 1111
History:	BGSC ← Singer S
16S rRNA gene:	KF597234
Genome sequence:	not available

Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A8 has demonstrated **mosquitocidal activity** against *Culex quinequefasciatus*, **nematicidal activity** against *Heterodera glycines,* and **molluscicidal activity** against *Biomphalaria glabrata* and *Dreissena polymorpha.*
Reference(s):	Favret ME, Yousten AA. J Invertebr Pathol. 1985 Mar;45(2):195-203 (PMID: 3981031)

BGSC 40A9

Original Code:	*Brevibacillus laterosporus* NRS 1645
History:	BGSC ← Singer S
16S rRNA gene:	KF597235
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A9 has demonstrated **mosquitocidal activity** against *Culex quinequefasciatus*, **nematicidal activity** against *Heterodera glycines.*
Reference(s):	Favret ME, Yousten AA. J Invertebr Pathol. 1985 Mar;45(2):195-203 (PMID: 3981031)

BGSC 40A10

Original Code:	*Brevibacillus laterosporus* NRS 1647
History:	BGSC ← Singer S
16S rRNA gene:	KF597236
Genome sequence:	not available
Growth conditions:	Nutrient Agar or other rich medium at 30°C
Why study it?	Strain 40A10 has demonstrated **mosquitocidal activity** against *Culex quinequefasciatus*, **nematicidal activity** against *Heterodera glycines* and *Trichostrongylus colubriformis.*
Reference(s):	Favret ME, Yousten AA. J Invertebr Pathol. 1985 Mar;45(2):195-203 (PMID: 3981031)

PAENBACILLUS SP.

BGSC 26A5

Original Code:	*Paenibacillus* sp. WRL-2904
History:	BGSC ← Singer S ← Bushby SRM
16S rRNA gene:	KF597218
Genome sequence:	not available
Growth conditions:	NYSM agar at 30°C
Why study it?	Strain 26A5 has demonstrated **molluscicidal activity** against the schistosomiasis vector *Biomphalaria glabrata* and nematicidal activity (Note: This strain was received as *B. brevis* but is reclassified here based on 16S rRNA sequence.)
Reference(s):	Singer S, Bair TB, Hammill TB, Berte AM, Correa-Ochoa MM, Stambaugh AD. J Ind Microbiol. 1994 Mar;13(2):112-9 (PMID: 7764671)

BGSC 35A1

Original Code:	*Paenibacillus* sp. JDR-2
History:	BGSC ← St John FJ
16S rRNA gene:	KF597225
Genome sequence:	Finished 7.18 Mb genome sequence available (GenBank CP001656)
Growth conditions:	TBAB, LB, Nutrient Agar, or other rich medium at 30°C
Why study it?	Strain 35A1 was isolated from sweet gum wood buried in surface soil. It is described as "aggressively xylanolytic" and is able to **utilize hemicellulosic polysaccharides**

Reference(s): St John FJ, Rice JD, Preston JF. Appl Environ Microbiol. 2006 Feb;72(2):1496-506 (PMID: 16461704); Chow V, Nong G, St John FJ, Rice JD, Dickstein E, Chertkov O, Bruce D, Detter C, Brettin T, Han J, Woyke T, Pitluck S, Nolan M, Pati A, Martin J, Copeland A, Land ML, Goodwin L, Jones JB, Ingram LO, Shanmugam KT, Preston JF. Stand Genomic Sci. 2012 Mar 19;6(1):1-10 (PMID: 22675593)

PAENIBACILLUS ALVEI

BGSC 33A1

Original Code: *Paenibacillus alvei* III_3DT-1A
History: BGSC ← Singer S
16S rRNA gene: KF597222
Genome sequence: not available
Growth conditions: NYSM agar at 30°C
Why study it? Strain 33A1 was solated from dead mosquito larvae obtained from Delhi, India. Moderate **mosquitocidal activity** has been demonstrated against *Culex quinquefasciatus.* Moderate **molluscicidal activity** has been demonstrated against *Biomphalaria glabrata* and *Dreissena polymorpha.* Strong **nemacticidal activity** demonstrated against the nematode *Heterodera glycines*.
Reference(s): Singer S. Nature. 1973 Jul 13;244(5411):110-1 (PMID: 4147722); Singer S. Adv Appl Microbiol. 1996;42:219-61 (PMID: 8865586)

