Acidobacteria

Svetlana N Dedysh, *Winogradsky Institute of Microbiology, Research Center of Biotechnology RAS, Moscow, Russia*

Jaap S Sinninghe Damsté, *NIOZ Royal Netherlands Institute for Sea Research, Utrecht University, AB Den Burg, The Netherlands*

Acidobacteria are one of the globally distributed and highly diverse phyla of the domain *Bacteria*. These microorganisms inhabit a wide variety of terrestrial and aquatic habitats and are particularly abundant in acidic soils, peatlands and mineral iron-rich environments. Owing to the difficulties in cultivating *Acidobacteria*, the taxonomically described diversity within this phylum remains limited. All characterised representatives are Gram-negative, nonspore-forming bacteria that display a variety of cell morphologies. Most characterised acidobacteria are chemoheterotrophs, although photoheterotrophic members have also been described. Cells of these bacteria contain a number of characteristic lipids, which may be responsible for their environmental adaptations. Genomes of acidobacteria are up to 10 Mbp in size and encode a wide repertoire of carbohydrate-active enzymes involved in breakdown, utilisation and biosynthesis of diverse carbohydrates. Their functional role in the environment includes the decomposition of various biopolymers and participation in the global cycling of carbon, iron and hydrogen.

Introduction

Acidobacteria raised considerable scientific interest at the turn of the century, when application of molecular techniques revealed the cosmopolitan distribution and high abundance of these microorganisms in various environments. The corresponding phylum has been created in order to accommodate the large number of 16S ribosomal ribonucleic acid (rRNA) gene sequences, which have been retrieved from various soils by means of cultivation-independent molecular techniques. These sequences displayed only a distant relationship to 16S rRNA gene sequences from characterised bacteria. By the end of the 1990s, this phylogenetic group encountered hundreds of 16S rRNA gene sequences detected not only in soils, but also in freshwater sediments, hot springs, acid mine drainages, peatlands, activated sludge and other habitats. In 1997, this rapidly expanding group received the status of a bacterial phylum and was named *Acidobacteria* (Ludwig *et al*., 1997), after the first cultured representative of this group, that is *Acidobacterium capsulatum*, an acidophilic heterotroph isolated from a mineral leaching environment (Kishimoto *et al*., 1991). Later, it has been realised that the diversity within this phylum is not restricted to acidophilic bacteria, but includes physiologically diverse organisms, which inhabit a wide range of environments (Barns *et al*., 1999). As revealed by molecular analysis, the phylogenetic diversity within *Acidobacteria* is nearly as great as in *Proteobacteria* (Hugenholtz *et al*., 1998). The number of major sequence clusters or subdivisions (SD) within *Acidobacteria* increased from 4 in 1997 (Ludwig *et al*., 1997) to 26 in 2007 (Barns *et al*., 2007). Despite their wide distribution in natural habitats, these bacteria remain a difficult object for microbiologists and are strongly underrepresented in culture collections. At the time of formal description in 1997, this group encountered only three species. Despite two decades of culturing efforts, the number of characterised species within this phylum has increased only to 50. The research on *Acidobacteria* is fuelled by the interest in understanding their functional roles in various niches in the biosphere and their cosmopolitan distribution and the possibility to extend the range of objects in screening for new metabolites and biologically active compounds. See also: **Phylogeny Based on 16S rRNA/DNA**; **Microbial Diversity**
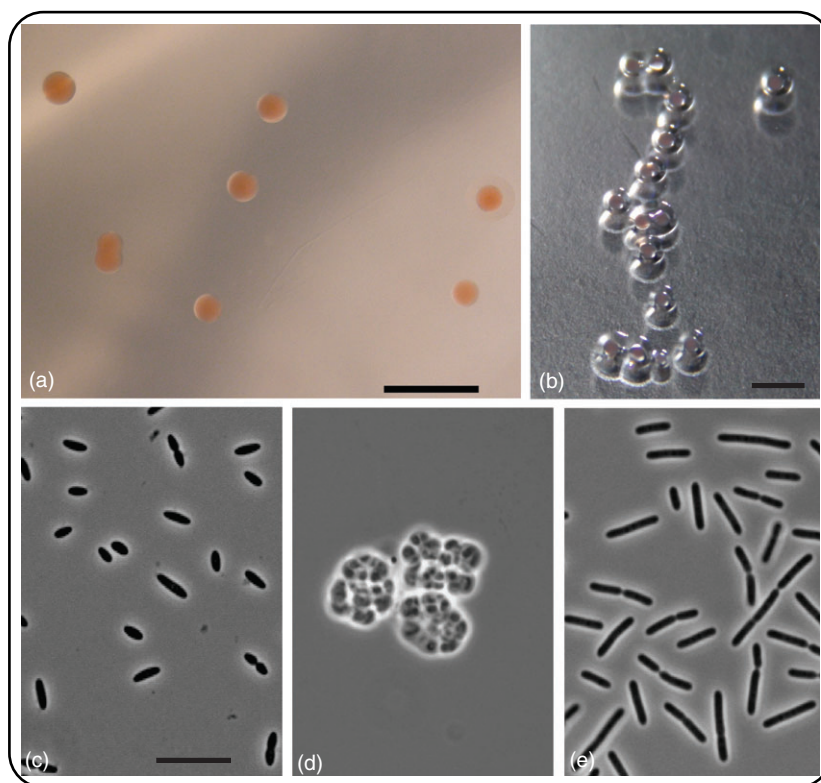
Figure 1 (a) Mini colonies produced by *Granulicella paludicola* OB1010[T] at the stage of isolation. Bar, 2 mm. (b) Development of depressions in the gellan-solidified medium during colony growth of *Bryocella elongata* SN10[T]. Bar, 5 mm. (c–e) Examples of cell morphologies of acidobacteria: *Granulicella rosea* TPO1014[T] (c), *Acidobacteriaceae* bacterium CCO287 (d), *Paludibaculum fermentans* P105[T] (e). Bar, 5 μm (applies to c–e).

