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REVIEW PAPER

The *Planctomycetia*: an overview of the currently largest class within the phylum *Planctomycetes*

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Abstract The phylum *Planctomycetes* comprises bacteria with uncommon features among prokaryotes, such as cell division by budding, absence of the bacterial tubulin-homolog cell division protein FtsZ and complex cell plans with invaginations of the cytoplasmic membrane. Although planctomycetes are ubiquitous, the number of described species and isolated strains available as axenic cultures is still low compared to the diversity observed in metagenomes or environmental studies. An increasing interest in planctomycetes is reflected by the recent description of a large number of new species and their increasing accessibility in terms of pure cultures. In this review, data from all taxonomically described species belonging to *Planctomycetia,* the class with the currently highest number of characterized members within the phylum *Planctomycetes*, is summarized. Phylogeny, morphology, physiology, ecology and genomic traits of its members are discussed. This comprehensive overview will help to acknowledge several aspects of the biology of these fascinating bacteria.

Keyword Bacteria · Taxonomy · Ecology · Morphology · Physiology · Genomics · Budding

The phylum *Planctomycetes*

The phylum *Planctomycetes* is a group of bacteria within the *Planctomycetes-Verrucomicrobia-Chlamydiae* (PVC) superphylum (Wagner and Horn 2006), which is presently also formed by *Lentisphaerae* and other sister phyla with *Candidatus* status (Lage et al. 2019). The first representative of this phylum was identified nearly one century ago and mistakenly classified as a floating fungus, which explains the name of the phylum (Gimesi 1924).

Taxonomically, the phylum *Planctomycetes* is presently divided into two classes, *Planctomycetia* (Krieg et al. 2010) and *Phycisphaerae* (Fukunaga et al. 2009). In addition to members of these two classes, Planctomycetes capable of anaerobic ammonium oxidation (anammox) (Strous et al. 1999) form the proposed *Candidatus* order Brocadiales (Jetten et al. 2010), a status that results from the current lack of an axenic culture for any described member of the order.

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Planctomycetes and other PVC members such as the *Chlamydiae* are unique in many aspects, such as their cell biology (van Niftrik and Devos 2017). The planctomycetal cell plan is distinctive from other bacteria because of invaginations of the cytoplasmic membrane which give rise to an enlarged periplasmic space in several strains (Boedeker et al. 2017; Devos 2014; Lage et al. 2013; Santarella-Mellwig et al. 2013). *Planctomycetes*, as well as *Chlamydiae,* are solely capable of dividing without the otherwise universal division protein FtsZ, which is unique in prokaryotes (Ouellette et al. 2020; Rivas-Marin et al. 2016a). Key proteins involved in cell division are still unknown (Wiegand et al. 2020c). The phenomenon of phagocytosis-like cell engulfment (exclusively known until now in eukaryotes and therefore quite unique in prokaryotes) was also spotted recently in the putative planctomycete *Candidatus* 'Uab amorphum' (Shiratori et al. 2019).

Presently, Planctomycetes are still mysterious bacteria (Lage et al. 2019; Wiegand et al. 2018) and, although ubiquitous, only a small percentage of the known diversity is covered by axenic cultures (Wiegand et al. 2018). The description of novel taxa and the expansion of our knowledge on the existing ones are equally important to have a better understanding of the biology of this fascinating group of bacteria. In fact, recent efforts in the development of new isolation techniques and sampling in different habitats resulted in the isolation of numerous strains in the last years (Boersma et al. 2020; Dedysh et al. 2020c; Devos et al. 2020; Kaushik et al. 2020; Kulichevskaya et al. 2017a; Kulichevskaya et al. 2020a; Kulichevskaya et al. 2020b; Kumar et al. 2020a; Kumar et al. 2020b; Kumar et al. 2020c; Lage et al. 2017; Pradel et al. 2020; Vitorino et al. 2020; Vitorino et al. 2021b; Wiegand et al. 2020c). Wiegand and collaborators made a remarkable contribution to the current planctomycete collection by bringing into culture and characterizing 79 planctomycetal strains, most of which are new taxa (Wiegand et al. 2020c). Furthermore, recent re-arrangements in the planctomycetal taxonomy have allowed the introduction of new taxonomic groups (Dedysh et al. 2020c).

The main goal of this overview article is to gather current knowledge on *Planctomycetia*, which is currently the class within the phylum *Planctomycetes* with the highest number of characterized members. This review, which puts the emphasis on taxonomy, is based on data available on the currently and effectively or validly described representatives. All compiled data from hitherto published species descriptions is given in Supplementary Table 1a-d while an overview of the major features and differences between each family is presented in Table 1. Based on the dataset, the phenotypic and genomic features of the taxa are discussed. Additionally, information on other isolates and environmental 16S rRNA gene sequences, when available, was obtained by searching for hits within the species threshold of 99% similarity of the 16S rRNA gene in the National Center for Biotechnology Information (NCBI) database using BLAST search (data given in Supplementary Table 1a).

The class *Planctomycetia*

Taxonomy

With a total of 108 formally described species, *Planctomycetia* is currently the best studied class within the phylum *Planctomycetes* (Supplementary Table 1a-d). By comparison, the current class *Phycisphaerae* consists of only 9 published species. More than half of the species described falling within the class *Planctomycetia* (70) were either published in 2019, 2020 or 2021, which reflects the increasing interest in an exploration of the diversity within this class. The class is currently subdivided into four orders, namely the type order *Planctomycetales* and the orders *Pirellulales, Isosphaerales* and *Gemmatales* (Dedysh et al. 2020c). The order *Planctomycetales* has only one family, *Planctomycetaceae*. The current order *Pirellulales* in turn is divided into three families, *Pirellulaceae, Lacipirellulaceae* and *Thermoguttaceae*. The orders *Isosphaerales* and *Gemmatales* harbour a single family, *Isosphaeraceae* and *Gemmataceae*, respectively. A partial 16S rRNA gene-sequence-based tree was computed based on all type strains to summarize the phylogeny of the families and orders within the class *Planctomycetia* (Fig. 1).

To achieve a better insight on the phylogenetic diversity within the class, we additionally searched for the respective full-length 16S rRNA gene sequences in the SILVA SSU Ref NR database (release 138.1 from 27 August 2020) (Quast et al. 2013) that putatively belong to class *Planctomycetia*. We found 4871 non-

Table 1 Overview on the main features of the families of the class *Planctomycetia*. NDA- no data available

	Order *Planctomycetales*	Order *Pirellulales*			Order *Isosphaerales*	Order *Gemmatales*
	Planctomycetaceae	*Pirellulaceae*	*Lacipirellulaceae*	*Thermoguttaceae*	*Isosphaeraceae*	*Gemmataceae*
Type genus/ species	*Planctomyces/ P. bekefii*	*Pirellula/ P.staleyi*	*Lacipirellula/ L. parvula*	*Thermogutta/ T. terrifontis*	*Isosphaera/ I. pallida*	*Gemmata/ G. obscuriglobus*
Fist taxonomically described member	*Planctomyces bekefii*	*Pirellula staleyi* (former *Planctomyces staleyi*)	*Bythopirellula goksoeyrii*	*Thermogutta terrifontis/ T. hypogea*	*Isosphaera pallida*	*Gemmata obscuriglobus*
Year/location of isolation of the first described member	1924/ Eutrophic lake in Budapest	1993/ Freshwater lake in the USA	2013/ Iron-hydroxide deposit in the Arctic Mid Ocean Ridge	2015/ Hot spring, Russia; deep gold mine, Africa	1987 / Hot spring in the USA	1984 / freshwater samples in Australia
Number of described species	29	39	13	3	13	11
Number of described genera	14	15	8	2	6	9
Habitats of taxonomically described species	Mostly marine but also freshwater and extreme	Mostly marine but also freshwater and extreme	Mostly marine but also freshwater and extreme	Extreme and deep surface	Mainly freshwater and terrestrial but also marine/extreme/deep surface	Manly freshwater but also terrestrial and extreme
Average duplication time (hours)	30.5 ± 8.9	15.3 ± 7.4	43.0 ± 26.6 h	NDA	29.9 ± 8.0	21.8 ± 14.5
Main respiratory mode	Aerobic	Aerobic	Aerobic	Facultatively anaerobic	Aerobic	Aerobic
Relation to temperature	Mostly mesophilic, but also rarely psychrotolerant	Mostly mesophilic, but also rarely psychrotolerant	Mesophilic	Thermophilic	Mostly mesophilic and psychrotolerant but also rarely thermotolerant	Mostly mesophilic, but also rarely psychrotolerant or thermophilic
Main polar lipids	(mono/di)phosphatidylglycerol, phosphatidyl-(mono/di) methylethanolamine, phosphatidylcholine, phosphocholine	Phosphatidylcholine, diphosphatidylglycerol, phosphatidylglycerol	Phosphatidyl-dimethylethanolamine	NDA	Phosphatidylcholine, phosphatidylglycerol, trimethylornithine and phosphocholine	Trimethylornithine
Major fatty acids	$C_{16:0}$, $C_{16:1}\omega7c$, $C_{18:1}\omega9c$	$C_{18:1}\omega9$, $C_{16:0}$	$C_{16:1}\omega9c$, $C_{16:0}$, $C_{18:1}\omega9$, $C_{16:1}\omega7c$, $C_{18:0}$	$C_{16:0}$, $C_{18:0}$, $C_{20:0}$	$C_{18:1}\omega9$, $C_{16:0}$, $C_{18:0}$	$C_{18:0}$, $C_{18:1}\omega5c$, $C_{16:1}\omega5c$
Most common cell shapes	Spherical to ovoid or rice/pear-shaped	Ovoid/pear-shaped/ elongated	Pear-Shaped/ovoid/ ellipsoidal	Coccoid to ellipsoidal	Spherical	Spherical
Most common form of cell aggregation	Aggregates and rosettes	Rosettes and aggregates	Aggregates	Aggregates	Aggregates and chains	Aggregates and rosettes
Colony pigmentation	Mostly pink and white/cream but also orange	Mostly pink and white/ cream but also orange	Hot pink to red or white/ unpigmented	White/cream	Mostly pink but also unpigmented/ milky yellow	Pink to red
Formation of stalks	Yes	No	No	No	No	Yes
Range of genome sizes/ average size (Mb)	5.16–8.92 / 6.9 ± 1.1	6.1—11.0 / 7.7 ± 1.2	4.3–6.83 / 6.1 ± 0.8	4.8	5.4–10.37 / 8.3 ± 1.7	4.81–12.4 / 9.1 ± 2.2

Table 1 continued

	Order *Planctomycetales*	Order *Pirellulales*			Order *Isosphaerales*	Order *Gemmatales*
	Planctomycetaceae	*Pirellulaceae*	*Lacipirellulaceae*	*Thermoguttaceae*	*Isosphaeraceae*	*Gemmataceae*
Range of G + C content /average value (mol%)	45.1–70.7 / 54.8 ± 6.6	49.5–62.4 / 56.5 ± 2.5	52.8–66.7 / 62.1 ± 5.3	57.3–66.6 / 60.8 ± 0.8	51.2–71.1 / 64.1 ± 6.0	57.0–71.3 / 63.5 ± 4.6
Presence of plasmids	Yes, rare	No	Yes, rare	No	Yes in most members and with often more than one	Yes, rare

redundant sequences in total, defined by a 99% identity threshold. However, a large part of the list of Operational taxonomic units (OTUs) corresponds to organisms that have not yet been cultivated, which underlines that only a small fraction of the known diversity of the class is presently covered by axenic cultures (approximately 2%) (Wiegand et al. 2018). In that regard, the class *Planctomycetia* is largely unexplored. Nevertheless, the current number of axenic cultures reflects the predicted abundance of this class within the phylum: in comparison, the number of OTUs for the phylum is 8657, of which more than half belong to the class *Planctomycetia* while only 2484 correspond to members of the class *Phycisphaerae* and the rest to other lineages. Based on the available information, *Planctomycetia* seems to be the most diverse class of the phylum *Planctomycetes*. However, this assumption is purely based on the present knowledge regarding the data available. As already discussed previously (Wiegand et al. 2018), the entire phylum *Planctomycetes* is still heavily underexplored and novel taxa and even lineages are most likely present in the environment but have not yet been discovered.