BGSC 33A2

Original Code: *Paenibacillus alvei* III_2E
History: BGSC ← Singer S
16S rRNA gene: KF597223
Genome sequence: not available
Growth conditions: NYSM agar at 30°C
Why study it? Strain 33A2 was solated from dead mosquito larvae obtained from Delhi, India. Moderate **mosquitocidal activity** has been demonstrated against *Culex quinquefasciatus.*
Reference(s): Singer S. Nature. 1973 Jul 13;244(5411):110-1 (PMID: 4147722); Singer S. Adv Appl Microbiol. 1996;42:219-61 (PMID: 8865586)

PAENIBACILLUS CHITINOLYTICUS

BGSC 39A1^T

Original Code: *Paenibacillus chitinolyticus* NRRL B-23119 (= DSM 11030 = IFO 15660 = LMG 18047)
History: BGSC ← Brumm P
16S rRNA gene: KF597227
Genome sequence: not available
Growth conditions: TBAB, LB, Nutrient Agar, or other rich medium at 28°C
Why study it? Strain 39A1^T is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work. As its name indicates, this strain produces **chitinase**. It was isolated from forest soil in Kaya, Kagoshima prefecture, Japan.
Reference(s): Mead DA, Lucas S, Copeland A, & 24 others. Stand Genomic Sci. 2012 Jul 30;6(3):381-400 (PMID: 23408395)

PAENIBACILLUS DENDRITIFORMUS

BGSC 30A1

Original Code:	*Paenibacillus dendritiformus* subsp. *dendron* T168
History:	BGSC ← Gutnick D
16S rRNA gene:	KF597219
Genome sequence:	not available
Growth conditions:	LB agar at 37°C
Why study it?	Strain 30A1 produces colonies with intricate, complex branching **pattern formation** on thin plates containing 0.5% peptone and 0.7-1.0% agar
Reference(s):	Tcherpakov M, Ben-Jacob E, Gutnick DL. Int J Syst Bacteriol. 1999 Jan;49 Pt 1:239-46 (PMID: 10028268)

BGSC 30A2

Original Code:	*Paenibacillus dendritiformus* subsp. *charalis* C168
History:	BGSC ← Gutnick D
16S rRNA gene:	KF597220
Genome sequence:	not available
Growth conditions:	LB agar at 37°C
Why study it?	Strain 30A2 produces colonies with intricate, complex chiral **pattern formation** on thin plates containing 0.5% peptone and 0.7-1.0% agar
Reference(s):	Tcherpakov M, Ben-Jacob E, Gutnick DL. Int J Syst Bacteriol. 1999 Jan;49 Pt 1:239-46 (PMID: 10028268)

PAENIBACILLUS LAUTUS

BGSC 36A2

Original Code:	*Paenibacillus lautus* Y412.MC10
History:	BGSC ← Brumm P
16S rRNA gene:	--
Genome sequence:	Finished 7.12 Mb genome sequence available (GenBank CP001793)
Growth conditions:	TBAB, LB, Nutrient Agar, or other rich medium at 30°C
Why study it?	Although strain 36A2 was **isolated from Obsidian Hot Spring**, Yellowstone National Park, Montana, USA, it is mesophilic, with a growth optimum of 37°C. Genomic content for this strain is more similar to that of a human **gut microbiome** isolate than to that of plant growth-promoting or pattern-forming members of the genus
Reference(s):	Mead DA, Lucas S, Copeland A, & 24 others. Stand Genomic Sci. 2012 Jul 30;6(3):381-400 (PMID: 23408395)

PAENIBACILLUS POLYMYXA

BGSC 25A2^T

Original Code:	*Paenibacillus polymyxa* NRRL B-4317^T
History:	BGSC ← NRRL ← Smith NR ← ATCC ← Kluyver AJ
16S rRNA gene:	KF597214
Genome sequence:	Scaffold WGS available (AFOX01000000)
Growth conditions:	LB, TBAB, Nutrient Agar, or other rich medium at 28°C
Why study it?	Strain 25A2^T is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work. It is an **antibiotic producer** with a genome sequence predicted to encode lipopeptide antibiotics tridecaptin and fusaricidin, antibiotic polymyxin, and a

	lantibiotic. Strains of *P. polymyxa* are often considered to be **plant growth-promoting** soil bacteria.
Reference(s):	Forsyth WG, Webley DM. J Gen Microbiol. 1950 Jan;4(1):87-91 (PMID: 15415560); Jeong H, Park SY, Chung WH, Kim SH, Kim N, Park SH, Kim JF. J Bacteriol. 2011 Sep;193(18):5026-7 (PMID: 21742878)

