Tautonia plasticadhaerens sp. nov., a novel species in the family Isosphaeraceae isolated from an alga in a hydrothermal area of the Eolian Archipelago

Christian Jogler · Sandra Wiegand · Christian Boedeker · Anja Heuer · Stijn H. Peeters · Mareike Jogler · Mike S. M. Jetten · Manfred Rohde · Nicolai Kallscheuer

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Abstract A novel planctomycetal strain, designated EIP\textsuperscript{T}, was isolated from an alga in the shallow hydrothermal vent system close to Panarea Island in the Tyrrhenian Sea. Cells of strain EIP\textsuperscript{T} are spherical, form pink colonies and display typical planctomycetal characteristics including division by budding and presence of crateriform structures. Strain EIP\textsuperscript{T} has a mesophilic (optimum at 30°C) and neutrophilic (optimum at pH 7.5) growth profile, is aerobic and heterotrophic. It reaches a generation time of 29 h (\(\mu\text{max} = 0.024 \text{ h}^{-1}\)). The strain has a genome size of 9.40 Mb with a G + C content of 71.1% and harbours five plasmids, the highest number observed in the phylum Planctomycetes thus far. Phylogenetically, the strain represents a novel species of the recently described genus Tautonia in the family Isosphaeraceae. A characteristic feature of the strain is its tendency to attach strongly to a range of plastic surfaces. We thus propose the name Tautonia plasticadhaerens sp. nov. for the novel species, represented by the type strain EIP\textsuperscript{T} (DSM 101012\textsuperscript{T} = LMG 29141\textsuperscript{T}).

Keywords Marine bacteria · Panarea · Biotic surfaces · Planctomycetes · Isosphaeraceae · Hydrothermal vent system

Introduction

The phylum Planctomycetes, along with Chlamydiae, Verrucomicrobia and others, forms the PVC super-phylum, which is of environmental, medical and biotechnological importance (Spring et al. 2016; Wagner and Horn 2006). Members of the phylum Planctomycetes occur in a broad range of habitats on Earth, with the largest number of species so far isolated from aquatic environments (Wiegand et al. 2018). Phylogenetically, the phylum is subdivided into the classes Phycisphaerae, Planctomycetia and Candidatus Brocadiaceae. Recent rearrangements in the class Planctomycetia led to a more strictly defined order
Planctomycetaceae and the introduction of the orders Pirellulales, Gemmatales and Isosphaerales (Dedysh et al. 2019). Species of the class Planctomycetia divide by budding, whereas members of the class Phycisphaerae divide by binary fission. Genome size ranges of 3–12 Mb and a G + C content of 40–71% have been observed in characterised strains of the phylum Planctomycetes (Ravin et al. 2018; Wiegand et al. 2020).

Strains clustering within Planctomycetia, the class with the currently highest number of characterised species in the phylum, have been shown to attach to various marine biotic surfaces, e.g. macroscopic phototrophs (Boersma et al. 2019; Bondoso et al. 2014, 2017; Peeters et al. 2020; Vollmers et al. 2017), on which they can be highly abundant (Bengtsson and Øvresås 2010). Such surfaces are suggested to serve as nutrient source, e.g. in the form of complex polysaccharides (Jeske et al. 2013; Lachnit et al. 2013). However, the survival of planctomycetal species appears counter-intuitive given their rather slow growth compared to natural competitors in this ecological niche (Frank et al. 2014; Wiegand et al. 2018). Strategies applied to compensate for lower growth rates may include the ability to produce bioactive secondary metabolites (Kallscheuer et al. 2019c; Panter et al. 2019), resistance against several antibiotics (Cayrou et al. 2010; Godinho et al. 2019) and/or a metabolism well-adapted to digestion of algae-derived compounds, including the above-mentioned polysaccharides. In this context, pili originating from conspicuous crateriform structures and an extremely enlarged periplasmic space observed in Planctomycetes may be involved in the uptake and intracellular cleavage of polymeric carbon sources, as shown for the model substrate dextran (Boedeker et al. 2017).