Genomic characteristics

Of all hitherto described species falling in the class *Planctomycetia*, the majority of the type strains have currently a genome sequence available in the NCBI database (as of October 2021), which has allowed in the recent years for a more extensive analysis of this group (Kallscheuer and Jogler 2021; Wiegand et al. 2020c) (Supplementary Table 1d). In total, in the NCBI database, 145 non-redundant genome assemblies belonging to cultured organisms taxonomically assigned to class *Planctomycetacia* are currently available (excluding Metagenome-assembled genomes (MAGs)). These genomes were used to compute a genomic multilocus-sequence analysis-based tree (MLST) (Alanjary et al. 2019) to visualize the phylogenetic organization of the current class *Planctomycetia* (Fig. 2). Furthermore, core information clustered in this study for all *Planctomycetia* species was additionally displayed in association to the tree (Fig. 2).

The genome size is highly variable among species within this class, with the smallest size of 4.3 Mb for "*Botrimarina hoheduenensis*" Pla111^{T}

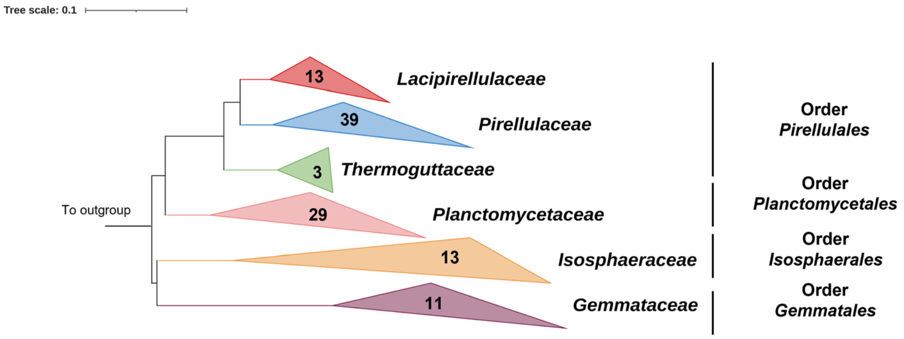

Fig. 1 Phylogeny of the families and orders of class *Planctomycetia*. The number of described species with 16S rRNA gene available are given. The partial 16S rRNA gene-based tree was constructed with MEGA X (Kumar et al., 2018) using type strain sequences, which were retrieved from the NCBI database. The alignment of sequences was performed with CLUSTALW (Larkin et al., 2007) and the phylogeny was inferred by using the Maximum Likelihood method and General Time Reversible mode using the gamma substitution and estimation of proportion of invariable sites option. Members belonging to the same family were collapsed and the number of species within each one presented. The outgroup consists of 3 members from the phylum *Verrucomicrobia*

(*Lacipirellulaceae*) (Wiegand et al. 2020a) and the biggest size of 12.4 Mb belonging to *Fimbriiglobus ruber* SP5^T (*Gemmataceae*) (Kulichevskaya et al. 2017a). Genome sizes are overall higher in planctomycetes from families such as *Isosphaeraceae* and *Gemmataceae*, which are almost exclusively present in terrestrial and freshwater habitats (Table 1). The DNA G + C content is also highly diverse, ranging from 45.1 mol% in *Gimesia aquarii* V144^T (*Planctomycetaceae*) (Wiegand et al. 2020b) to 71.3 mol% in *Urbifossiella limnaea* ETA_A1^T (*Gemmataceae*) (Kallscheuer et al. 2020d). The higher values are also correlated with planctomycetes that are inhabitants of terrestrial environments (Table 1). In general, more than 40% of the protein-coding genes are associated with unknown functions (Wiegand et al. 2020c).

Data on genome-encoded features in the central carbon metabolism was also gathered when available. All examined strains harbour genes coding for enzymes involved in glycolysis (Embden-Meyerhof-Parnas pathway or the alternative Entner-Doudoroff pathway), although, in some cases, not all genes could be identified. The same was noticed for the tricarboxylic acid cycle and gluconeogenesis. Most species had a fully functional pentose phosphate pathway but no planctomycetal genome analysed so far showed a complete glyoxylate shunt pathway. This pathway is normally required for anaplerosis during growth with fatty acids or acetate as sole carbon and energy source (Chew et al. 2019). The lack of genes for this pathway might support the hypothesis that members of class *Planctomycetia* prefer sugars over carboxylic acids as carbon and energy sources.

The bioactive potential of this class was also evidenced by the presence of related biosynthetic gene clusters in most available genomes (Wiegand et al. 2020c; Wiegand et al. 2018). These showed to be rich in different genes encoding large multimodular proteins such as Non-ribosomal peptide synthetases (NRPSs) and Polyketide synthases (PKSs), as well as in genes for production of terpenes, ectoines and antibiotics such as bacteriocins and lanthipeptides, among others (Kallscheuer and Jogler 2021; Wiegand et al. 2020c; Wiegand et al. 2018). The production of antimicrobial compounds empowers members of this class with the ability to compete against other fast-growing bacteria for space and food resources, rendering them competitive in challenging environments.

Morphology

Morphologically, members of the class *Planctomycetia* are mostly spherical to ovoid, elongated or pear-shaped and 0.5 to 2.5 µm in diameter or length and can form aggregates, rosettes and even chains (Supplementary Table 1b). Most species also have the capacity to produce extracellular materials (*e.g.* holdfast or mucus substances or fibrous materials) that allows them to live in an attached life style in biofilms. Most species also display crateriform pits, either

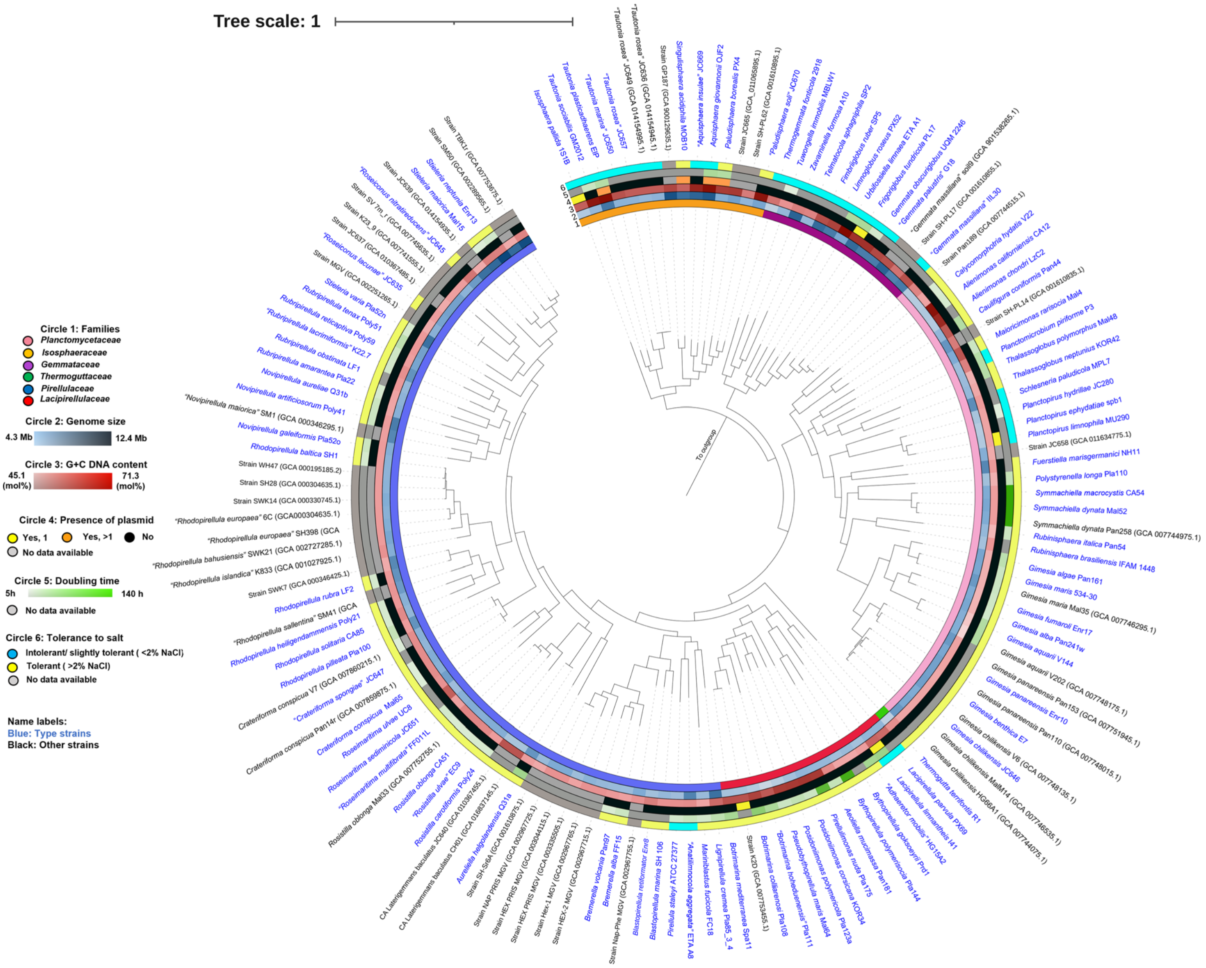

Fig. 2 Multi-locus- sequence analysis-based tree (MLST) showing the phylogenomics of class *Planctomycetia* and a summary of the core information clustered in this study. All genomes currently available in the NCBI database of organisms assigned to the class *Planctomycetia* were utilized to construct the MLS tree, which was computed using the autoMLST: Automated Multi-Locus Species Tree pipeline using default gene parameters (Alanjary et al., 2019). The outgroup consists of three members from phylum *Actinobacteria* (*Streptomyces* spp.). Name labels in blue correspond to type strains of the described species and names in black correspond to other strains with the genome available at GenBank. Excluded species with currently no genome available are *Rhodopirellula lusitana*, *Thermostilla marina*, *Novipirellula caenicola*, *N. rosea*, *Bremerella cremea*, *Thermogutta hypogea*, "*Singulispaera mucilagenosa*", *S. rosea, Tundrisphaera lichenicola, Planctomyces bekefii, P. stranskae* and *P. guttaeformis*. The datasets containing the summarized information of *Planctomycetia* species were added to the tree using the Interactive Tree Of Life (iTOL) v5 online tool (Letunic and Bork, 2021)

distributed uniformly over the cell surface or only on the reproductive pole. Overall, members of the class *Planctomycetia* display what is considered a typical planctomycetal cell structure, including a complex pattern of cytoplasmic membrane invaginations (Boedeker et al. 2017; Lage et al. 2019; Wiegand et al. 2018). Colony colours within the class range from unpigmented/white/beige to pink/red or orange. The pigmentation is caused by the production of carotenoids (Kallscheuer et al. 2019), while their exact function remains to be elucidated.