A Long-standing Mystery of Being 'Nonculturable'

The main reason why this widespread bacterial group remains poorly represented by characterised strains is that the commonly used cultivation approaches are not fully appropriate for isolating *Acidobacteria*. As many members of this phylum are slow-growing oligotrophs, they are easily outcompeted by fast-growing bacteria on media containing readily oxidisable carbon substrates or are inhibited by high substrate concentrations, which are uncommon in their natural habitat. It has been shown, however, that many acidobacteria can be cultured using modified cultivation techniques. The use of low-nutrient media and gellan gum as the solidifying agent is one of the strategies to culture them (Janssen *et al*., 2002; Sait *et al*., 2002; Davis *et al*., 2005; Dedysh, 2011). Extending the incubation time up to several months and selecting mini colonies is another useful approach (Davis *et al*., 2011). At the stage of isolation, these bacteria produce very small (50–500 μm in diameter) colonies, which can be observed and picked with the use of a dissecting microscope (**Figure 1a**). The use of plant-derived polymers as growth substrates also works well for isolation of acidobacteria as many of them possess hydrolytic capabilities (Sait *et al*., 2002; Pankratov *et al*., 2008; Pankratov and Dedysh, 2010; Eichorst

et al., 2011). Some acidobacteria are able to degrade gellan gum, so that their development is accompanied by the formation of depressions in gellan-solidified media (**Figure 1b**). The use of mildly acidic media (pH 3.5–5) is recommended for isolating SD1 and 3 *Acidobacteria*, which display a preference for acidic conditions. Successful isolation of acidobacteria in cocultures with other microorganisms has also been reported. In some cases, this approach may be more efficient than a routine 'single-colony pick-up' strategy. For example, microaerophilic representatives of this phylum, *Telmatobacter bradus* and *Chloracidobacterium thermophilum*, were originally isolated in cocultures with other bacteria (Bryant *et al*., 2007; Pankratov *et al*., 2012). In case of the phototrophic *Chl. thermophilum*, not only oxygen concentration, but also the availability of various essential nutrients, such as a reduced sulfur source, bicarbonate, branched chain amino acids and vitamin B_{12}, played a crucially important role in cultivation. Many of the earlier listed approaches are often used in combination. In addition, the use of different molecular techniques greatly facilitates the surveillance of isolation and purification procedures. Thus, isolation of *Acidobacteria* appears to be feasible, while comprehensive characterisation of these slow-growing bacteria still represents a big challenge. As a consequence, characterised diversity within the *Acidobacteria* remains limited.

Cell Biology

Currently described *Acidobacteria* display a wide variety of cell shapes including short and long rods, ovoids and sarcina-like aggregates (**Figure 1c–e**). Formation of elongated (up to 100–150 μm long) filament-like cells (*T. bradus*), cell chains (genera *Acidicapsa* and *Granulicella*), cell rosettes (*Bryocella elongata*) or highly pleomorphic cells (*Blastocatella fastidiosa*) has also been reported. The cells are Gram-negative, nonspore-forming and, in most cases, divide by binary fission. Budding-like division has so far been reported for some members of the *Blastocatellaceae* only (Foesel *et al.*, 2013). Formation of specialised dormant cell forms has not yet been described for acidobacteria. Production of amorphous extracellular polysaccharides (EPS) and formation of large capsules are most typical for members of the family *Acidobacteriaceae*, representatives of the genera *Granulicella, Acidicapsa, Acidobacterium, Bryocella, Terriglobus* and *Occallatibacter*. Presumably, these EPS provide protection against environmental stress and enable bacterial survival under unfavourable conditions including high acidity and low temperatures. Formation of outer-membrane vesicles can often been observed in cultures of these bacteria. The presence of S-layers has been reported only for *Paludibaculum fermentans* (Kulichevskaya *et al.*, 2014). Pigments synthesised by the *Acidobacteria* vary from pale pink to red in *Acidobacteriaceae*, from yellow to dark yellow in 'Vicinamibacteraceae' and from pink to orange in *Blastocatellaceae* and *Pyrinomonadaceae*. *Chl. thermophilum* produces greenish-brown cultures.
See also: **Bacterial Cells**; **Bacterial Cell Wall**; **Binary Fission in Bacteria**; **Polysaccharides: Bacterial and Fungal**

Taxonomy and Systematics

The taxonomically described acidobacteria belong to 28 genera and 50 species. These characterised bacteria, however, represent only 7 out of 26 currently recognised SDs (1, 3, 4, 6, 8, 10 and 23). Each of these SDs is equivalent to a class level (**Figure 2**).