The cell envelope architecture of species of the phylum Planctomycetes was investigated based on super-resolution microscopic techniques and developed genetic tools (Jogler et al. 2011; Jogler and Jogler 2013; Rivas-Marin et al. 2016), which confirmed presence of peptidoglycan (Jeske et al. 2015; van Teeseling et al. 2015) and a cell envelope similar to that of Gram-negative bacteria (Boedeker et al. 2017; Devos 2014). However, in contrast to canonical bacteria, Planctomycetes lack otherwise essential divisome proteins, including FtsZ (Jogler et al. 2012; Pilhofer et al. 2008). In their genomes, 40–55% of the automatically annotated genes are of unknown function (Wiegand et al. 2020), which is a strong motivation to study the planctomycetal cell biology in greater detail.

To extend the collection of axenic cultures of Planctomycetes and as a basis for further study of their cell biology and metabolism, here we describe a novel strain, ELPT, isolated from an alga sampled in the Tyrrhenian Sea close to the island Panarea.

Materials and methods

Isolation of the novel strain and cultivation

For the isolation and cultivation of strain ELPT, M1H NAG ASW medium was used. Liquid and solid M1H NAG ASW medium was prepared as previously described (Boersma et al. 2019). Strain ELPT was isolated from an alga gathered from hydrothermal area A26 (location: 38.6392 N 15.1051 E). With an average depth of 26 m, A26 is the deepest spot of a plateau located between the small islands Le Guglie and Lisca Bianca around 2.5 km east of the island Panarea, Italy. The geology of area A26 in the shallow-marine hydrothermal system close to Panarea is described elsewhere (Kürzinger 2019). Algal pieces were sampled on the 10th of September 2013 at a depth of 25 m and a water temperature of 19.4 °C. The sampled material was initially washed with sterile seawater containing 20 mg/L cycloheximide to prevent fungal growth. Afterwards, washed algal pieces were swabbed over a plate with M1H NAG ASW medium containing 8 g/L gellan gum, 1000 mg/L streptomycin, 200 mg/L ampicillin and 20 mg/L cycloheximide, which was subsequently incubated at 20 °C for four weeks. The 16S rRNA gene of the strains obtained was amplified by PCR with the primers 8f (5′-AGA GTT TGA TCM TGG CTC AG-3′) and 1492r (5′-GGY TAC CTT GTT AGC ACT T-3′) and then sequenced following a previously published protocol (Rast et al. 2017). This step was performed in order to check whether isolated strains represent members of the phylum Planctomycetes.

Determination of pH and temperature optimum

The pH optimum and range were determined in M1H NAG ASW medium at 28 °C. The following buffers (each 100 mM) were used: 2-(N-
morpholino)ethanesulfonic acid (MES) for pH 5.0 and 6.0, 4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid (HEPES) for pH 7.0, 7.5 and 8.0, 3-(4-(2-hydroxyethyl)piperazin-1-yl)propane-1-sulfonic acid (HEPPS) for pH 8.5 and N-cyclohexyl-2-aminoethanesulfonic acid (CHES) for pH 9.0 and 10.0. The temperature optimum and range were determined in standard M1H NAG ASW medium at pH 7.5. Growth was assessed by measuring the optical density at 600 nm (OD600). The average of OD600 values from three biological replicates was used for calculation of the growth rates. To this end, the natural logarithm of average OD600 values (ln(OD600)) was plotted against the cultivation time. The slope of the linear range of the curve (at least five data points) was used as maximal growth rate \( l \) (in h\(^{-1}\)). The generation time \( t_d \) (in h) was calculated using the equation \( t_d = \ln(2)/l \).

Microscopy protocols

Phase contrast and field emission scanning electron microscopy were performed as previously described (Boersma et al. 2019).

Genome information and analysis of genome-encoded features

Genome and plasmid sequences of strain ElP\(^T\) are available from GenBank under accession numbers CP036426–CP036431. The 16S rRNA gene sequence of strain ElP\(^T\) can be found under accession number MK559970. DNA isolation and genome sequencing was carried out as part of a previous study (Wiegand et al. 2020). Numbers of carbohydrate-active enzymes were obtained from the CAZY database (Lombard et al. 2014). Gene clusters potentially involved in the production of secondary metabolites were determined using antiSMASH 4.0 (Blin et al. 2017).