Members of the class *Planctomycetia* divide by budding (Lage et al. 2019; Wiegand et al. 2020c). This is a striking difference to most other bacteria, which divide by binary fission, including members of the class *Phycisphaerae* (Fukunaga et al. 2009), as well as the anammox planctomycetes (van Niftrik and Jetten 2012). Budding in bacteria is a rare division mode shared only by a scarce number of taxa, such as

Caulobacter spp. and *Hyphomicrobium* spp., and diverges from the budding normally associated to yeasts (Stackebrandt et al. 1988). Planctomycetal budding is characterized by the outgrowth of a bud from the mother cell, which is regularly on the polar side of the cell but can be formed laterally (Vitorino et al. 2020; Wiegand et al. 2020c). Furthermore, other unique division variations such as the formation of a tubular neck-like structure between the mother and daughter cells and consecutive budding were also spotted in different *Planctomycetia* strains (Boersma et al. 2020; Kohn et al. 2016; Lage 2013; Vitorino et al. 2020).

Ecology

Data on the ecology of the currently described members of the class was gathered (Supplementary Table 1a) and summarized in Fig. 3. Marine and brackish environments are well-known habitats for members of the class and material used for strain isolation included diverse sources such as water, sediments, marine organisms like algae, plants and invertebrates (*i.e.* sponges, shrimps), etc. (Fig. 3a). In particular, macroalgae are hotspot organisms that harbour planctomycetal diversity (Bengtsson and Ovreas 2010; Bondoso et al. 2014b, 2017; Lage and Bondoso 2011, 2014). In fact, environments rich in organic carbon sources such as macroalgal biofilms that are composed of Extracellular polymeric substances (EPS) seem to favour the presence of members of the class *Planctomycetia*. Furthermore, strains belonging to the families *Pirellulaceae* and *Lacipirellulaceae* were isolated from natural (wood pellets) or artificial (polystyrene particles or polyethylene) materials retrieved from marine/brackish environments (Fig. 3a). On the other hand, freshwater and terrestrial environments, seem to be promising spots for the isolation of members of the families *Gemmataceae* and *Isosphaeraceae* (Fig. 3b). Strains affiliated to all families were also isolated from ‘extreme’ environments (such as hot springs and hydrothermal vents) (Fig. 3b). The ranges regarding temperature preference points towards potential differences in the capacity of different taxa to adapt to such conditions. Also, deep-surface environments such as gold mines served as a source for the isolation of *Isosphaeraceae* and *Thermoguttaceae* (Fig. 3b).

Although no strains were isolated from oil/petroleum/metal-contaminated environments so far, a variety of environmental 16S rRNA sequences likely belonging to the families *Pirellulaceae*, *Planctomycetaceae* and *Gemmataceae* were detected (Fig. 3b). The indication of the presence of strains belonging to this class in such environments demonstrates that *Planctomycetia* members are promising organisms to be studied in the context of bioremediation (either with hydrocarbons or metals). So far, only uncultured *Planctomycetaceae*, *Gemmataceae*, *Lacipirellulaceae* and *Thermoguttaceae* were detected in anaerobic reactors/activated sludge or wastewater treatment plants (Fig. 3b). Taken together, known members of this class, although mostly distributed in marine and freshwater environments, appear to adapt well to a variety of different habitats (Fig. 3).

In terms of the geographical distribution of known *Planctomycetia* (Fig. 4), sampling and isolation campaigns focused on a limited number of locations around the globe, in particular the European coast. The Mediterranean Sea around Italy, including the Aeolian Islands, turned out to be a promising location for the isolation of members of all families with exception of *Gemmataceae*. A variety of strains from the families *Pirellulaceae*, *Lacipirellulaceae* and *Planctomycetaceae* was also obtained from German coastlines of the North and Baltic Sea and the Spanish and French coastlines/islands (Wiegand et al. 2020c). The North Coast of Portugal in the Atlantic ocean is also inhabited by diverse *Planctomycetaceae* and *Pirellulaceae* (Bondoso et al. 2014b, 2017; Lage and Bondoso 2011, 2014), as well as the Norwegian coast (Bengtsson and Ovreas 2010). Additional coastlines from which *Planctomycetaceae* and *Pirellulaceae* were isolated are the Californian coast (Wiegand et al. 2020c) and the eastern Australian coast (Izumi et al. 2013). Valu Fa Ridge in the Southwest Pacific is also a location with abundant *Pirellulaceae* and *Planctomycetaceae*, as well as *Lacipirellulaceae* (Storesund et al. 2018). Numerous locations in Russia, namely peat bogs, subarctic lands and lakes, also serve as habitats for a variety of known *Gemmataceae* and *Isosphaeraceae*, as well as some *Pirellulaceae* and *Lacipirellulaceae* (Dedysh and Ivanova 2019; Ivanova et al. 2016; Kulichevskaya et al. 2017a, 2015, 2017b). An isolation campaign in India also revealed diversity of *Planctomycetia* (Gaurav et al. 2021; Kaushik et al. 2020; Kumar et al. 2020a; Kumar et al. 2020b; Kumar

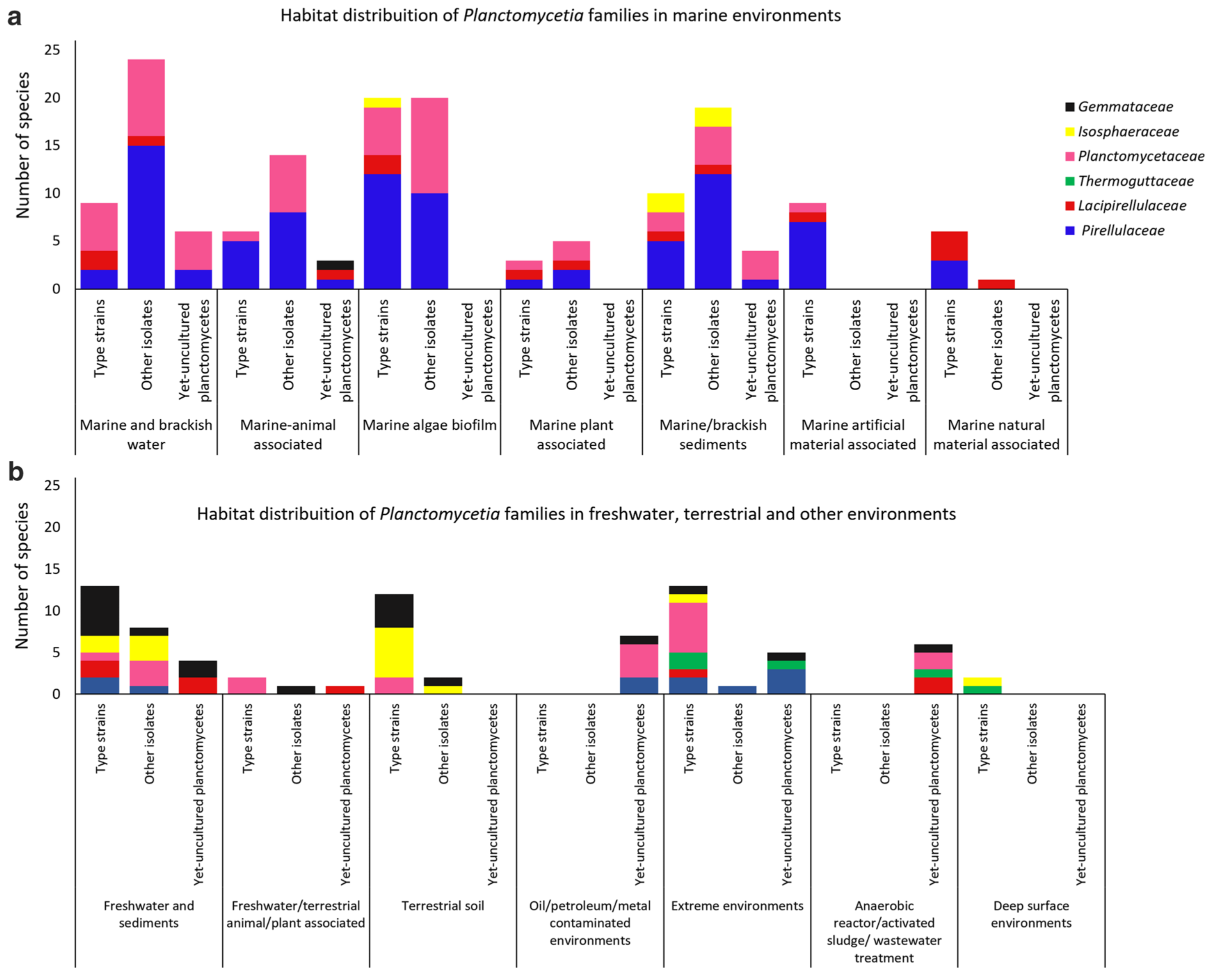

Fig. 3 Habitat distribution of the currently taxonomically described members of the families within the class *Planctomycetia*. In (**a**), the marine and brackish water ecosystems display a very distinctive planctomycetal distribution compared to freshwater/terrestrial/other environments (**b**). Data from type strains was obtained from species description studies and information on other isolates and environmental 16S rRNA gene sequences, when available, was obtained by searching for hits defined by a threshold of 99% similarity of the 16S rRNA gene, in the NCBI database using the BLAST search

et al. 2021a; Kumar et al. 2020c; Kumar et al. 2021b; Kumar et al. 2021c). Based on NCBI data, additional locations with shown planctomycetal variety include territories in the United States and India but also other regions on the globe, including China, Mexico, Antarctica, Pacific Ocean, Philippines, Indonesia, Papua New Guinea, Japan and South Korea (Fig. 4), which makes them good candidates for future diversity and isolation studies. Taken together, known members of the class *Planctomycetia* seem to be well distributed around the globe and found when searched for (Fig. 4). Exploring different niches and locations is crucial to help bringing new taxa into pure culture and unveil the untapped planctomycetal diversity.

Physiology and metabolism

Most of the currently described members of the class *Planctomycetia* are aerobic (Lage et al. 2019; Wiegand et al. 2020c) while members of the class *Phycisphaerae* are mostly facultatively or strictly anaerobic (Dedysh et al. 2020a; Wiegand et al. 2018). In general, *Planctomycetia* comprises heterotrophic, neutrophilic, and mesophilic strains (Supplementary Table 1c). Members of this class are rather slow-growing bacteria, with the shortest doubling time of around 5 h (Yadav et al. 2018) and the largest of up to 140 h (Salbreiter et al. 2020), both belonging to family *Planctomycetaceae*. A variety of species have a motile

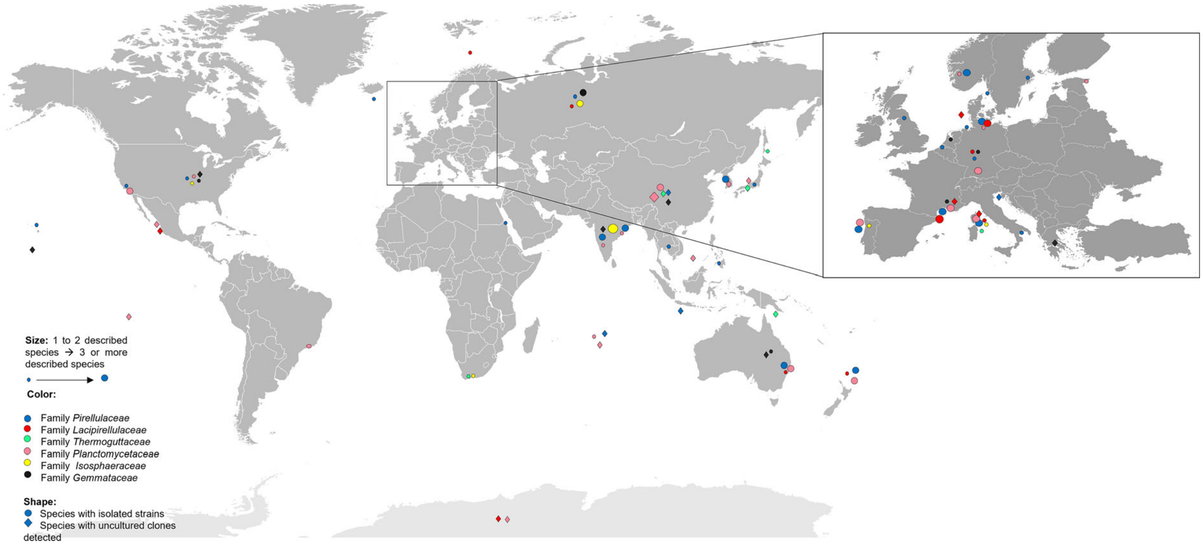

Fig. 4 Geographical distribution of the currently taxonomically described members of the families within the class *Planctomycetia*. Data from type strains was obtained from species description studies and information on other isolates and environmental 16S rRNA gene sequences, when available, was obtained by searching for hits, defined by a threshold of 99% similarity of the 16S rRNA gene, in the NCBI database using the BLAST search

stage in a dimorphic lifecycle (Gade et al. 2005). Most *Planctomycetia* are resistant to several antibiotics (Supplementary Table 1c) (Cayrou et al. 2010; Godinho et al. 2019; Ivanova et al. 2021b), *e.g.* the beta-lactam ampicillin and the aminoglycoside streptomycin, which are the components of a common antibiotic mixture used in isolation medium for the selective enrichment of planctomycetes (Lage and Bondoso 2012; Wiegand et al. 2020c) and also glycopeptides (Godinho et al. 2019). Although most species do not require vitamins for growth, the use of vitamin B_{12} (cyanocobalamin) as supplement enhances their growth.