The class *Acidobacteria* (SD1) includes a single order *Acidobacteriales* and a single family *Acidobacteriaceae*. Much of the currently described acidobacterial diversity belongs to this family. It accommodates 11 genera of acidophilic or mildly acidophilic, chemoheterotrophic bacteria, most of which have obligate aerobic lifestyle. Two known exceptions are the genera *Telmatobacter* and *Acidobacterium*. *T. bradus* is a facultatively anaerobic bacterium that can grow only under reduced oxygen tension or fully anoxic conditions. Anaerobic growth occurs by means of fermenting sugars and several polysaccharides, including crystalline and amorphous cellulose. *A. capsulatum* is also capable of weak growth under anoxic conditions by means of fermentation, but it has a clear preference for aerobic lifestyle. Members of the *Acidobacteriaceae* are mesophiles, but many species display tolerance of low temperatures and resilience to multiple freeze–thaw cycles, which allow them to thrive in northern soils and wetlands. The preferred growth substrates are various sugars, though several organic acids and polyalcohols can also be utilised by some strains. Many representatives of this family are capable of degrading complex substrates, such as cellulose, starch, pectin, xylan and chitin.

The class 'Bryobacteria' (SD3) accommodates the order 'Bryobacterales' and the family *Bryobacteraceae*. At present, this family includes two described members with validly published names, the strictly aerobic chemoheterotroph *Bryobacter aggregatus* and the iron-reducing, facultatively anaerobic chemoheterotroph *P. fermentans*. These are mildly acidophilic, mesophilic and psychrotolerant bacteria that utilise various sugars, some organic acids and polysaccharides, but not cellulose or chitin. Representatives of the class 'Bryobacteria' are among the most abundant acidobacteria in various soils as well as in boreal and tundra wetlands.