Phylogenetic analysis

In both, the 16S rRNA gene sequence- and the MLSA-based phylogenetic tree (Fig. 1), strain ElP\(^T\) clusters monophyletically with Tautonia sociabilis GM2012\(^T\) (Kovaleva et al. 2019). The two strains share a 16S rRNA gene sequence similarity of 96.5% (Fig. 2), which is above the recommended genus threshold of 94.5%, but below the species threshold of 98.7% (Stackebrandt and Ebers 2006; Yarza et al. 2014). Comparison at the 16S rRNA gene level thus suggests that strain ElP\(^T\) represents a novel species in the genus Tautonia, family Isosphaeraceae. This finding is in line with an ANI of 79.8% obtained during comparison of strain ElP\(^T\) and T. sociabilis, since this value is below the threshold of 95% for strains belonging to the same species (Kim et al. 2014). For a more extensive evaluation, additional phylogenetic markers were taken into account. Indeed, affiliation of strain ElP\(^T\) to the genus Tautonia and simultaneous delineation (Kallscheuer et al. 2019d). Three 16S rRNA genes of bacterial strains from the PVC superphylum, but outside of the phylum Planctomycetes (accession numbers AJ229235, NR_146840 and NR_027571), were used as the outgroup. The multi-locus sequence analysis (MLSA) was performed according to a previously published protocol (Kallscheuer et al. 2019d). The genomes of Gemmata obscuriglobus (accession number CP042911), Rhodopirellula baltica (accession number BX119912.1) and Gimesia maris (accession number CP043931) served as outgroup. The average nucleotide identity (ANI) was calculated using OrthoANI (Lee et al. 2016). The average amino acid identity (AAI) was obtained using the aai.rb script of the enveomics collection (Rodriguez-R and Konstantinidis 2016), while the percentage of conserved proteins (POCP) was calculated as described by Qin et al. (2014). The rpoB nucleotide sequences were taken from publicly available planctomycetal genome annotations and the sequence identities for the described 1200 bp sequence fragment were determined as previously described (Bondoso et al. 2013). Alignment and matrix calculation were performed with Clustal Omega (Sievers et al. 2011).

Results and discussion

Phylogenetic analysis

In both, the 16S rRNA gene sequence- and the MLSA-based phylogenetic tree (Fig. 1), strain ElP\(^T\) clusters monophyletically with Tautonia sociabilis GM2012\(^T\) (Kovaleva et al. 2019). The two strains share a 16S rRNA gene sequence similarity of 96.5% (Fig. 2), which is above the recommended genus threshold of 94.5%, but below the species threshold of 98.7% (Stackebrandt and Ebers 2006; Yarza et al. 2014). Comparison at the 16S rRNA gene level thus suggests that strain ElP\(^T\) represents a novel species in the genus Tautonia, family Isosphaeraceae. This finding is in line with an ANI of 79.8% obtained during comparison of strain ElP\(^T\) and T. sociabilis, since this value is below the threshold of 95% for strains belonging to the same species (Kim et al. 2014). For a more extensive evaluation, additional phylogenetic markers were taken into account. Indeed, affiliation of strain ElP\(^T\) to the genus Tautonia and simultaneous delineation
from *T. sociabilis* is supported by AAI, rpoB similarity and POCP values of 76.3%, 90.5% and 65.7%, respectively (Fig. 2). These values fall above the recommended genus thresholds of 60–80% (AAI), 75.5–78% (rpoB) and 50% (POCP) for delineation of prokaryotic genera, but below the thresholds of 95% (AAI) and 96.3% (rpoB) for differentiation of species (Kallscheuer et al. 2019d; Konstantinidis and Tiedje 2005; Qin et al. 2014). *T. sociabilis* was clearly established as the current closest relative of strain EIP$^T$ since lower similarity values were obtained for comparison with species of other known genera in the family *Isosphaeraceae*, namely *Isosphaera, Singulisphaera, Aquisphaera, Paludisphaera* and *Tundrisphaera*. For comparison of strain EIP$^T$ with species of the mentioned genera, AAI and 16S rRNA gene similarity values are below the genus threshold, while in most cases the POCP was found to be at or slightly above the genus threshold of 50% (Fig. 2). Similarity of rpoB is used as phylogenetic marker in the order *Planctomycetales* (Bondoso et al. 2013) and a genus threshold of 75.5–78% was
recently proposed based on new strains in the family *Pirellulaceae* (former members of *Planctomycetaceae*) (Kallscheuer et al. 2019d). Based on the obtained values (Fig. 2), the *rpoB* genus threshold is probably not applicable to the family *Isosphaeraceae*.