Analysis of carbohydrate utilization patterns of *Planctomycetia* assessed by traditional assays (Supplementary Table 1c) showed that most species are capable of using diverse sugars and other complex polysaccharides as carbon and energy source. Furthermore, most species can also utilize peptone, yeast extract, urea, nitrate, and ammonium as nitrogen sources. *N*-acetyl glucosamine can act both as a source of carbon and nitrogen (Schlesner 1994). Members of *Gemmataceae* and *Isosphaeraceae* and, more specifically, strains isolated from the microbial community inhabiting boreal *Sphagnum* peat bogs and lichen-dominated tundra wetlands, also show the ability to grow on compounds like xylan, pectin, starch, lichenan, cellulose, chitin and polysaccharides of microbial origin, which demonstrates their versatile hydrolytic capabilities and wide repertoires of carbohydrate-active enzymes (Dedysh and Ivanova 2019; Rakitin et al. 2021).

The fatty acid (FA) composition present in the various families is dominated by $C_{16:0}$ with the exception of the family *Gemmataceae*, in which $C_{18:0}$ and $C_{16:1}\omega5c$ are the major fatty acids. Besides $C_{16:0}$, the families *Pirellulaceae*, *Lacipirellulaceae* and *Isosphaeraceae* also have $C_{18:1}\omega9c$ as another major FA and the representatives of *Thermoguttaceae* have a large content of $C_{18:0}$. In general, the *Planctomycetaceae* possesses $C_{16:1}\omega7c$. Although a comprehensive analysis on all the described species is not available, FA profiles are, to a certain extent, taxonomically indicative. The main respiratory quinone found in this class is menaquinone 6 (MK-6).

In the following sections, data will be discussed at the family level, including the main distinctive features between the six families of class *Planctomycetia* which are summarized in Table 1. Furthermore, particular aspects of *Planctomycetia* species currently described will also be presented.

Family *Planctomycetaceae*

The type family *Planctomycetaceae* currently comprehends 14 genera and 29 species and is the second largest family in terms of isolated and studied members (Table 1). The type genus *Planctomyces* comprises three members, including the first planctomycete, *Planctomyces bekefii* (Gimesi 1924). The genus is constituted by as-yet-uncultivated planctomycetes with validly published names, namely the type species *P. bekefii*, *P. stranskae* and *P. guttaeformis* (Gimesi 1924; Starr and Schmidt 1984). Certain pieces of information are available for these taxa, however, it is crucial to bring them into pure culture to allow a full description, as already evidenced by Dedysh et al. (Dedysh et al. 2020b). The remaining described species are listed in Table 2, as well as their main features.

Members of this family are mostly spherical to ovoid but can also be rice/pear-shaped. *Thalassoglobus polymorphus* Mal48^{T}, as the name indicates ("polymorphus": multiform, various shapes of the cells), has typically pear-shaped cells but other forms (such as coccoid and ovoid cells) are also observed (Rivas-Marin et al. 2020c). Members of *Planctomycetaceae* can be generally found in aggregates or rosettes, often harbour stalk-like structures and many members produce a holdfast structure. Morphologically, members of the genus *Planctomyces* are distinct: *P. bekefii* has a unique morphotype of rosettes formed by cells separated through stalk-like structures, which was the morphotype initially used for the distinction of this phylum (Dedysh et al. 2020b; Gimesi 1924). The other two *Planctomyces* species have also distinctive morphotypes: *P. stranskae* was described as a bulbiform bacterium with numerous multifibrillar appendages and bristles extending from the spherical end of the cell, while *P. guttaeformis* is described as a bulb-shaped bacterium with only one prominent multifibrillar appendage, like a spike (but not a stalk) (Starr and Schmidt 1984). Other species also possess distinct morphological features, such as *Caulifigura coniformis* Pan44^{T}, which has an uncommon cell texture comprised of triangles or rectangles (resembling a pinecone) (Kallscheuer et al. 2020e), and *Schlesneria paludicola* MPL7^{T}, which has short stalk-like structures which resemble twisted fibrils connecting the cells (Kulichevskaya et al. 2007). *Thalossoglobus neptunius* KOR42^{T} differs from others by being the only family member capable of occasional aggregation in filaments (Kohn et al. 2020a). *Calycomorphotria hydatis* V22^{T} possesses striking cell internal characteristics, such as putative filamentous cytoskeletal elements (Schubert et al. 2020). Although all known class members divide by budding, several members of this family have distinctive variations of the cell division process, such as polar and lateral budding in *Alienimonas chondri* LzC2^{T} (Vitorino et al. 2020; Vitorino et al. 2021a), consecutive budding in *A. californiensis* CA12^{T} (Boersma et al. 2020) and the formation of a tubular-like structure between mother and daughter cells in *A. chondri* LzC2^{T}, *Planctopirus hydrillae* JC280^{T} (Yadav et al. 2018) and *Fuerstiella marisgermanici* NH11^{T} (Kohn et al. 2016; Kohn et al. 2019). Most members are white/cream to pink pigmented while species *Maioricimonas rarisocia* (type strain Mal4^{T}) and *Rubinisphaera brasiliensis* (type strain IFAM 1448 ^{T}) are orange coloured (Kallscheuer et al. 2019; Rivas-Marin et al. 2020b; Schlesner 1989).

The family comprises, in general, heterotrophic, mesophilic, aerobic and neutrophilic organisms, although some members such as the strains isolated from the microbial communities inhabiting boreal tundra wetlands can be psychrotolerant and/or acid-tolerant (Supplementary Table 1c). Overall, the most common fatty acids found in the family are palmitic acid ($C_{16:0}$), palmitoleic acid ($C_{16:1}\omega7c$) and $C_{18:1}\omega7$ but some members display a different lipid profile, such as *F. marisgermanici* NH11^{T}, which is mainly constituted by fatty acids $C_{16:1}\omega6c$ and $C_{18:1}\omega7c$ (Kohn et al. 2016; Kohn et al. 2019), *R. italica* Pan54^{T} with the uncommon fatty acid $C_{15:0}$ iso2-O (Kallscheuer et al. 2020b) and *A. chondri* LzC2^{T} which produces iso-$C_{15:0}$ and *anteiso*-$C_{15:0}$ in major amounts (Vitorino et al. 2020, 2021a). Additional uncommon fatty acids (either $C_{14:0}$,3-OH or $C_{16:1}$iso) are also part of the lipid composition of most known members of the genus *Gimesia.* The main polar lipids found in the family are phosphatidylglycerol, diphosphatidylglycerol, phosphatidylcholine, phosphatidyl-dimethylethanolamine, phosphocholine and phosphatidyl-monomethylethanolamine besides a variety of non-identified lipids. *Planctomicrobium piriforme* P3^{T} is different from other family members by having a specific polar lipid composition (diacylglycerol-*O*-(*N*,*N*,*N*-trimethyl)homoserine lipid plus phosphocholine (Kulichevskaya et al. 2015).

Table 2 Main features of the described species of family *Planctomycetaceae*

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Alienimonas californiensis (Boersma et al. 2020)	CA12	*Macrocystis pyrifera* kelp	Monterey Bay, California	Pink	Spherical to ovoid	a	11	5.5	70.7
Alienimonas chondri (Vitorino et al. 2020)	LzC2	Macroalga *Chondrus crispus*	Porto, Portugal	Pink	Spherical to ovoid	r	NDA	5.3	68.3
Calycomorphotria hydatis (Schubert et al. 2020)	V22	Water/sediments of a fish tank	Braunschweig, Germany	Pink	Spherical to grain ice	r	10	5.2	53.9
Caulifigura coniformis (Kallscheuer et al. 2020e)	Pan44	Red biofilm, hydrothermal area	Island Panarea, Italy	White	Pear	r	32	6.8	63.2
Fuerstiella marisgermanici (Kohn et al. 2016)	NH11	Crustacean shell	Wadden Sea, Germany	Cream	Pear to ovoid	a	NDA	8.9	55.9
Gimesia alba (Wiegand et al. 2020b)	Pan241w	Organic material, hydrothermal vent	Panarea Island, Italy	White	Short grain-rice	a,r	14	7.8	49.6
Gimesia algae (Wiegand et al. 2020b)	Pan161	Alga, hydrothermal vent	Panarea Island, Italy	White	Short grain-rice	a,r	25	7.9	50.2
Gimesia aquarii (Wiegand et al. 2020b)	V144	Ornamental sea water aquarium	Braunschweig, Germany	Orange	Short grain-rice	a,r	32	7.4	45.1
Gimesia fumaroli (Wiegand et al. 2020b)	Enr17	Marine hot lake gas escape	Panarea island, Italy	White	Short grain-rice	a,r	15	7.7	49.5
Gimesia maris (Bauld and Staley 1976)	534–30	Seawater	Deception Pass, U.S.A	NDA	Ovoid	NDA	13–24	7.8	50.45
Gimesia chilikensis (Kumar et al. 2020a)	JC646	Sediments	Chilika lagoon, India	White	Pear to ovoid	r	NDA	7.6	53.2
Gimesia panareensis (Wiegand et al. 2020b)	Enr10	Rust biofilm at a hot lake gas escape	Panarea Island, Italy	Cream	Short grain-rice	a,r	NDA	7.8	53.7
Gimesia benthica (Wang et al. 2020)	E7	Deep- sea water sample	Northwest Indian Ocean	White	Ovoid	a,r	NDA	8.0	52.8
Maioricimonas rarisocia (Rivas-Marin et al. 2020b)	Mal4	Marine sediments	Coast of S'Arenal, Spain	Orange	Pear	a	17	7.7	63.4
Planctomicrobium piriforme (Kulichevskaya et al. 2015)	P3	Peat soil of a littoral wetland	Valaam Island, Russia	Unpigmented	Ellipsoidal to pear	r	30	6.3	58.8