The class *Blastocatellia* (SD4) currently comprises the single order *Blastocatellales*, which includes two families of aerobic chemoheterotrophic bacteria, the *Blastocatellaceae* and *Pyrinomonadaceae*, and the family 'Chloracidobacteriaceae' of microaerophilic anoxygenic photoheterotrophic bacteria. Cells are nonmotile, do not form capsules, divide by binary fission and/or budding (genus *Blastocatella*). The *Blastocatellaceae* accommodates the genera *Blastocatella, Aridibacter, Tellurimicrobium* and *Stenotrophobacter*. These are mesophilic and thermotolerant bacteria, which display a broad growth pH range (4.0–9.0). They utilise mainly complex proteinaceous compounds such as casamino acids, peptone or yeast extract, although protocatechuate, few sugars and amino acids can also be utilised by several species. Some representatives are able to degrade chitin or cellulose (*Aridibacter*). Members of the *Blastocatellaceae* are slow-growing K-strategists that prefer oligotrophic growth conditions and are able to survive drought and nutrient limitation; these bacteria are quite common in arid soils and soil crusts. The family *Pyrinomonadaceae* includes the genera *Pyrinomonas, Arenimicrobium* and *Brevitalea*. These are mesophilic or thermophilic and mildly acidophilic bacteria that also display a preference for complex proteinaceous substrates. *Brevitalea aridisoli* is capable of degrading cellulose and xylan; *Pyrinomonas methylaliphatogenes* degrades xylan and xanthan. The latter acidobacterium is also capable of scavenging atmospheric H_2, which enables its survival under nutrient limitation (Greening *et al.*, 2015). These bacteria inhabit arid and geothermally heated soils. The family 'Chloracidobacteriaceae' accommodates a unique representative, i.e. microaerophilic anoxygenic photoheterotrophic bacterium *Chl.thermophilum* (Bryant *et al.*, 2007). This is the only currently described phototrophic member of the phylum *Acidobacteria*. *Chl. thermophilum* synthesises bacteriochlorophyll (BChl) and has a photosynthetic apparatus resembling that of obligately anaerobic members of *Chlorobiales* (i.e. comprising chlorosomes as light-harvesting antenna complexes, the Fenna–Matthews–Olson, BChl *a*-binding protein (FmoA) and homodimeric type-1 photochemical reaction centre). In contrast to green sulfur bacteria, however, BChl biosynthesis and some other cellular processes in *Chl. thermophilum* are oxygen-dependent. This bacterium is incapable of autotrophic carbon fixation and relies on the utilisation of organic carbon sources (branched chain amino acids), reduced sulfur sources and oxygen for BChl and carotenoid biosynthesis, although bicarbonate is also required for growth (Tank and Bryant, 2015). The type strain of *Chl. thermophilum* is classified as a moderate
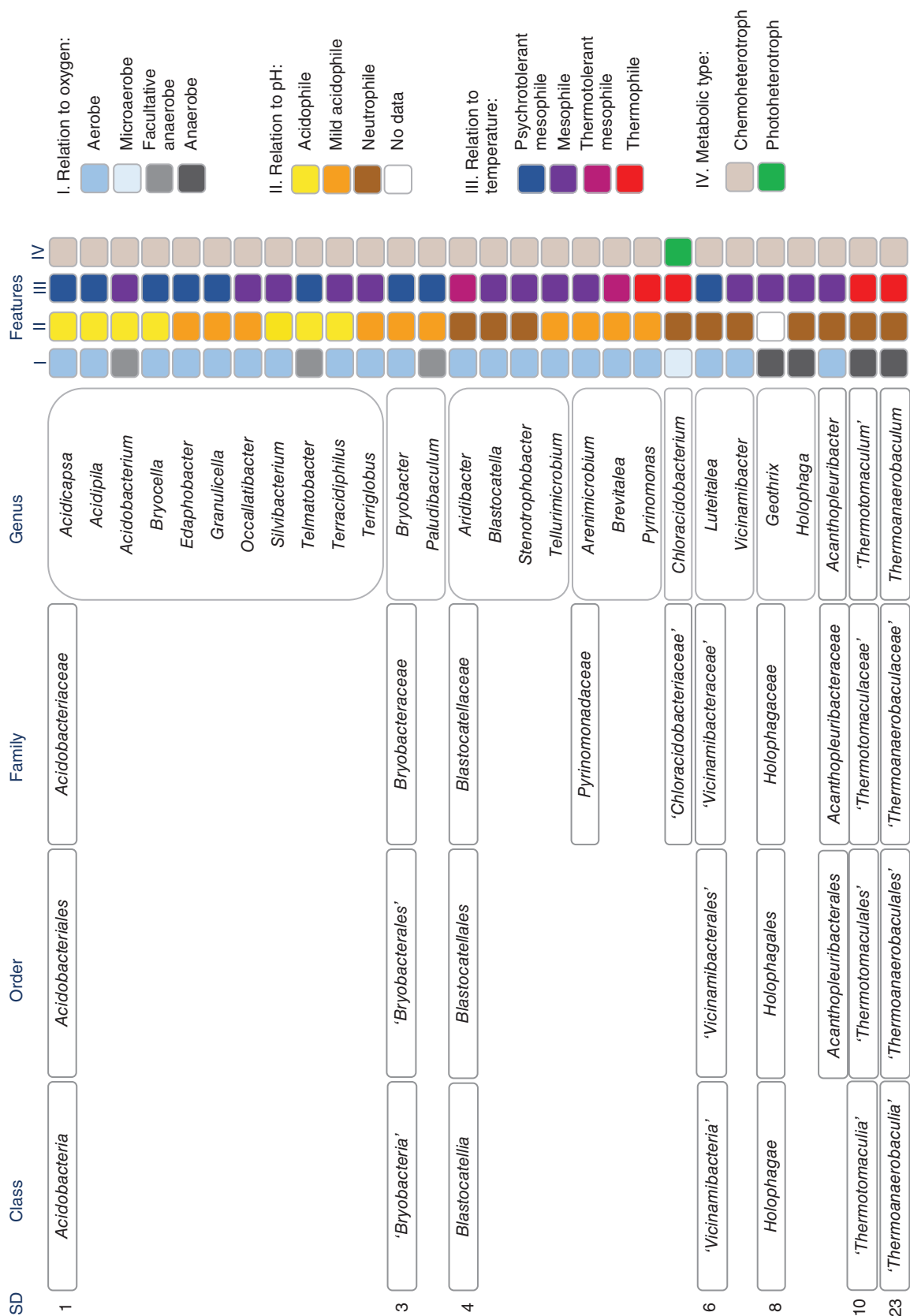
Figure 2 The current taxonomic structure of the phylum *Acidobacteria* and physiological characteristics of taxonomically described representatives. SD, subdivision. The names given in parentheses remain to be validly published. Two additional representatives of the classes *Acidobacteriia* and '*Bryobacteria*' with determined genome sequences, '*Candidatus* Koribacter versatilis' and '*Candidatus* Solibacter usitatus', are not included in this diagram because no detailed information regarding their physiology is currently available.

thermophile, but different ecotypes of these bacteria are adapted to specific temperatures of their habitats.

The class 'Vicinamibacteria' (SD6) accommodates the order 'Vicinamibacterales' and the family 'Vicinamibacteraceae'. This family includes two described members, Vicinamibacter silvestris and Luteitalea pratensis. Cells of these acidobacteria are nonmotile and do not form capsules. These aerobic, neutrophilc and mesophilic bacteria were isolated from soils and grow chemoheterotrophically on sugars, complex proteinaceous compounds, some organic acids and nucleic acids.

The class Holophagae (SD8) accommodates two orders, the Holophagales and Acanthopleuribacterales. The Holophagales includes the family Holophagaceae containing two taxonomically described members. Holophaga foetida is a strictly anaerobic, homoacetogenic bacterium that degrades methoxylated aromatic compounds to acetate and is capable of transferring methyl groups from phenylmethylethers to sulfide, forming methanethiol and dimethyl sulfide. Geothrix fermentans is also a strict anaerobe that oxidises acetate as well as several other simple organic and long-chain fatty acids with Fe(III) as the electron acceptor. Nitrate, Mn(IV), fumarate and the humic acid analogue 2,6-antraquinone disulfonate can also be used as alternative electron acceptors. In addition to anaerobic respiration, G. fermentans can also grow by fermentation of citrate or fumarate. The order Acanthopleuribacterales includes the family Acanthopleuribacteraceae with a single described representative, Acanthopleuribacter pedis. This strictly aerobic chemoheterotroph was isolated from a specimen of the chiton Acanthopleura japonica and utilises only a very limited number of growth substrates including glucose and several amino acids.