Morphological and physiological analyses

Basic features of strain EIP\(^T\) comprising cell morphology, growth and mechanism of cell division are summarised in Table 1 and compared to *T. sociabilis*, *Isosphaera pallida*, *Tundrisphaera lichenicola*, *Singulisphaera acidiphila*, *Paludisphaera borealis* and *Aquisphaera giovannonii* (Bondoso et al. 2011; Giovannoni et al. 1987; Kovaleva et al. 2019; Kulichevskaya et al. 2008, 2016, 2017). Morphological features of EIP\(^T\) cells harvested during the exponential growth phase were analysed using phase contrast and scanning electron microscopy (Fig. 3). Strain EIP\(^T\) forms spherical cells with a typical diameter of 1.4–2.0 μm (Fig. 3a, c), which occur either as single cells or form smaller aggregates of 25–40 cells. Cells divide by budding with the bud having the same shape as the mother cell (Fig. 3a). Cell size and shape of EIP\(^T\) are comparable to the type species of known genera in the family *Isosphaeraceae*, with the exception of *I. pallida*, which forms cells that are considerably larger. All seven compared strains follow the same mode of division and contain crateriform structures on the entire cell surface (no data available for *T. sociabilis*). The colonies of EIP\(^T\) have a pink pigmentation, suggesting the production of carotenoids. The colour is similar to the species chosen for comparison, with the exception of *S. acidiphila* and the closely related *T. sociabilis*, which lack pigmentation (Table 1). Once isolated, colonies of strain EIP\(^T\) were observed to grow at the plastic boundary of the Petri dish, only half connected to the agar surface. This tendency to stick to plastic surfaces necessitated the use of glassware for handling of the strain. For example, cells stuck strongly to plastic pipettes, making their transfer difficult. This immediate adsorption towards plastic

![Figure 2](image-url)
Table 1 Phenotypic and genotypic features of strain ElP<sup>T</sup> compared to closely related strains. The genome analysis is based on GenBank accession numbers for strain ElP<sup>T</sup> (CP003642–CP0036431), *Tautonia sociabilis* (GCA_003977685.1), *Isosphaera pallida* (CP002353–CP002354), *Singulisphaera acidiphila* (CP003364–CP003367), *Paludisphaera borealis* (CP019082–CP019084) and *Aquisphaera giovannonii* (CP042997–CP042999). The genome of *Tundrisphaera lichenicola* has not been sequenced yet.