Table 2 continued

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Planctopirus limnophila (Hirsch and Müller 1985)	MU 290	Freshwater	Lake Plußsee, Germany	Pink to red	Spherical to ovoid	r	NDA	5.4, 1 plasmid: 0.04	53.8
Planctopirus hydrillae (Yadav et al. 2018)	JC280	Surface of plant *Hydrilla verticillata*	Alkaline lake, India	Dark pink	Spherical to ovoid	a	5	5.8	53.8
Planctopirus ephydatiae (Yadav et al. 2018)	spb1	*Ephydatia* sp. sponge	Lake Constance, Germany	Pink	Ovoid to spherical	a,r	NDA	5.2	53.7
Polystyrenella longa (Peeters et al. 2020a)	Pla110	Polystyrene particles	Heiligendamm, Germany	White	Pear	r	21	6.1	50.3
Rubinisphaera brasiliensis (Schlesner 1989)	IFAM 1448	Water sample in a salt pit	Rio de Janeiro (Brasil)	Orange	Spherical to ovoid	r	NDA	6	56.5
Rubinisphaera italica (Kallscheuer et al. 2020b)	Pan54	Algal surface, hydrothermal area	Island Panarea, Italy	White	Pear	a,r	18	6.7	48.8
Schlesneria paludicola (Kulichevskaya et al. 2007)	MPL7	Acidic soil (Sphagnum peat bog)	Tomsk region, Russia	Unpigmented	Ellipsoidal	r	NDA	8.7	55.7
Symmachiella dynata (Salbreiter et al. 2020)	Mal52	Algae in the Mediterranean Sea	S'Arenal, Mallorca, Spain	White	Ovoid to pear	a	70–140	7.8	55.3
Symmachiella macrocystis (Salbreiter et al. 2020)	CA54	*Macrocystis pyrifera*	Monterey Bay, CA, USA	White to cream	Ovoid to pear or rod	a	70–140	7.6	55.2
Thalassoglobus neptunius (Kohn et al. 2020a)	KOR42	Biofilm of *Posidonia oceanica*	France, Corsica	Cream	Spherical	a,r, c	NDA	6.7	52.8
Thalassoglobus polymorphus (Rivas-Marin et al. 2020c)	Mal48	Algal surface	Coast of S'Arenal, Spain	Beige	Pear, coccoid or ovoid	a	29	6.4	50.3

**NDA*, no data available; *a*, aggregates; *r*, rosetes; *c*, chains

Although menaquinone 6 is the main respiratory quinone found in the class, an additional one, menaquinone 7 (MK-7), was found in *P. hydrillae* JC280^{T} (Yadav et al. 2018).

As referred previously, members of this family are geographically widely distributed (Fig. 4) and present in a variety of marine habitats, such as sediments, the water column and in association with macro- and microalgae, plants and animals (Fig. 3). *Gimesia* spp. are particularly widely spread in different marine locations and have also been isolated and detected in extreme environments, such as hot lakes and petroleum- and metal-contaminated sites (Supplementary Table 1a) which makes the members of the genus *Gimesia* promising organisms for future studies dealing with bioremediation of contaminated locations. Some members of the family such as *Planctopirus* spp., *P. piriforme* and *S. paludicola* are exclusively found in freshwater associated environments.

Members of family *Planctomycetaceae* turned out to be good candidates for future studies focusing on bioactive molecules: *P. limnophila, P. hydrillae* and *R. brasiliensis* strains showed antimicrobial activity (Graca et al. 2016; Jeske et al. 2016; Yadav et al. 2018). Additionally, the first detected phage capable of infecting a planctomycete was observed in *P. ephydatiae* spb1^{T} and posteriorly isolated and characterized (Kohn et al. 2020b).

The average genome size in this family is approximately 6.9 ± 1.1 Mb and it ranges from 5.16 to 8.92 Mb. The mean DNA G + C content is 54.8 ± 6.6 mol% (the lowest of the class) and it ranges from 45.1 to 70.7 mol%. *P. limnophila* MU 290 ^{T}, the only family member harbouring a plasmid, is considered a model organism for planctomycetal studies and has been one of the few successfully genetically modified planctomycetes (Boedeker et al. 2017; Jeske et al. 2016; Rivas-Marin et al. 2016b; Rivas-Marin et al. 2020a).

During the analysis of the family, we encountered a taxonomic conflict regarding the genus *Gimesia*. The 16S rRNA gene comparison between *G. benthica* E7^{T} and *G. chilikensis* JC646^{T} indicated that these two species are very similar (99.9% similarity). Both species descriptions were published almost at the same time (May and June 2020) (Kumar et al. 2020a; Wang et al. 2020) and both names are currently valid. The resulting conflict required reassessment of the phylogeny of the two strains. In fact, Wiegand and collaborators already employed several phylogenetic markers (*rpoB* gene identity, Average nucleotide identity (ANI), Amino acid identity (AAI) and percentage of conserved proteins) to re-analyse phylogenetic positions and concluded that the two strains belong to the same species (in this case, *G. chilikensis*, which was published and validated first) (Wiegand et al. 2020b). By the comparative analysis of our data clustered for both strains (Supplementary Table 1) we corroborate that these strains are indeed highly similar in morphological and physiological traits. Strain E7 should therefore be re-classified as a strain of the species *G. chilikensis*.

Family *Pirellulaceae*

The family *Pirellulaceae* is the group with the highest number of studied members in the entire class *Planctomycetia* (Table 1) and comprises 15 described genera and 39 species. The type genus *Pirellula* is constituted by a single species, *Pirellula staleyi* (Schlesner and Hirsch 1987) that was the first *Pirellulaceae* isolated, although it was originally named *Planctomyces staleyi* (Staley 1973) and then *Pirella staleyi* (Schlesner and Hirsch 1984). All described species are listed in Table 3 and their main traits presented. Very recently, an additional member of this family, *Candidatus* "Laterigemmans baculatus" was described (Kumar et al. 2021a), which possesses the *Candidatus* status due to the loss of viability in the laboratory culture (Kumar et al. 2021a).

Members of the family *Pirellulaceae* are often ovoid/pear-shaped/elongated ("pirellula" = small pear) and rosettes are the most common form of aggregation, with exception of species *Rhodopirellula solitaria* CA85^{T} that does not aggregate at all (Supplementary Table 1b). The recently described *Candidatus* "Laterigemmans baculatus" was the first reported rod-shaped planctomycete in the family (Kumar et al. 2021a). Stalk-like structures have never been observed in members of this family. Most species have a motile stage and produce a holdfast structure or fibrous materials. A strong glycocalyx or extracellular polymeric substance (which renders the cells adhesive) were additionally observed for some members of the genus *Rubripirellula* (*R. obstinata* LF1^{T} and *R. tenax* Poly51^{T}) (Bondoso et al. 2015; Kallscheuer et al. 2020c). The main colony colours in the family are white and pink while *Stieleria varia* Pla52^T is the sole member of the family to form orange-pigmented colonies (Surup et al. 2020).

Current data on known *Pirellulaceae* shows that they are wide-spread around the globe (Fig. 4) and live mostly in a variety of marine habitats (Fig. 3). Members of the genus *Rhodopirellula* seem to be the most disseminated one in these environments (Supplementary Table 1a) and they are often strongly associated with different macroalgal species (Bondoso et al. 2017; Lage and Bondoso 2011, 2012; Schlesner et al. 2004; Winkelmann and Harder 2009). Strains from the genera *Pirellula* and "*Anatilimnocola*" were only found in freshwater environments. *Pirellulaceae* strains belonging to additional genera, such as *Novipirellula* and *Rubripirellula*, were isolated from non-natural and abiotic surfaces like polystyrene or polyethylene particles. One strain affiliated to the genus *Bremerella* was isolated from an anaerobic, sulfide- and sulfur-rich spring in Oklahoma (Elshahed et al. 2007) and an uncultured clone putatively from the same genus was detected in chromium-contaminated tannery sludge, which indicates that *Bremerella* spp. may be promising organisms with relevance in bioremediation studies.

In general (Supplementary Table 1c), *Pirellulaceae* are heterotrophs and aerobes, with few exceptions capable of microaerobic or anaerobic growth, such as *Rhodopirellula rubra*, *Rhodopirellula lusitana* and *Blastopirellula marina*. They all divide by polar budding, with the exception of the recently described *Candidatus* "Laterigemmans baculatus", which is also capable of lateral budding (Kumar et al. 2021a). Overall, *Pirellulaceae* are neutrophilic and mesophilic, with a few psychrotolerant species. Members of this family have the smallest generation times of the current class *Planctomycetia*, with a mean value of 15.3 ± 7.4 h, with exception of *Aureliella helgolandensis* Q31a^T, which has a relatively high doubling time (41 h). Some members require vitamin B_{12} for growth. Phosphatidylcholine, diphosphatidylglycerol and phosphatidylglycerol are the main polar lipids found in the studied strains, however, a chemotaxonomic analysis was not presented in a considerable number of studies describing members of this family. Moreover, still unknown (phospho)lipids are also present in most species. Studies with *Novipirellula rosea* LHWP3^T (Roh et al. 2013) showed that it produces an extra polar lipid rare in the family: phosphatidylethanolamine. The major fatty acids found in members of this family are oleic/elaidic acid ($C_{18:1}\omega9$) and palmitic acid ($C_{16:0}$), while *P. staleyi* ATCC 27377 ^{T} also produces the long-chain unsaturated fatty acid $C_{20:1}\omega11c$ and *Mariniblastus fucicola* FC18^T the $C_{14:0}$ myristic acid in major amounts, which are unique in the family. *M. fucicola* FC18^T is also the only member in the class *Planctomycetia* to produce menaquinone 5 (MK-5) besides the standard menaquinone 6 (MK-6) found in planctomycetes.

As briefly discussed previously, *Planctomycetia* have the genomic potential to produce secondary metabolites with potential biotechnological applications (Kallscheuer and Jogler 2021). The natural function of such compounds is probably linked to the survival in complex and competitive habitats such as macroalgae biofilms (Graca et al. 2016). In fact, *Pirellulaceae* have been demonstrated to be promising organisms for bioprospection, in particular *Bremerella* members. Cell extracts of these bacteria have been linked to anti-cancer activity (Calisto et al. 2019), *Roseimaritima ulvae* UC8^T showed antimicrobial activity (Graca et al. 2016) and diverse strains from the genus *Rhodopirellula* showed antimicrobial and anti-cancer activities (Calisto et al. 2019; Graca et al. 2016; Jeske et al. 2016). Members of the genus *Stieleria* were the source for the isolation of a new type of secondary metabolite with moderate antimicrobial activity named stieleriacine (Kallscheuer et al. 2020a; Sandargo et al. 2020). Moreover, *R. rubra* LF2^T was studied for its adequacy as a supplementary food source for *Daphnia magna* (Marinho et al. 2019, 2018).

R. baltica SH1^T was the first planctomycete with a sequenced genome (Glockner et al. 2003) and currently 64 genomes of strains belonging to this family are available. The average genome size in this family is approximately 7.7 ± 1.2 Mb with a minimum and maximum size of 6.1 and 11.0 Mb, respectively. The mean DNA G + C content is 56.5 ± 2.5 mol% and it ranges from 49.5 to 62.4 mol%. No current member of the family harbours a plasmid.

A phylogenetic analysis of the family led to a taxonomic conflict between the validly published genus *Stieleria* and the more recently and not yet validated name of the genus "*Roseiconus*" (Kumar et al. 2020c). This is possibly related to the fact that the genus description of *Stieleria* was not published in a taxonomy journal, but in the context of the analysis of identified stieleriacines. Based on the 16S rRNA gene comparison between the five taxa (2 species of "*Roseiconus*" and 3 species of *Stieleria*), we found that "*Roseiconus lacunae*" JC635^T is more similar to other *Stieleria* than to "*Roseiconus nitratireducens*", with a 16S rRNA gene sequence similarity of 99.36% between "*R. lacunae*" JC635^T and its closest relative *S. neptunia* Enr13^T. On the other hand, "*R. nitratireducens*" JC645^T shares 96.9% 16S rRNA gene similarity with its closest relative *S. maiorica* Mal15^T. Following the rules of priority, these analysis suggest that "*Roseiconus lacunae*" JC635^T is a strain that belongs to species *S. neptunia* and that "*R. nitratireducens*" JC645^T is probably a new species within the genus *Stieleria* (following the well-established thresholds for delineation of new species of 98.7% and new genera of $< 94.5\%$ (Yarza et al. 2014)). However, the use of the 16S rRNA gene as sole phylogenetic marker is not always reliable for phylogenetic inference in the phylum *Planctomycetes* (Kallscheuer et al. 2020a; Kohn et al. 2020b; Wiegand et al. 2020b). Re-analysis of the phylogenetic position of both "*Roseiconus*" species using other phylogenetic markers is thus envisaged, ideally before the names of the genus "*Roseiconus*" and the proposed species belonging to the genus are validly published.