The only currently described representative of the class 'Thermotomaculia' (SD10), 'Thermotomaculum hydrothermale', was isolated from a deep sea hydrothermal vent chimney. It is strictly anaerobic, neutrophilic and moderately thermophilic bacterium capable of fermentative growth on complex proteinaceous substances.

Finally, the only known representative of the class 'Thermoanaerobaculia' (SD23), Thermoanaerobaculum aquaticum, is a strictly anaerobic thermophile, which was isolated from a freshwater hot spring. This bacterium is capable of fermentative growth on pyruvate or proteinaceous substrates as well as reducing Fe(III) and Mn(IV). **See also**: **Prokaryotic Systematics: Theoretical Overview in the Light of Molecular Advances**; **Acidophiles**; **Anaerobes**; **Biology of Green Sulfur Bacteria**

Genomic Potential

For the most recent analysis of the genome-encoded potential of Acidobacteria, the reader is referred to the detailed review by Kielak and coauthors (2016). Mesophilic representatives of this phylum have relatively large genomes, ranging in size between 4 and 10 Mbp. Genomes of thermophilic Acidobacteria are smaller, 2.7–3.8 Mbp. The very first analysis of three genomes from soil acidobacteria revealed their potential to participate in the cycling of plant-, fungal- and insect-derived organic matter (Ward et al., 2009). The genomes encode a wide repertoire of carbohydrate-active enzymes involved in breakdown, utilisation and biosynthesis of diverse structural and storage carbohydrates. Notably, the proportion of genes encoding various glycoside hydrolases in acidobacterial genomes is nearly the same as in genomes of the Bacteroidetes, the bacterial phylum with well-recognised hydrolytic potential. Further genome analyses were also supportive for placing the Acidobacteria in the list of organisms involved in hydrolysis and utilisation of various biopolymers in nature (Rawat et al., 2012; Kielak et al., 2016).

Acidobacterial genomes have a large proportion of genes encoding for transporters (Ward et al., 2009; Challacombe et al., 2011; Kielak et al., 2016). The high number of different transport systems facilitates the acquisition of a broad range of substrate categories, including amino acids, peptides, siderophores, cations or anions. The presence of a broad substrate range of transporters for nutrient uptake suggests an advantage of Acidobacteria in complex environments and adaptation to oligotrophic conditions, such as nutrient-limited soil conditions.

The gene clusters containing protein-coding genes for capsular polysaccharides as well as free EPS synthesis and export are also present in the genomes providing the cells with protection from environmental stresses and increasing their resilience to fluctuating temperatures (Rawat et al., 2012).

Identification of enzymes involved in energy-generation in Pyrinomonas methylaliphatogenes revealed multiple genes encoding a hydrogenase of the Group 5 [NiFe]-hydrogenases, a recently discovered class of enzymes known to catalyse high-affinity H_2 oxidation during persistence of certain Actinobacteria (Greening et al., 2015). An eight-gene operon encoding this hydrogenase is expressed under nutrient-limiting conditions, thus allowing this acidobacterium to consume H_2 in a high-affinity, first-order kinetic process. The genes encoding similar (>75% amino acid sequence identity) hydrogenases have also been identified in some other acidobacteria isolated from nongeothermal environments, such as 'Candidatus Solibacter usitatus', Edaphobacter aggregans and Granulicella mallensis.

The genome of Chl. thermophilum, the only known chlorophototroph in the phylum Acidobacteria, is composed of two chromosomes, 2.7 and 1.0 Mbp in size (Garcia Costas et al., 2012a). These contained genes to produce chlorosomes, the Fenna–Matthews–Olson protein, BChl a and c as principal pigments and type-1, homodimeric reaction centres. However, the genome lacked genes for all known CO_2 fixation pathways, as well as genes for assimilatory nitrate and sulfate reduction, vitamin B_{12} synthesis and the synthesis of branched-chain amino acids. These genome-inferred insights into the physiology and metabolism of Chl. thermophilum were of key importance for isolating this unique bacterium in an axenic culture (Tank and Bryant, 2015).

One additional important aspect in genome mining of Acidobacteria is related to search for novel bioactive compounds. The presence of genes predicted to encode macrolide glycosylases and polyketide synthases in genomes of uncultivated acidobacteria suggested that they might also be producers of yet-uncharacterised antimicrobial compounds (Parsley et al., 2011). **See also**: **Bacterial Genomes**; **Glycosidases: Functions, Families and Folds**; **Bacterial Membrane Transport: Superfamilies of Transport Proteins**