| Feature                        | ElP<sup>T</sup> | Tautonia sociabilis GM2012<sup>T</sup> | Isosphaera pallida IS1B<sup>T</sup> | Tundrisphaera lichenicola P12<sup>T</sup> | Singulisphaera acidiphila MOB10<sup>T</sup> | Paludisphaera borealis PX4<sup>T</sup> | Aquisphaera giovannonii OJF2<sup>T</sup> |
|-------------------------------|----------------|--------------------------------------|-----------------------------------|------------------------------------------|------------------------------------------|------------------------------------------|------------------------------------------|
| **Phenotypic characteristics**|                |                                      |                                   |                                         |                                         |                                         |                                         |
| **Shape**                     | Spherical      | Spherical                            | Spherical                         | Spherical                                | Spherical                                | Spherical                                | Spherical                                |
| **Diameter (µm)**             | 1.7 ± 0.3      | 1.7–2.9                              | 2.5–3.0                           | 2.2–3.0                                  | 1.6–2.6                                  | 1.5–2.5                                  | 1.6–2.0                                  |
| **Colour**                    | Pink           | White                                | Pink                              | Pink                                     | White                                    | Bright pink                             | Pink                                     |
| **Relation to oxygen**        | Aerobic        | Strictly aerobic                      | Strictly aerobic                   | Strictly aerobic                         | Strictly aerobic                         | Aerobic                                 | Strictly aerobic                         |
| **Temperature range (optimum) (°C)** | 10–33 (30)    | 37–46 (42)                           | 34–55 (41)                        | 4–28 (15–22)                             | 4–33 (20–26)                             | 6–30 (15–25)                            | 10–35 (30)                              |
| **pH range (optimum)**        | 6–0.8.5 (7.5)  | 5.5–9.0 (7.5)                        | 7.8–8.8                           | 4.5–6.8 (5.5–6.0)                        | 4.2–7.5 (5.0–6.2)                       | 3.5–6.5 (5.0–5.5)                      | 6.5–9.5 (7.5–8.5)                       |
| **Division**                  | Budding        | Budding                              | Budding                           | Budding                                  | Budding                                  | Budding                                 | Budding                                 |
| **Dimorphic life cycle**      | n.o.           | n.d.                                 | n.d.                              | n.d.                                     | n.d.                                     | n.d.                                    | n.d.                                    |
| **Motility**                  | No             | No                                   | Yes, phototactic gliding          | No                                       | No                                       | No                                       | No                                       |
| **Crateriform structures**    | Ubiquitous     | n.d.                                 | Ubiquitous                        | Ubiquitous                               | Ubiquitous                               | Ubiquitous                              | Ubiquitous                              |
| **Fimbriae**                  | Yes            | n.d.                                 | Yes                               | n.d.                                     | Yes                                      | n.d.                                    | Yes                                      |
| **Capsule**                   | Yes            | n.d.                                 | No                                | n.d.                                     | Yes                                      | n.d.                                    | Yes                                      |
| **Stalk**                     | n.o.           | n.d.                                 | n.d.                              | No                                       | No                                       | n.d.                                    | n.d.                                    |
| **Holdfast structure**        | n.o.           | n.d.                                 | Yes                              | Yes                                      | Yes                                      | n.d.                                    | n.d.                                    |
| **Genomic characteristics**   |                |                                      |                                   |                                         |                                         |                                         |                                         |
| **Genome size (bp)**          | 9,395,224      | 6,760,005                            | 5,529,304                         | n.d.                                     | 9,755,686                                | 7,651,896                               | 10,526,296                              |
| **Plasmids**                  | 5              | n.d.                                 | 1                                 | n.d.                                     | 3                                        | 2                                       | 2                                        |
| **G + C (%)**                 | 71.1 ± 0.8     | 70.1                                 | 62.5 ± 3.2                        | 62.2 ± 6.2                               | 66.3 ± 4.1                               | 70.8 ± 0.5                              | 85.7                                    |
| **Coding density (%)**        | 84.7           | 85.0                                 | 84.7                              | n.d.                                     | 83.5                                     | 86.1                                    | 85.7                                    |
| **Completeness (%)**          | 98.28          | 98.28                                | 98.28                             | n.d.                                     | 98.28                                    | 96.55                                   | 96.55                                   |
| **Contamination (%)**         | 5.17           | 3.45                                 | 0                                 | n.d.                                     | 6.90                                     | 3.45                                    | 5.17                                    |
| **Total genes**               | 7707           | 5183                                 | 3828                              | n.d.                                     | 7689                                     | 5961                                    | 7953                                    |
| **Genes/Mb**                  | 820            | 767                                  | 692                               | n.d.                                     | 788                                      | 779                                     | 756                                     |
| **Giant genes**               | 0              | 0                                    | 0                                 | n.d.                                     | 1                                        | 0                                       | 1                                       |
| **All protein-coding genes**  | 7556           | 5084                                 | 3761                              | n.d.                                     | 7540                                     | 5855                                    | 7835                                    |
| **Protein-coding genes/Mb**   | 804            | 752                                  | 680                               | n.d.                                     | 773                                      | 765                                     | 744                                     |
| **Hypothetical proteins**     | 3399           | 3175                                 | 1821                              | n.d.                                     | 4316                                     | 3154                                    | 3328                                    |
| **tRNAs**                     | 100            | 84                                   | 51                                | n.d.                                     | 81                                       | 83                                      | 107                                     |
| **16S rRNA genes**            | 3              | 1                                    | 3                                 | n.d.                                     | 8                                        | 3                                       | 3                                       |

n.o. not observed, n.d. not determined
surfaces might be related to the extracellular matrix abundantly produced by strain ElP T (Fig. 3e). The strain was determined to be non-motile as are the other reference species, except *I. pallida*, which displays phototactic gliding motility (Giovannoni et al. 1987).