Family *Lacipirellulaceae*

The current family *Lacipirellulaceae* comprises 8 genera and 13 species (Table 1 and 4). *Bythopirellula goksoeyrii* Pr1d^T (initially described as *"Bythopirellula goksoyri"*), was the first identified member of this family (Storesund and Ovreas 2013, 2021), however, the type genus is *Lacipirellula* and the type species *L. parvula* (Dedysh et al. 2020c).

Most known members of this family were isolated in marine habitats, either on natural (algae, wood, sediments) or artificial (polyethylene) surfaces (Fig. 3). Dedysh and collaborators (Dedysh et al. 2020c) also demonstrated that several members are preferably found in low-oxygen aquatic habitats, which is corroborated by the isolation and detection of strains in sites such as wastewater treatment plants, hydrothermal vents and the gut microbiome of some aquatic invertebrates (Supplementary Table 1a). The genus *Lacipirellula* is the sole genus of the family to be exclusively found in freshwater habitats.

Members of this family are overall pear-shaped/ovoid/ellipsoidal and cells are mostly observed in aggregates (Supplementary Table 1b), although rosettes were additionally found in *L. parvula* PX69^T and *Posidoniimonas corsicana* KOR34^T (Dedysh et al. 2020c; Wiegand et al. 2020a). No stalks were observed. Most members produce fibrous extracellular materials or a holdfast structure which helps in cell aggregation. *Aeoliella mucimassa* Pan181^T was described as forming very fibrous materials and slime (Wiegand et al. 2020a) and *Bythopirellula polymerisocia* Pla144^T was found to be able to attach to polymeric material (Wiegand et al. 2020a). *Pirellulimonas nuda* Pla175^T differs from its relatives by an uncommon absence of matrix or fibers (Wiegand et al. 2020a). Members from this family are either unpigmented/white or hot pink/red pigmented, with currently no orange-pigmented species.

In general, *Lacipirellulaceae* are aerobic, mesophilic, neutrophilic and heterotrophic, with the exception of *L. parvula* PX69^T which is microaerobic and facultatively anaerobic (Supplementary Table 1c). This family has the highest mean doubling time (43.0 h ± 26.6 h) of the class *Planctomycetia* with the lowest doubling time of 17 h of *Pseudobythopirellula maris* Mal64^T and the highest of *B. polymerisocia* Pla144^T(94 h). The fatty acids $C_{16:1}\omega 9c$, palmitic acid ($C_{16:0}$), oleic/elaidic acid ($C_{18:1}\omega 9$), palmitoleic acid ($C_{16:1}\omega 7c$) and stearic acid ($C_{18:0}$) are the major ones found in this family, although a chemotaxonomic analysis was not presented for most members. The same is true for the polar lipid content: the only compound detected until now was dimethylphosphatidylethanolamine in *L. parvula* PX69^T (Dedysh et al. 2020c).

Although the family *Lacipirellulaceae* was only recently introduced, the biotechnological potential of its members is already starting to be unveiled: antimicrobial activity was recently detected in *L. parvula* PX69^T (Belova et al. 2020). Similar to *Pirellulaceae* and *Planctomycetaceae*, *Lacipirellulaceae* are present in complex habitats rich in microbial diversity, and we can hypothesize that production of antimicrobial metabolites by these organisms can give them advantage to survive in such environments.

The average genome size in this family is 6.1 ± 0.8 Mb and it ranges from 4.30 to 6.83 Mb. The average DNA G + C content is 62.1 ± 5.3 mol% and it ranges from 52.8 to 66.7 mol% (Supplementary

Table 3 Main features of the described species of family *Pirellulaceae*

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
“*Anatilimnocola aggregata*” (Kallscheuer et al. 2020d)	ETA_A8	Duck pound	Wolfenbuettel, Germany	White	Round to rice	a	20	9.0	57.8
Aureliella helgolandensis (Kallscheuer et al. 2020f)	Q31a	Jellyfish *Aurelia aurita*	Island Helgoland, North sea	Lucid white	Acorn	a,r	41	8.4	55.3
Blastopirellula marina (Schlesner 1986)	SH 106	Brackish water	Baltic Sea	White	Ovoid to ellipsoidal	r	NDA	6.7	57.0
Blastopirellula retiformator (Kallscheuer et al. 2020g)	Enr8	Hydrothermal area	Tyrrhenian Sea, Italy	White	Ovoid to pear	a	NDA	6.1	59.2 ± 2.6
Bremerella cremea (Lee et al. 2013)	LHWP2	Dead ark clam	Gangjin Bay, Korea	Cream	Ovoid	a	NDA	NDA	49.5
Bremerella volcania (Rensink et al. 2020)	Pan97	Red biofilm in Hot Lake	Tyrrhenian Sea, Italy	White to cream	Pear	a,r	9	6.5	56.2
Bremerella alba (Godinho et al. 2021)	FF15	Alga Fucus *spiralis*	Foz, Portugal	White	Oblong	a,r	18	6.4	54.5
Crateriforma conspicua (Peeters et al. 2020c)	Mal65	Algae	Coast of El Arenal, Spain	Pink	Pear	r	8	7.2	57.8
“*Crateriforma spongiae*” (Kumar et al. 2021b)	JC647	Sponge from genus *Spongia*	Rameswaram, India	Pale pink	Pear to ovoid	r	NDA	6.9	57.8
Lignipirellula cremea (Peeters et al. 2020b)	Pla85_3_4	Pellets, near a wastewater treatment plant	Warnow river, Germany	Cream	Spherical to pear	a,r	26	9.6	61.4
Mariniblastus fucicola (Lage et al. 2017)	FC18	Alga *Fucus spiralis*	Carreço, Portugal	Light-pink	Ovoid or pear	r	13	6.5	53.4
Novipirellula artificiosorum (Kallscheuer et al. 2020i)	Poly41	Polystyrene particles	Heiligendamm, Germany	Light pink	Acornshaped	r	18	9.2	55.3
Novipirellula aureliae (Kallscheuer et al. 2020i)	Q31b	Jellyfish *Aurelia aurita*	Island Heligoland, Germany	Lucid white	Acornshaped	a	18	7.3	52.9
Novipirellula galeiformis (Kallscheuer et al. 2020i)	Pla52o	Wood	Heiligendamm, Germany	Light pink	Acornshaped	a	18	7.4	55.8
Novipirellula caenicola (Yoon et al. 2015)	YM26-125	Iron sand	Murohama Beach, Japan	Pink	Spherical	NDA	NDA	NDA	57.5

Table 3 continued

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Novipirellula rosea (Roh et al. 2013)	LHWP3	Dead ark clam	Southern coastal of Korea	Pink to red	Ovoid	NDA	NDA	NDA	53.0
Pirellula staleyi (Schlesner and Hirsch 1984)	ATCC 27,377	Freshwater	Lake Lansing, USA	Pink	Pear or teardrop	r	13	6.2	57.5
Rhodopirellula baltica (Schlesner et al. 2004)	SH1	Water	Kiel Fjord, Baltic Sea	Pink to red	Ovoid, elipsoidal,	r	12	7.1	55.4
Rhodopirellula lusitana (Bondoso et al. 2014a)	UC17	Alga *Ulva* sp.	North coast of Portugal	Pink	Ovoid or pear	r	8.5–14	NDA	54.6
Rhodopirellula rubra (Bondoso et al. 2014a)	LF2	Alga *Laminaria* sp.	North coast of Portugal	Red	Pear or club	r	8.5–14	8.5	56.1
Rhodopirellula heiligendammensis (Kallscheuer et al. 2020 h)	Poly21	Polyethylene particles	Heiligendamm, Germany	Coral pink	Ovoid to pear	a	11	7.2	56.5 ± 2.4
Rhodopirellula pilleata (Kallscheuer et al. 2020 h)	Pla100	Polyethylene particles	Warnow river, Germany	Pink	Elongated pear	a	21	8.5	55.8 ± 1.5
Rhodopirellula solitaria (Kallscheuer et al. 2020 h)	CA85	*Macrocystis pyrifera*	Monterey Bay, CA, USA	Cream	Pear	s	11	6.8	58.0 ± 2.8
Roseimaritima ulvae (Bondoso et al. 2015)	UC8	Green alga Ulva sp.	North coast of Portugal	Light pink	Spherical to ovoid	r	NDA	8.1	57.0
Roseimaritima sediminicola (Kumar et al. 2020b)	JC651	Sediment sample	Satapada region, India	Light pink	Spherical to pear	r	NDA	6.2	62.4
Roseimaritima multifibrata (Wiegand et al. 2021)	FF011L	Alga *Laminaria* sp.	Helgoland Island, Germany	Pink to red	Pear	a,r	14.1	7.2	54.5
Rosistilla carotiformis (Waqqas et al. 2020)	Poly24	Polyethylene particles	Heiligendamm, Germany	Pink	Elongated pear	r	11	7.4	55.7
Rosistilla oblonga (Waqqas et al. 2020)	CA51	*Macrocystis pyrifera*	Monterey Bay, CA, USA	Unpigmented	Pear	r	9	7.3	58.2
Rosistilla ulvae (Wiegand et al. 2021)	EC9	Alga *Ulva* sp.	Helgoland Island, Germany	Red	Elongated pear	a,r	11	7.5	57.9

Table 3 continued

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Rubripirellula obstinata (Bondoso et al. 2015)	LF1	Brown alga *Laminaria* sp.	North coast of Portugal	Pink to red	Pear-shaped, ovoid	r	NDA	6.6	56.1
Rubripirellula amarantea (Kallscheuer et al. 2020c)	Pla22	Polyethylene particles	Warnow river, Germany	Pink	Spherical, grain rice	r	10	7.0	53.7 ± 0.9
Rubripirellula reticaptiva (Kallscheuer et al. 2020c)	Poly59	Polyethylene particles	Heiligendamm, Germany	Pink	Spherical, grain rice	r	16	7.9	54.8 ± 1.7
Rubripirellula tenax (Kallscheuer et al. 2020c)	Poly51	Polyethylene particles	Heiligendamm, Germany	Pink	Spherical, grain rice	r	25	8.0	56.2 ± 2.1
Rubripirellula lacrimiformis (Wiegand et al. 2021)	K22.7	Alga *Fucus* sp.	Helgoland Island, Germany	Pink	Pear	a,r	13	8.5	57.3
"*Roseiconus nitratireducens*" (Kumar et al. 2020c)	JC645	Sediment	Chilika lagoon, India	Pink	Spherical to oval	a	NDA	8.2	60.0
"*Roseiconus lacunae*" (Kumar et al. 2020c)	JC635	Sediment	Chilika lagoon, India	Pink	Cone to pear	a	NDA	7.9	55.1
Stieleria maiorica (Kallscheuer et al. 2020a)	Mal15	Sediments	Island Mallorca, Spain	Pink	Spherical to pear	r	7.5	9.9	59.3
Stieleria neptunia (Sandargo et al. 2020)	Enr13	Leaves of plant *Posidonia* sp.	Panarea island, Italy	Pink	Spherical to ovoid	a	13	11.0	58.9
Stieleria varia (Surup et al. 2020)	Pla52n	Wood particles	Heiligendamm, Germany	Light orange	Ovoid to spherical	r, c	11	9.6	56.0