Characteristic Lipids

Acidobacterial species of SD1, 3 and 4 are characterised by a quite unique membrane-spanning lipid, *iso*-diabolic acid (**1** in **Figure 3**) (Sinninghe Damsté *et al*., 2011, 2014). The only other known bacteria that produce these lipids are *Thermoanaerobacter* species. Although the mechanism of biosynthesis of *iso*-diabolic acid is unknown, it is thought to be produced by condensation of two *iso*-C_{15} fatty acids, which is a commonly occurring and abundant fatty acid of acidobacteria. The presence of these membrane-spanning lipids in combination with the presumed presence of large polar head groups makes these lipids hard to extract with commonly used extraction methods (Sinninghe Damsté *et al*., 2011) and this explains why *iso*-diabolic acid is commonly missed by more conventional methods of membrane lipid analysis, even though it may represent up to 50% of the fatty acids. *Iso*-diabolic acid occurs also with an additional methyl group (i.e. **2**), and in SD4 acidobacteria (excluding *Chl. thermophilum*) *iso*-diabolic acid occurs predominantly ether bound to a glycerol moiety (**3–4**) (Sinninghe Damsté *et al*., 2014). These acidobacteria also biosynthesise other monoethers (e.g. **5**). The presence of these specific lipids indicates that the membranes of these bacteria contain *iso*-diabolic acid-based membrane-spanning lipids such as tetraesters **6** and **7** and diester/diethers **8** and **9**. This suggests that the structurally closely related 'orphan' branched tetraethers (e.g. **10** and **11**), which occur widespread in soils, peat bogs and lakes (Schouten *et al*., 2013), and which have been shown to have the bacterial stereoconfiguration of the glycerol moieties (Weijers *et al*., 2006), are potentially also produced by *Acidobacteria*. Indeed, traces of **10** were reported in two species of SD1 acidobacteria (Sinninghe Damsté *et al*., 2011), but no acidobacteria have been found yet that produce branched tetraethers as their main membrane lipids. It is currently unknown why some acidobacteria produce these specific membrane-spanning lipids. Changes in pH and temperature did not substantially affect the amount of *iso*-diabolic acid (Sinninghe Damsté *et al*., 2011, 2014).

Another group of characteristic lipids present in some SDs of the *Acidobacteria* are the bacteriohopanepolyol (BHP) derivatives, which are used as membrane rigidifiers. Garcia Costas *et al*. (2012a,b) identified intact BHPs (e.g. **12** and **13**) in *Chl. thermophilum*. A subsequent study analysed 38 different strains from various SDs (1, 3, 4, 6, 8, 10 and 23) for C_{30} hopenes and BHPs (Sinninghe Damsté *et al*., 2017). They were detected in all strains of SD1 and SD3, but not in SD4 (except for *Chl. thermophilum*), 6, 8, 10 and 23. This was in good agreement with the presence of genes required for hopanoid biosynthesis in the available genomes of cultivated acidobacteria. Analysis of environmental metagenomes suggested that also SD2 acidobacteria and one other groups closely related to SD1 and SD3 acidobacteria would be capable of BHP biosynthesis, but this requires confirmation by isolation and cultivation. The phylogeny of the key gene for BHP biosynthesis, *shc*, showed that this gene in *Chl. thermophilum* is most closely related to that of cyanobacteria, which probably explains why this is the only SD4 acidobacterium capable of BHP biosynthesis (Sinninghe Damsté *et al*., 2017). This is in line with the observation that only <20% of identified genes of

Chl. thermophilum are most closely related to those of other acidobacteria (Garcia Costas *et al*., 2012a,b). Of special interest is the SD1 acidobacterium *Candidatus* 'Koribacter versatilis' as it produces 2,3-dimethyl BHPs, which is unprecedented (Sinninghe Damsté *et al*., 2017). This is in accordance with the presence of the genes encoding for the proteins responsible for these methylation reactions (Welander *et al*., 2010; Welander and Summons, 2012). However, no other acidobacterium so far has been possessing these genes or produces methylated hopanoids, making it an exception rather than the rule.

As mentioned before, *Chl. thermophilum* is the only acidobacterium isolated so far that is photosynthetic and consequently produces a series of bacteriochlorophyll *c* derivatives, not only with farnesol as the esterifying alcohol but also with straight-chain alcohols (e.g. **14**) (Garcia Costas *et al*., 2012b). In addition, it produces a series of carotenoids with the somewhat uncommon carotenoid echinenone (**15**) as the most abundant one. Once more, this demonstrates the peculiar (chemo)taxonomic position of *Chl. thermophilum* as an SD4 acidobacterium. **See also**: **Lipids**

Ecology and Functions in a Biosphere

As judged by the proportion of *Acidobacteria*-affiliated 16S rRNA and 16S rRNA gene reads in sequence pools retrieved from various environments, members of this phylum are particularly abundant in diverse soil habitats, where they represent between 5% and 50% of the total bacterial community (Janssen, 2006; Lee *et al*., 2008; Jones *et al*., 2009; Lauber *et al*., 2009; Foesel *et al*., 2014). Most common representatives of soil-inhabiting acidobacteria belong to SDs 1, 2, 3, 4 and 6. SDs 1 and 3 are more typical for acidic soils, while SDs 4 and 6 are characteristic for arid soil environments. *Acidobacteria* are also among the major bacterial phyla in various wetlands, including extensive acidic *Sphagnum*-dominated peatlands, where they inhabit both oxic and anoxic peat layers (Dedysh *et al*., 2006, Dedysh, 2011; Serkebaeva *et al*., 2013). Peat-inhabiting acidobacteria belong mostly to SD1 and 3, although some subarctic wetlands may contain a relatively high proportion of SD2 *Acidobacteria*. The wide distribution of acidobacteria in soils and peatlands is also confirmed by the presence and relatively high abundance of the branched tetraethers (e.g. **10** and **11** in **Figure 3**), which are presumed to be derived from *Acidobacteria* (Schouten *et al*., 2013).