In M1H NAG ASW medium, strain ElP T was able to grow over a temperature range of 10–33 °C and a pH range of 6.0–8.5 (Fig. 4). Strain ElP T was found to be aerobic, heterotrophic, mesophilic and neutrophilic. Optimal growth was observed at 30 °C and pH 7.5, which led to a maximal growth rate of 0.024 h⁻¹, corresponding to a generation time of 29 h (Fig. 4). The family *Isosphaeraceae* appears to be heterogeneous regarding temperature and pH preferences. *S. acidiphila, T. lichenicola* and *P. borealis* favour lower temperatures (15–26 °C) compared to strain ElP T (30 °C), whereas *I. pallida* and *T. sociabilis* are thermophiles with optimal growth at 41–42 °C and a temperature range allowing growth up to 55 °C (Table 1). With regard to pH, *I. pallida* and *A. giovannonii* are adapted to slightly alkaline growth conditions (pH 8–9), whereas *S. acidiphila, T. lichenicola* and *P. borealis* require more acidic environments (pH 5–6). Strain ElP T and *T. sociabilis* grow optimally under neutral conditions (pH 7–7.5). These differences likely reflect the different natural habitats from which the strains were isolated. *I. pallida* was isolated from a hot spring, explaining the preference for higher temperatures, while e.g. *S. acidiphila* was isolated from a *Sphagnum* peat moss, which are typically found in nutrient-poor and acidic peat bogs (Giovannoni et al. 1987; Kulichevskaya et al. 2008).

**Fig. 3** Microscopy images and cell size plot of strain ElP T. The mode of cell division (a) and a general overview of the cell morphology (b, d, e) is shown. Cells tend to form aggregates surrounded by an extracellular matrix (d + e). The scale bar is 1 μm. For determination of the cell size (c) at least 100 representative cells were counted manually or by using a semi-automated object count tool.
Genomic characteristics

The complete genome of strain \textit{EIP}^T has a size of 9.40 Mb, distributed among the chromosome (8.67 Mb) and five plasmids (with sizes of 0.28, 0.14, 0.12, 0.09 and 0.09 Mb). While plasmids are scarce among Planctomycetes, the family \textit{Isosphaeraceae} is exceptional in that regard (Ivanova et al. 2017). Five strains of this family harbour at least one plasmid (no data available for \textit{T. sociabilis}), while four plasmids was the current maximum observed in strain SH-PL62 (Ivanova et al. 2017). Strain \textit{EIP}^T maintains five extrachromosomal replicons in parallel, making it a potential resource for future planctomycetal genetic tool development.

The \textit{G} + \textit{C} content of strain \textit{EIP}^T is 71.1%. In its genome, 7707 genes were annotated, of which 7556 are putative protein-coding genes. The number of hypothetical proteins is 3399, corresponding to 45% of the total number of putatively annotated proteins. The number of protein-coding genes yields 804 encoded proteins per Mb and a coding density of 84.7%. 100 tRNAs and three copies of the 16S rRNA gene were identified. The genomic characteristics of the compared strains are quite heterogeneous (Table 1). With 5.53 Mb \textit{I. pallida} has by far the smallest genome, while the genomes of strain \textit{EIP}^T, \textit{S. acidiphila} and \textit{A. giovannonii} fall in a size range of 9.4–10.6 Mb. Their \textit{G} + \textit{C} content varies from 62 to 71%, with strain \textit{EIP}^T showing the highest \textit{G} + \textit{C} content of the compared strains. One giant gene (> 5 kb) was found in \textit{S. acidiphila} and \textit{A. giovannonii}, while the other three strains lack giant genes. The genome of \textit{T. lichenicola has not been sequenced yet and could thus not be used for comparison.}