PAENIBACILLUS THIAMINOLYTICUS

BGSC 34A1^T

Original Code:	*Paenibacillus thiaminolyticus* NRRL B-4156^T
History:	BGSC ← NRRL
16S rRNA gene:	KF597224
Genome sequence:	not available
Growth conditions:	TBAB, LB, Nutrient Agar, or other rich medium at 26°C
Why study it?	Strain 34A1^T is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work. The thiaminase enzyme has potential **antitumor activity** (see PMID: 22431205)
Reference(s):	Nakamura LK. Int J Syst Bacteriol. 1990 Jul;40(3):242-6 (PMID: 2397192)

PAENIBACILLUS VALIDUS

BGSC 38A1^T

Original Code:	*Paenibacillus validus* NRS-1000^T (= LMG 11161 = NBRC 15382 = NCIMB 12782 = NRRL B-14484 = NRRL NRS-639)
History:	BGSC ← NRRL ← Smith NR ← Porter J R ← Bredemann G
16S rRNA gene:	KF597226
Genome sequence:	not available
Growth conditions:	TBAB, LB, Nutrient Agar, or other rich medium at 28°C
Why study it?	Strain 38A1^T is the **nomenclatural type strain** of the species and therefore a standard strain for taxonomic work.
Reference(s):	Heyndrickx M, Vandemeulebroecke K, Scheldeman P, Hoste B, Kersters K, De Vos P, Logan NA, Aziz AM, Ali N, Berkeley RC. Int J Syst Bacteriol. 1995 Oct;45(4):661-9 (PMID: 7547285)

PAENIBACILLUS VORTEX

BGSC 31A2^T

Original Code:	*Paenibacillus vortex*
History:	BGSC ← Ben-Jacob E
16S rRNA gene:	KF597221
Genome sequence:	not available
Growth conditions:	LB agar
Why study it?	Strain 31A2^T shows complex **pattern formation** through cooperative motility on thin plates containing 0.8% peptone, 0.5% NaCl, 0.5% K_2HPO_4, 2% agar at 30°C
Reference(s):	Ben-Jacob E, Cohen I, Gutnick DL. Annu Rev Microbiol. 1998;52:779-806 (PMID: 9891813); Ben Jacob E, Becker I, Shapira Y, Levine H. Trends Microbiol. 2004 Aug;12(8):366-72 (PMID: 15276612); Ingham CJ, Ben Jacob E. BMC Microbiol. 2008 Feb 25;8:36 (PMID: 18298829)

GROWTH MEDIA

TGY

Tryptone	5.0 g
Yeast extract	5.0 g
Glucose	1.0 g
K_2HPO_4	1.0 g
Agar (if desired)	20.0 g
Tap water	1.0 L

Adjust pH to 7.0
Autoclave at 121°C for 15 minutes

NYSM

Nutrient broth	8.0 g
Yeast extract	0.5 g
$CaCl_2 \cdot 2H_2O$	0.70 mM
$MnCl_2 \cdot 4H_2O$	0.05 mM
$MgCl_2 \cdot 6H_2O$	1 mM
Agar (if desired)	15.0 g
H_2O	1.0 L

Autoclave at 121°C for 15 minutes

LB (MILLER)

Tryptone	10.0 g
Yeast extract	5.0 g
NaCl	10.0 g
Agar (if desired)	15.0 g
H_2O	1.0 L

NUTRIENT BROTH

Available in off-the-shelf formulation from many vendors

TRYPTOSE BLOOD AGAR BASE (TBAB)

Available in off-the-shelf formulation from many vendors. The bacteria in this catalog do not require the addition of blood.

TRYPTICASE SOY AGAR (TSA)

Available in off-the-shelf formulation from many vendors

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Cover: *Paenibacillus dendritiformus* colony pattern formation. Color added for effect. Image courtesy of Eshel Ben Jacob.