**NDA*, no data available; *a*, aggregates; *r*, rosetes; *c*, chains; *s*, single

Table 4 Main features of the described species of family *Lacipirellulaceae*

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering *	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Lacipirellula parvula (Dedysh et al. 2020c)	PX69	Boreal lake water	Vologda region, Russian	Unpigmented	Ellipsoidal	a,r	NDA	6.9	61.2
Lacipirellula limnantheis (Kallscheuer et al. 2020d)	I41	Duck pound	Wolfenbuettel, Germany	White	Pear-shaped	a	43	6.8, 1 plasmid: 0.05	62.0
Aeoliella mucimassa (Wiegand et al. 2020a)	Pan181	Hydrothermal vent area offshore	Panarea island	White	Pear-shaped	a	21	6.6	58.0
Botrimarina colliarenosi (Wiegand et al. 2020a)	Pla108	Wood pellets stored in na incubator	Hohe Düne, Germany	Hot pink to red	Pear-shaped	a	53.3	5.3	65.4 ± 3.8
"*Botrimarina hoheduenensis*" (Wiegand et al. 2020a)	Pla111	Incubator	Hohe Düne, Germany	Hot pink to red	Pear-shaped	a	34.7	4.3	63.1 ± 2.6
Botrimarina mediterranea (Wiegand et al. 2020a)	Spa11	Seawater	Costa Brava, Spain	White	Pear-shaped	a	36.5	5.9	64.1
Bythopirellula goksoeyrii (Storesund and Ovreas 2013)	Pr1d	Iron-hydroxide deposit	Arctic Mid Ocean Ridge	Unpigmented	Oval or egg-shaped	a	NDA	6.5	52.8
Bythopirellula polymerisocia (Wiegand et al. 2020a)	Pla144	Polyethylene waste	Unterwarnow, Germany	White	Pear-shaped	a	93.7	6.1	52.9 ± 2.2
Pirellulimonas nuda (Wiegand et al. 2020a)	Pla175	Wood pellets, near a wastewater treatment plant	Unterwarnow, Germany	Hot pink to red	Pear-shaped	a	80.6	6.6	66.5
Posidoniimonas corsicana (Kohn et al. 2020a)	KOR34	Biofilm of *Posidonia oceanica*	France, Corsica	Cream	Ovoid to pear-shaped	a,r	18	6.8	66.7
Posidoniimonas polymericola (Wiegand et al. 2020a)	Pla123a	Wood pellets stored in an incubator	Heiligendamm, Germany	White	Pear-shaped	a	23.1	6.3	66.5 ± 3.2
"*Adhaeretor mobilis*" (Wiegand et al. 2021)	HG15A2	Alga *Laminaria* sp.	Helgoland Island, Germany	Cream	Egg-shaped	a,r	38.7	6.0	55.1
Pseudobythopirellula maris (Wiegand et al. 2020a)	Mal64	Phytoplancton, public beach	Mallorca island	White	Pear-shaped	a	16.9	5.1	66.2 ± 0.9

**NDA*, no data available; *a*, aggregates; *r*, rosetes

Table 5 Main features of the described species of family *Thermoguttaceae*

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Thermogutta hypogea (Slobodkina et al. 2015)	SBP2	Deep gold mine	South Africa	NDA	Ellipsoidal	a	NDA	NDA	66,6
Thermogutta terrifontis (Slobodkina et al. 2015)	R1	Hot spring	Kunashir Island, Russia	NDA	Ellipsoidal	a	NDA	4.8	57,3
Thermostilla marina (Slobodkina et al. 2016)	SVX8	Sand, fluid and seawater,shallow submarine hydrothermal vent	Vulcano Island, Italy	NDA	Coccoid	a	NDA	NDA	58,5

**NDA*, no data available; *a*, aggregates

Table 6 Main features of the described species of family *Isosphaeraceae*

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Aquisphaera giovannonii (Bondoso et al. 2011)	OJF2	Sediments of a freshwater aquarium	Porto, Portugal	Light pink	Spherical	a	24–48	10.4, 2 plasmids (0.13 + 0.02)	70.8 ± 0.5
"*Aquisphaera insulae*" (Kumar et al. 2021c)	JC669	Rhizospheric soil	Loktak lake, India	Light pink	Spherical to oval	a	NDA	10.0	68.5
Isosphaera pallida (Giovannoni et al. 1987)	1S1B	Hot spring	Oregon, North America	Pink	Spherical	c	NDA	5.4, 1 plasmid (0.06)	62.5
Paludisphaera borealis (Kulichevskaya et al. 2016)	PX4	Acidic wetlands, *Sphagnum* peat bog	Obukhovskoye, Yaroslavl region, Russia	Pink	Spherical	c	32	7.5, 2 plasmids (0.11 + 0.04)	66.0
"*Paludisphaera soli*" (Kaushik et al. 2020)	JC670	High altitude soil sample	Garhwal region in the Western Himalaya	Pink	Spherical to ovoid	a	NDA	7.9	70.4
Singulisphaera acidiphila (Kulichevskaya et al. 2008)	MOB10	Acidic wetlands, *Sphagnum* peat bog	Yaroslavl region in Northern Russia	Unpigmented	Spherical	a	NDA	9.6, 3 plasmids (0.05 + 0.04 + 0.03)	62.2
"*Singulispaera mucilagenosa*" (Zaicnikova et al. 2011)	Z0071	Water formed by fungal community grown on decaying spruce wood	Russia	Milky yellow	Spherical	p	NDA	NDA	51.2
Singulisphaera rosea (Kulichevskaya et al. 2012a)	S26	Acidic wetlands, *Sphagnum* peat bog	Tver region in Northern Russia	Pink	Spherical	c	NDA	NDA	62.2
Tautonia sociabilis (Kovaleva et al. 2019)	GM2012	Microbial mat from a thermal water stream, tunnels of the gold mine	Gold mine TauTona in South Africa	NDA	Spherical	a	13–21	6.7	70.1

Table 6 continued

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering*	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
"*Tautonia marina*" (Gaurav et al. 2021)	JC650	Sediments	Balugaon (Chilika Lake), India	Pale pink	Spherical to oval	a	NDA	7.1	63.9
"*Tautonia rosea*" (Gaurav et al. 2021)	JC657	Sediments	Satapada (Chilika Lake), India	Dark pink	Spherical to oval	a	NDA	7.0	62.7
Tautonia plasticadhaerens (Jogler et al. 2020)	ElP	Alga from a hydrothermal vent system	Panarea Island in the Tyrrhenian Sea, Italy	Pink	Spherical	a	29	9.4, 5 plasmids (0.28 + 0.14 + 0.12 + 0.09 + 0.09)	71.1
Tundrisphaera lichenicola (Kulichevskaya et al. 2017b)	P12	Shallow peatland	Nadym region, Russia	Pink	Spherical	a c	35.3	NDA	61.2–62.2

**NDA*, no data available; *a*, aggregates; *c*, chains; *p*, pairs

Table 7 Main features of the described species of family *Gemmataceae*

Species	Type strain ID	Source of isolation	Region of origin	Colony color	Cell shape	Type of clustering	Doubling time (h)	Genome size (Mb)	G + C content (mol %)
Fimbriiglobus ruber (Kulichevskaya et al. 2017a)	SP5	Acidic sphagnum-dominated peatbog	Yaroslavl region, Russia	Dark pink to red	Spherical	a	NDA	12.4	64.2
Gemmata obscuriglobus (Franzmann and Skerman 1984)	UQM 2246	Water	Maroon Dam, Australia	Pink	Spherical to ovoid	a	13	9.2	67.2
"*Gemmata massiliana*" (Aghnatios et al. 2015)	IIL30/	Water network in a hospital	Marseille, France	Pink	Spherical	a	NDA	9.3	64.07
"*Gemmata palustris*" (Ivanova et al. 2021a)	G18	Peat sample from a fen	Vologda oblast, Russia	Pink	Spherical	a	NDA	9.2	65.0
Limnoglobus roseus (Kulichevskaya et al. 2020b)	PX52	Water from na upper oxic layer of the boreal eutrophic lake	Vologda region, Russia	Pink	Spherical	a,r	NDA	9.3	65.6
Telmatocola sphagniphila (Kulichevskaya et al. 2012b)	SP2	Upper oxic layer of a *Sphagnum*-dominated peat bog	Tver region, Russia	Pink	Spherical	r	NDA	NDA	58.5
Urbifossiella limnaea (Kallscheuer et al. 2020d)	ETA_A1	Duck pound	Wolfenbuettel, Germany	Pink to red	Sperical	a	33	7.80	71.3
Frigoriglobus tundricola (Kulichevskaya et al. 2020a)	PL17	Water collected in a shallow littoral wetland in a forested tundra	Nadym region, Russia	Pink	Spherical	c, a	35	9.8, 1 plasmid (0.24)	67.4
Thermogemmata fonticola (Elcheninov et al. 2020)	2918	Sediments and water mixture from a terrestrial hot spring	Kamchatka, Russia	Light pink to pink	Spherical	a	NDA	4.8	60.4
Tuwongella immobilis (Seeger et al. 2017)	MBLW1	Sater sample collected from a freshwater lake	Lake at the University of Queensland, Australia	Pink	Spherical	s	6	NDA	57
Zavarzinella formosa (Kulichevskaya et al. 2009)	A10	Peat soil of a *Sphagnum* peat bog	Tomsk region, West Siberia	Pink	Ellipsoid	r	NDA	10.1	59.1

**NDA*, no data available; *a*, aggregates; *r*, rosetes; *c*, chains; *s*, single; *p*, pairs

Table 1d). The presence of a plasmid was only reported in one member, *L. parvula* PX69^T (Dedysh et al. 2020c).

Family *Thermoguttaceae*

The family *Thermoguttaceae* is underrepresented in terms of isolated strains and is constituted by only 2 genera and 3 species (Table 1 and 5). The genus *Thermogutta* includes two species, *T. terrifontis* and *T. hypogea* (Slobodkina et al. 2015). An additional strain of this genus that was initially designated "*Thermopirellula anaerolimosa*" VM20-7 was isolated from an anaerobic sludge blanket and described as an obligate anaerobic hydrogen-producing thermophilic bacterium (Liu et al. 2012). However, the genus '*Thermopirellula*' was not formally described and thus the strain was added as a member of the species *T. terrifontis* (Slobodkina et al. 2015). The genus *Thermostilla* has only one species, *T. marina* (Slobodkina et al. 2016).

Members of this family are coccoid to ellipsoidal, form aggregates and are motile. No pink or orange pigmentation was observed in this family, as all members are white/cream pigmented (Supplementary Table 1b).

They can be found in extreme environments (such as hot springs, hydrothermal vents, high-temperature horizons) and deep-subsurface sites (such as gold mines) and were also detected in anaerobic reactors (Fig. 3b and Supplementary Table 1a).

All current members are thermophilic, facultatively anaerobic and capable of microaerobic growth, neutrophilic, halotolerant and chemoorganotrophic (Supplementary Table 1c). Palmitic acid ($C_{16:0}$), stearic acid ($C_{18:0}$) and eicosanoid acid ($C_{20:0}$) are the major fatty acids in the family and *T. marina* produces an additional fatty acid (11-methyl $C_{18:0}$) (Slobodkina et al. 2016). Data on polar lipid and respiratory quinone content is currently not available.