Genome-based analysis of the primary and secondary metabolism

The genome sequences of species belonging to the family \textit{Isosphaeraceae} provide important information on their metabolic capabilities. The suggested capability of Planctomycetes to degrade high molecular weight sugars is likely reflected by high numbers of carbohydrate-active enzymes encoded in their genomes, while production of secondary metabolites is often related to interactions with the abiotic and biotic environment, including response to external stress factors. The compared members of the family \textit{Isosphaeraceae} harbour between 109 and 317 carbohydrate-active enzymes and a clear correlation between the number of enzymes and the genome size was observed (Table 2). Only \textit{S. acidiphila} slightly deviates from this trend. It has the second largest genome of the compared species, but is only ranked 3rd with regard to the number of carbohydrate-active enzymes. Strain \textit{EIP}^T has a 5% smaller genome, but its number of carbohydrate-active enzymes is around 10% higher. Analysis of the distribution to the different enzyme families shows that glycoside hydrolases and glycosyl transferases account for 80–90% of the total number in all five strains. \textit{A. giovannonii} has a considerably higher number of enzymes of the glycoside hydrolase family, which is 2.5 times as high as in strain \textit{EIP}^T (second highest number of enzymes of this family) and almost seven times as high.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{fig4}
\caption{Temperature and pH optimum of \textit{EIP}^T. The graphs show the average growth rates obtained from cultivation of the strain in M1H NAG ASW medium in biological triplicates.}
\end{figure}
Whether a higher number of carbohydrate-active enzymes is related to a higher versatility during degradation naturally-occurring polysaccharides remains to be elucidated.

To gain a first insight into the secondary metabolism, numbers of genes coding for polyketide synthases (PKSs), non-ribosomal peptide synthetases (NRPSs) and other genes involved in the synthesis of terpenoids, bacteriocins or resorcinol were analysed (Table 2). A correlation between the number of gene clusters and the genome size could also be observed in this case. Five genes/gene clusters were found in species with genome sizes of 5–7 Mb, six in species with 7–10 Mb and seven clusters in A. giovannonii with > 10 Mb genome size. Strain EIP\textsuperscript{T} is an exception to this trend since only four clusters were observed, although the strain has the second largest genome of those compared. All six strains harbour 2–3 genes putatively involved in terpenoid biosynthesis.

Genes coding for phytoene synthase isoenzymes (CrtB; catalysing the initial step during carotenoid biosynthesis) were identified in the pink-pigmented strains (see Table 1), however, genes in T. sociabilis and S. acidiphila might well code for closely related squalene synthases. Since the pathway for carotenoid biosynthesis in Planctomycetes has not been discovered yet, additional conclusions cannot be drawn from the genome sequence at this stage. At least one type I PKS-encoding gene is present in all six strains, while three of the strains also harbour a putative type III PKS gene. Type II PKSs were not observed in the compared strains. Two of the strains appear to be capable of bacteriocin production, while a single NRPS-encoding gene was observed in A. giovannonii. The six species may harbour additional gene clusters involved in the production of small molecules, these, however, might

**Table 2** Numbers of carbohydrate-active enzymes and secondary metabolite-associated gene clusters in EIP\textsuperscript{T} in comparison to other species in the family Isosphaeraceae. The analysis is based on GenBank accession numbers for strain EIP\textsuperscript{T} (CP036426–CP036431), Tautonia sociabilis (GCA_003977685.1), Isosphaera pallida (CP002353–CP002354), Singulisphaera acidiphila (CP003364–CP003367), Paludisphaera borealis (CP019082–CP019084) and Aquisphaera giovannonii (CP042997–CP042999).