Cells of soil- or peat-inhabiting acidobacteria are usually observed as being attached to particles of nondecomposed organic material (**Figure 4**), which agrees well with their suggested role as slow-acting decomposers of plant-, fungi- and insect-derived polymers (Pankratov *et al*., 2011, 2012; Štrursová *et al*., 2012; Rawat *et al*., 2012; García-Fraile *et al*., 2015; Ivanova *et al*., 2016). This environmental role of *Acidobacteria* has remained unnoticed for a long time owing to their slow growth rates. Members of this phylum become particularly important in the econiches where well-known and fast-acting bacterial decomposers are absent or numerically insignificant. In northern acidic wetlands, for example, *Acidobacteria* appear to functionally replace the *Firmicutes* and *Bacteroidetes*, two
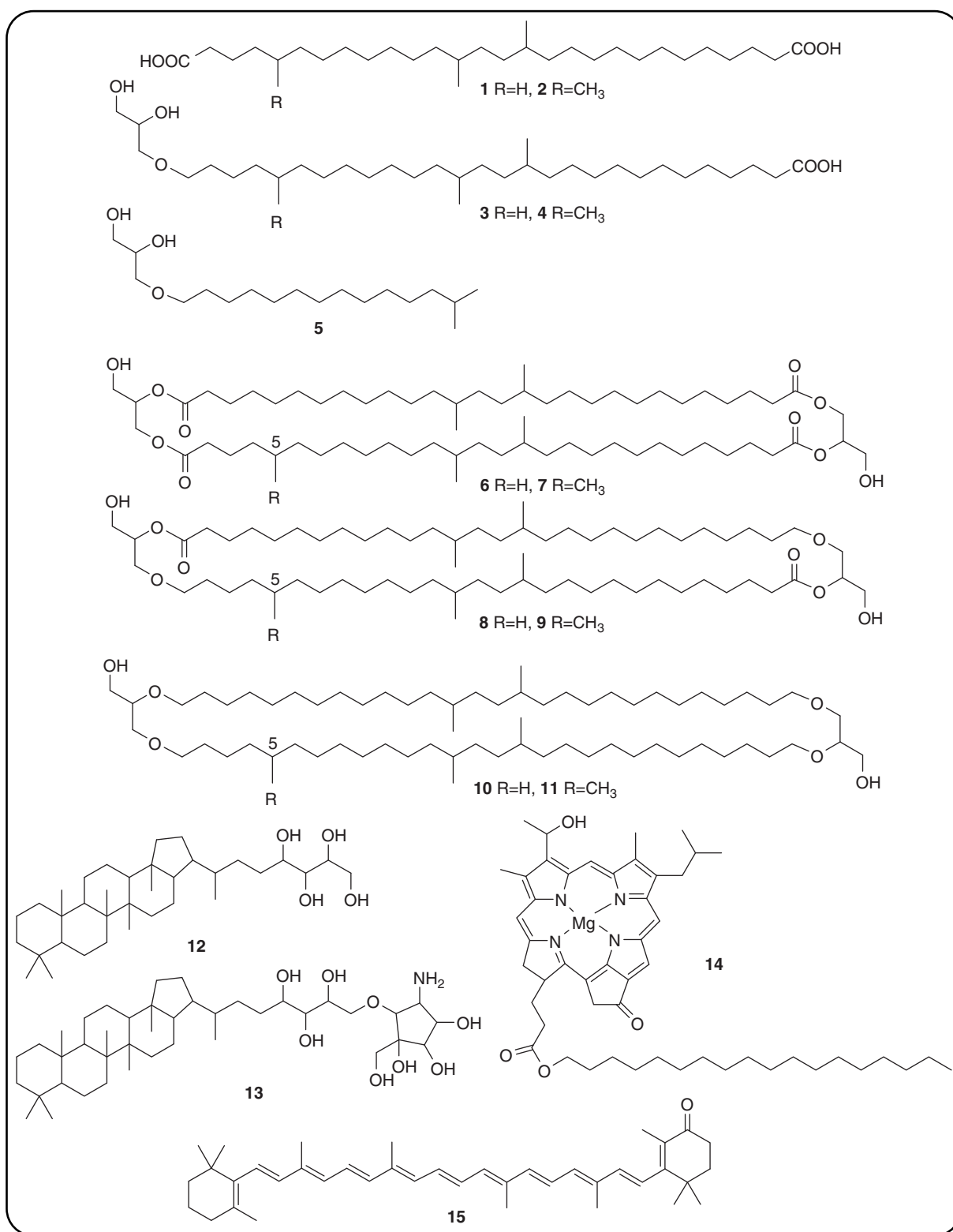
Figure 3 Structures of some lipids characteristic for *Acidobacteria*: **1** – *iso*-diabolic acid, **2** – *iso*-diabolic acid with an additional methyl group, **3** and **4** – *iso*-diabolic acid ether bound to a glycerol moiety, **5** – other monoethers synthesised by acidobacteria, **6** and **7** – tetraesters, **8** and **9** – diester/diethers, **10** and **11** – structurally related 'orphan' branched tetraethers which are widespread in terrestrial habitats, **12** and **13** – bacteriohopanepolyol derivatives, **14** – derivatives of bacteriochlorophyll *c* with straight-chain esterifying alcohols and **15** – the uncommon carotenoid echinenone produced by *Chl. thermophilum*.
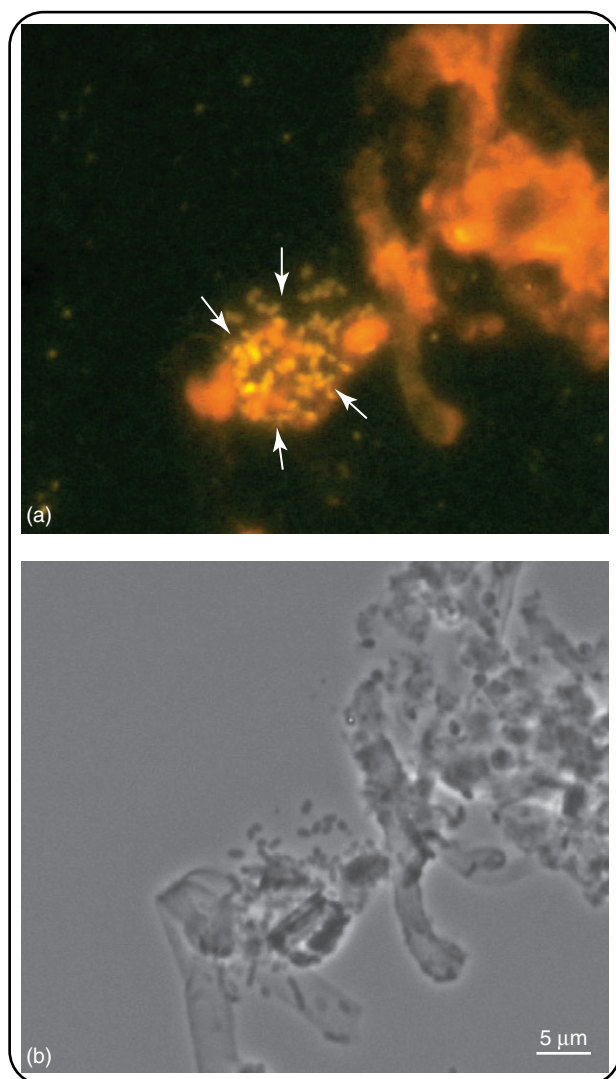
Figure 4 Specific detection of cells of peat-inhabiting acidobacteria (indicated by white arrows) attached to semidecomposed organic material. Epifluorescent micrograph of *in situ* hybridisation with *Acidobacteria*-specific Cy3-labeled probe HoAc1402 (a) and the corresponding phase-contrast image (b) are shown.