Only one member (*Thermogutta terrifontis* R1^T) has a genome sequence available for further analyses: with 4.8 Mb, the genome is relatively small and no plasmids are present (Supplementary Table 1d). The average DNA G + C content between the three current members is 60.8 ± 0.8 mol% and the range is from 57.3 to 66.6 mol%.

Family *Isosphaeraceae*

The family *Isosphaeraceae* is constituted by 6 genera and 13 published species (Table 6).

The type genus *Isosphaera* was the first described genus of the family. The type species is *Isosphaera pallida* (Giovannoni et al. 1987).

Members of this family (Supplementary Table 1b) have spherical cells which are found singly, in pairs, aggregates or even chains (filaments). Cells connected by chains were observed in *Paludisphaera borealis* PX4^T, *Tundrisphaera lichenicola* P12^T and *Isosphaera pallida* 1S1B^T (Giovannoni et al. 1987; Kulichevskaya et al. 2017b, 2016). *I. pallida* 1S1B^T is the only planctomycete that forms long filaments with often more than one hundred cells (Giovannoni et al. 1987). No stalk-like structures were observed in members of this family. Cells are non-motile and colonies pink pigmented while *Singulisphaera acidiphila* MOB10^T and "*Singulisphaera mucilagenosa*" Z0071^T are the sole unpigmented/milky-yellow-pigmented members of the family. Distinctive characteristics are observed in some species, such as phototactic gliding motility in *I. pallida* 1S1B^T (Giovannoni et al. 1987) and the tendency to attach strongly to plastic surfaces for *Tautonia plasticadhaerens* ElP^T, a characteristic that justifies its name (Jogler et al. 2020).

Members of this family are primarily found in freshwater and terrestrial environments (Fig. 3). The majority of the isolated strains were retrieved from boreal regions in Russia and acidic wetlands (Fig. 4), while other species such as *I. pallida* and *T. sociabilis* were isolated from extreme environments such as hot springs (Giovannoni et al. 1987) and a deep subsurface environment (gold mine) (Kovaleva et al. 2019), respectively. The genus *Tautonia* is the only genus of the family with isolates from marine environments, in this case macroalgae biofilms and sediments (Jogler et al. 2020).

Members of this family are heterotrophic, neutrophilic, mesophilic and aerobic, although some members such as *P. borealis* and *Singulisphaera spp.* are also capable of microaerobic growth (Supplementary Table 1c). As most members were isolated from cold regions and acidic wetlands, most species are also acid-tolerant and psychrotolerant, while others isolated from extreme environments are thermotolerant, which is the case for *I. pallida* 1S1B^T and *T. sociabilis* (Giovannoni et al. 1987; Kovaleva et al.

2019). Almost all known members are salt-sensitive, with the exception of the strains isolated from marine environments belonging to the genus *Tautonia* (Gaurav et al. 2021; Jogler et al. 2020). The average doubling time in the family is 29.9 ± 8.0 h and *Aquisphaera giovannonii* OJF2^T has the highest doubling time (48 h) of the family, although this data is not available for most of the other family members. The major fatty acids in the family are oleic/elaidic acid ($C_{18:1}\omega9$), palmitic acid ($C_{16:0}$) and stearic acid ($C_{18:0}$). Members of the genus *Singulisphaera* produce an additional rare fatty acid: $C_{18:2}\omega6c,12c$. The main polar lipids are phosphatidylcholine, phosphatidylglycerol, trimethylornithine and phosphocholine.

The average genome size in this family is 8.3 ± 1.7 Mb, the average DNA G + C content is 64.1 ± 6.0 mol% (the highest in the class) and almost all known members possess more than one plasmid, which is very distinctive in comparison to the other families. The *I. pallida* type strain IS1B^T has the smallest genome of the family (5.4 Mb) and *A. giovannonii* OJF2^T the largest one (10.4 Mb).

Family *Gemmataceae*

The family *Gemmataceae* contains 9 genera and 11 species, which are listed in Table 7. *Gemmata* was the first identified genus with the description of *G. obscuriglobus* UQM 2246 ^{T} (Franzmann and Skerman 1984).

Gemmataceae are mostly spherical and can be found singly and more often in shapeless aggregates, although some species can assemble in rosettes or in short chains, such as the cells of *Frigoriglobus tundricola* PL17^T (Kulichevskaya et al. 2020a). Stalk-like structures are observed in some species, namely *Limnoglobus roseus* PX52^T, *Telmatocola sphagniphila* SP2^T and *Zavarzinella formosa* A10^T. All known members are pink/red-pigmented. The cytoplasmic membrane invaginations (a characteristic cell biological features of planctomycetes) can be rearranged in an even more complex way in some *Gemmataceae* (Sagulenko et al. 2014), which is the case of *G. obscuriglobus*, which shows a very complex cytoplasmic membrane invagination system (Santarella-Mellwig et al. 2013). In fact, several studies regarding cell structure, division and genetic manipulation have focused on this species (Boedeker et al. 2017; Jeske et al. 2015; Rivas-Marin et al. 2016b; Sagulenko et al. 2014; Sagulenko et al. 2017). A tubulo-vesicular network was also reported in *G. obscuriglobus*, which is unique among prokaryotes and reveals similarities with the endocytosis that is exclusively associated with eukaryotes (Acehan et al. 2014). Taken together, these studies demonstrated how complex and unique it is the *Planctomycetes* cell biology. Other distinctive morphotypes are also seen in this family, such as the cells from *T. sphagniphila* SP2^T which cluster in unique dendriform-like structures (Kulichevskaya et al. 2012b). *Z. formosa* A10^T is the only taxon of the family forming a holdfast structure, which supports aggregation in rosettes besides the formation of abnormally thick stalk-like structures (Kulichevskaya et al. 2009).

Known members of the family are found in freshwater and terrestrial environments (Fig. 3). "*G. massiliana*" IIL30^T was initially isolated from a water network in a hospital (Aghnatios et al. 2015) and consequently *Gemmata*-like organisms have been hypothesized as possible opportunistic human pathogens (Aghnatios and Drancourt 2016), however, this still remains to be clarified (Wiegand et al. 2018).

Thermogemmata fonticola 2918 ^{T} is the only *Gemmataceae* member isolated from a terrestrial hot spring (Elcheninov et al. 2020). Furthermore, uncultured strains belonging to this species were detected in other hot springs (including the radioactive Paralana hot spring in Australia), in sediments from an U.S. Department of Energy contaminated site (Abulencia et al. 2006) and associated with the marine invertebrate *Pocillopora meandrina* found in the Pacific Ocean.

The family comprises, in general, heterotrophic, mesophilic, neutrophilic and aerobic organisms, however, a small number of members are also psychrotolerant (*F. tundricola* and *T. sphagniphila*) or thermophilic (*T. fonticola*) or acid tolerant (*e.g. Frigoriglobus ruber* SP5^T and *T. sphagniphila*) (Supplementary Table 1c). All the isolated strains are halophobic. The average doubling time in the family is 21.8 ± 14.5 h, however, this data is not available for all members. Strain MBLW1^T of the species *Tuwongella immobilis* has a low doubling time (6 h) in comparison to the other family members (Seeger et al. 2017). The main fatty acids in the family are stearic acid ($C_{18:0}$), $C_{18:1}\omega5c$ and $C_{16:1}\omega5c$. In *T. fonticola* 2918 ^{T}, $C_{20:0}$ fatty acids were also detected. The fatty acid composition in *F. ruber* SP5^T differs from the other family members as it includes $C_{20:1}\omega9c$, $C_{16:1}\omega9c$ and $C_{16:0}$ as the major fatty acids. In this family, the fatty acid $C_{18:1}\omega7c$ is produced in major amounts by only *L. roseus* PX52^T and the uncommon fatty acid (βOH-$C_{16:1}$) by *F. tundricola* PL17^T. The main polar lipid is trimethylornithine, although others such as phosphatidylglycerol, dimethylphosphatidylethanolamine, monomethylornithine and dimethylornithine can be present.

The average genome size in this family is approximately 9.1 ± 2.2 Mb (among the highest in the class). The largest genome of the class *Planctomycetia* (and even of the entire phylum) belongs to *F. ruber* SP5^T (12.4 Mb), while *T. fonticola* 2918 ^{T} has a small genome (4.81 Mb) compared to the average size in the family (9.1 Mb). The average DNA G + C content is 63.5 ± 4.6 mol% and *Urbifossiella limnaea* ETA_A1^T has the highest DNA G + C content of the class *Planctomycetia* (71.3 mol%). *F. tundricola* PL17^T is the only member of the family that possesses a plasmid.

Conclusions

In this overview article, the clustered data obtained from species description studies dealing with members of the class *Planctomycetia*, allowed for a more holistic view and comparison of phylogeny, ecology, morphology, physiology, and genomic traits of the cultured taxa in this group. Shared as well as distinctive (or even unique) features of the different families are presented and discussed. This overview showed the importance of a complete characterization of the novel taxonomic groups, namely genomic information, chemotaxonomy and physiology of the strains, to allow a better discrimination between taxa.

The last decades were a great momentum for the discovery of planctomycetes and in particular of the class *Planctomycetia*. However, the planctomycetal scientific community faces the great challenge of bringing into culture much of the biodiversity that still stays beyond our capacity of isolation. The bias in the number of isolated strains towards the class *Planctomycetia* and specifically towards mesophilic, neutrophilic and aerobic members may be due to several factors such as the uniform isolation techniques and growth conditions, the media formulation used, the use of selective factors like *N*-acetylglucosamine as the only source of carbon and nitrogen and also our unawareness of the nutritional and metabolic requirements of so far non-culturable planctomycetes. In fact, the media developed for isolation are based on the knowledge gathered on the nutritional needs of the isolated strains which are mainly from the class *Planctomycetia*. As the majority of the isolated planctomycetes are resistant to betalactam antibiotics and streptomycin, a mixture of these antibiotics is currently used to achieve an enrichment of planctomycetes, making it impossible to isolate non-resistant planctomycetes. Furthermore, most planctomycetes seem to be resistant to most classes of antibiotics, however, the mechanisms behind these resistances are still unknown. It is hypothesized that many of the antimicrobial resistance genes in pathogens are obtain via horizontal gene transfer events from environmental bacteria, which is why it is also important to gather knowledge on the resistome-mobilome of highly resistant bacteria such as the planctomycetes.

To overcome the isolation difficulties here discussed, new strategies are needed to bring the untapped diversity of uncultured clades of planctomycetes into culture. This can possibly by achieved by the exploitation of less investigated ecological niches and by focusing on different culture conditions (such as anaerobic growth) and testing new medium formulations (*e.g.* by incorporating nutrients from the isolation environments or the use of other selective antibiotics). The development and refinement of novel isolation techniques is also essential, such as the use of *in-situ* methodologies, which recently proved to be useful to isolate novel taxa. As many strains have long doubling times, it is always needed to wait for a long period to allow slow growing planctomycetes to appear in culture. Another approach should be the dilution of the initial inoculum or its cell sorting to obtain single cell cultures per well in order to avoid completion from fast growing bacteria.

Thanks to the isolation and description of many species that lead to a taxonomic revolution in the phylum in the last years, scientists became aware of several aspects of the cell biology of this group. The availability of many planctomycetal strains and genomes will facilitate the investigation of the secrets in their cell biology. In the light of more than 40% of the genome-encoded proteins with an unknown function, their genomes are another enigmatic feature of their divergent morphology and physiology. Future studies with members of the current family *Planctomycetia* will contribute to understand their division mode, their resistance to antibiotics, the function behind many genes, their complex structure, the role played in many ecosystems and the biotechnological potential that starts to be discovered.

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Data availability Data generated or analysed during this study is included in this published article (and its supplementary information files).

Declarations

Conflicts of interest The authors declare that there is no conflict of interest.

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