| Feature                        | EIP\textsuperscript{T} | Tautonia sociabilis GM2012\textsuperscript{T} | Isosphaera pallida IS1B\textsuperscript{T} | Singulisphaera acidiphila MOB10\textsuperscript{T} | Paludisphaera borealis PX4\textsuperscript{T} | Aquisphaera giovannonii OJF2\textsuperscript{T} |
|--------------------------------|-------------------------|-----------------------------------------------|---------------------------------------------|-------------------------------------------------|-------------------------------------------|-----------------------------------------------|
| Genome size (Mb)               | 9.40                    | 6.76                                          | 5.53                                        | 9.76                                            | 7.65                                       | 10.53                                         |
| Carbohydrate-active enzymes    |                         |                                               |                                             |                                                 |                                           |                                               |
| Glycoside Hydrolase Family     | 59                      | n.d.                                          | 21                                          | 49                                              | 52                                        | 142                                           |
| Glycosyl Transferase Family    | 123                     | n.d.                                          | 74                                          | 117                                             | 86                                        | 120                                           |
| Polysaccharide Lyase Family    | 3                       | n.d.                                          | 2                                           | 1                                               | 0                                         | 3                                             |
| Carbohydrate Esterase Family   | 13                      | n.d.                                          | 5                                           | 9                                               | 9                                         | 17                                            |
| Carbohydrate-Binding Family    | 16                      | n.d.                                          | 7                                           | 14                                              | 21                                        | 35                                            |
| Total number                   | 214                     | n.d.                                          | 109                                         | 190                                             | 168                                       | 317                                           |
| Secondary metabolite-associated clusters |           |                                               |                                             |                                                 |                                           |                                               |
| Terpenoid                      | 3                       | 2                                             | 3                                           | 3                                               | 2                                         | 2                                             |
| Type I Polyketide synthase     | 1                       | 1                                             | 1                                           | 2                                               | 3                                         | 2                                             |
| Type II Polyketide synthase    | 0                       | 0                                             | 0                                           | 0                                               | 0                                         | 0                                             |
| Type III Polyketide synthase   | 0                       | 0                                             | 1                                           | 0                                               | 1                                         | 1                                             |
| Non-ribosomal peptide synthetase| 0                       | 0                                             | 0                                           | 0                                               | 0                                         | 0                                             |
| Bacteriocin                    | 0                       | 2                                             | 0                                           | 1                                               | 0                                         | 1                                             |
| Resorcinol                     | 0                       | 0                                             | 0                                           | 0                                               | 0                                         | 0                                             |
| Total number                   | 4                       | 5                                             | 5                                           | 6                                               | 6                                         | 7                                             |
have escaped the in silico prediction by the AntiSMASH tool.

Taken together, comparison of morphological, physiological and genomic features in the heterogeneous family *Isosphaeraceae* supports the results of the phylogenetic analysis, which leads us to the conclusion that strain EiPT represents a novel species in the genus *Tautonia*. Thus, we propose the name *Tautonia plasticadhaerens* for this species, represented by the type strain EiPT (DSM 101012T = LMG 29141T).

Emended genus description of *Tautonia* Kovaleva et al. (2019)

The description of the genus is as previously published (Kovaleva et al. 2019), with the following modification: species of this genus are mesophilic or thermod tolerant.

*Tautonia plasticadhaerens* sp. nov.

Plas.tic.ad.hae’rens. N.L. neut. n. *plasticum* plastic; L. pres. part. *adhaerens* adhering, sticking to; N.L. part. adj. *plasticadhaerens* attaching to plastic, due to the tendency of the type strain to attach strongly to plastic surfaces.

Cells are spherical (diameter 1.7 ± 0.3 μm), occur as single cells or small aggregates and divide by budding. Stalk-free and non-motile cells, which contain crateriform structures covering the entire cell surface. Cells produce an extracellular matrix and strongly attach to plastic surfaces. Colonies are pink.

Cells of the type strain grow over a temperature range of 10–33 °C (optimum 30 °C) and at pH 6.0–8.5 (optimum 7.5). The genome of the type strain has a size of 9.40 Mb, which is distributed among the chromosome and five plasmids. The G + C content is 71.1%.

The type strain is EiPT (DSM 101012T = LMG 29141T), isolated from an alga close to Panarea Island in September 2013.

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Author contributions NK wrote the manuscript and analysed the cultivation data, SW performed the genomic and phylogenetic analysis, AH and MJ isolated the strains and performed the initial cultivation and strain deposition, SHP and CB performed the light microscopic analysis and prepared the LM pictures, MSMJ contributed to text preparation and revised the manuscript, MR performed the electron microscopic analysis and prepared the SEM pictures, CJ supervised AH and the study. All authors read and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

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