major bacterial hydrolytic groups known to be key players in biopolymer degradation in various habitats.

The question of how these slow-growing bacteria, which do not produce specialised dormant cell forms, become abundant members within soil microbial communities has received significant research attention. One of the possible mechanisms used by these bacteria for persistence in nutrient-starved soil ecosystems was offered by a recent discovery of atmospheric H_2 consumption by *Acidobacteria* (Greening *et al.*, 2015). This capability is owing to the possession of a high-affinity [NiFe]-hydrogenase, which is similar to those present in *Actinobacteria*. It has been suggested that trace H_2 gas oxidation may be a relatively conserved persistence mechanism among dominant soil phyla, such as *Actinobacteria* and *Acidobacteria* (Greening *et al.*, 2015). By

consuming atmospheric H_2, *Acidobacteria* contribute to global hydrogen cycling.

Acidobacteria appear to be particularly abundant in mineral, Fe-rich acidic environments (Barns *et al.*, 2007; Blöthe *et al.*, 2008; Kleinsteuber *et al.*, 2008; Lu *et al.*, 2010). Notably, the first described member of the phylum, *A. capsulatum*, was isolated from this type of habitat (Kishimoto *et al.*, 1991). Among taxonomically characterised acidobacteria, the ability to use Fe(III) as the electron acceptor in anaerobic respiration was demonstrated only for *G. fermentans* (Coates *et al.*, 1999). However, *A. capsulatum*, several other members of the *Acidobacteriaceae* and *P. fermentans* are capable of dissimilatory Fe(III) reduction under strict anoxic or micro-oxic conditions (Blöthe *et al.*, 2008; Lu *et al.*, 2010; Kulichevskaya *et al.*, 2014). Thus, *Acidobacteria* seem to play a role in the cycling of iron in various ecosystems.

The knowledge on environmental distribution and abundance of photoheterotrophic, *Chloracidobacterium*-like organisms remains limited, although they were detected in most mat communities in the alkaline hot spring of Yellowstone National Park and also in thermal springs of other geographic locations. The data regarding the relative abundance and ecological role of marine representatives of the *Acidobacteria* are also limited. The screening of metagenomic Mediterranean deep-sea libraries revealed a number of acidobacterial fosmids, most of which affiliated with SD6 and 11 (Quaiser *et al.*, 2008). Moreover, the number of *Acidobacteria*-related sequences showed a significant increase of their relative proportion in plankton libraries as a function of increasing depth, suggesting that some members of this phylum are well adapted to deep oceanic waters. Clearly, there is a major lack of knowledge about acidobacteria that thrive in marine and terrestrial anoxic environments. **See also**: **Bacterial Ecology**; **Soils and Decomposition**; **Mire Ecosystems**

Acknowledgements

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