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Predatory Organisms with Untapped Biosynthetic Potential

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1 **Predatory organisms with untapped biosynthetic potential. A description of**
2 **eight novel *Coralloccoccus* species: *Coralloccoccus aberystwythiensis* sp. nov.,**
3 ***Coralloccoccus carmarthensis* sp. nov., *Coralloccoccus exercitus* sp. nov.,**
4 ***Coralloccoccus interemptor* sp. nov., *Coralloccoccus llansteffanensis* sp. nov.,**
5 ***Coralloccoccus praedator* sp. nov., *Coralloccoccus sicarius* sp. nov., and**
6 ***Coralloccoccus terminator* sp. nov.**

7
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17 Running Title: Eight novel *Coralloccoccus* species.

18
19 **Abstract**

20 *Coralloccoccus* spp. are common soil-dwelling organisms which kill and consume prey
21 microbes through the secretion of antimicrobial substances. Two species of *Coralloccoccus*
22 have been described previously (*Coralloccoccus coralloides* and *Coralloccoccus exiguus*).

23 A polyphasic approach was taken to characterise antimicrobial, biochemical and
24 phenotypic properties of eight *Coralloccoccus* spp. strains and the two type strains. We also
25 report here the genome sequence of the *C. exiguus* type strain (DSM 14696^T).

26 The genomes of the eight candidate strains, *C. exiguus* DSM 14696^T and *C.*
27 *coralloides* DSM 2259^T, had an average nucleotide identity below 95% and digital DNA-DNA
28 hybridisation scores less than the 70% lower bound for species identity, indicating they
29 belong to distinct species.

30 All ten strains, including the two type strains, were thoroughly characterised,
31 including biochemical analysis of their fatty acid methyl esters, substrate utilisation and

32 sugar assimilation. Each strain gave a distinct profile of properties, which together with their
33 genomic differences supports the proposal of the eight candidate strains as novel species:
34 *Coralloccoccus exercitus* sp. nov. (AB043A^T = DSM 108849^T = NBRC 113887^T), *Coralloccoccus*
35 *interemptor* sp. nov. (AB047A^T = DSM 108843^T = NBRC 113888^T), *Coralloccoccus*
36 *aberystwythensis* sp. nov. (AB050A^T = DSM 108846^T = NBRC 114019^T), *Coralloccoccus*
37 *praedator* sp. nov. (CA031B^T = DSM 108841^T = NBRC 113889^T), *Coralloccoccus sicarius* sp.
38 nov. (CA040B^T = DSM 108850^T = NBRC 113890^T), *Coralloccoccus carmarthenensis* sp. nov.
39 (CA043D^T = DSM 108842^T = NBRC 113891^T), *Coralloccoccus llansteffanensis* sp. nov. (CA051B^T
40 = DSM 108844^T = NBRC 114100^T) and *Coralloccoccus terminator* sp. nov. (CA054A^T = DSM
41 108848^T = NBRC 113892^T).

42

43 **Importance**

44 *Coralloccoccus* is a genus of 'wolf-pack' predators with broad prey ranges and whose
45 genomes contain large numbers of biosynthetic gene clusters for secondary metabolite
46 production. Eight *Coralloccoccus spp.* strains were thoroughly characterised using
47 phylogenetic and phylogenomic analyses, growth assays, microscopic imaging, biochemical
48 activity assays, fatty acid profiling, predatory activity assays and antibiotic resistance
49 profiling. The strains exhibited distinct patterns of drug resistance, which mirrored their
50 possession of diverse sets of biosynthetic genes. Multiple metrics confirmed that each strain
51 belonged to a novel species within the *Coralloccoccus* genus.

52 Taxonomic assignment of environmental isolates to novel species allows us to begin
53 to characterise the diversity and evolution of members of this biotechnologically important
54 bacterium, which is important as it can guide bioprospecting efforts for novel biologically
55 active metabolites and antimicrobials.

56

57 **Introduction**

58 Myxobacteria are virtually ubiquitous deltaproteobacteria commonly found in
59 temperate topsoil (Dawid, 2000). Their lifestyle is unusual amongst bacteria, with
60 populations cooperatively responding to starvation by forming multicellular fruiting bodies
61 containing spores, while vegetative growth is supported by their predation of a broad range
62 of prey organisms (Morgan et al., 2010; Livingstone et al., 2017). Myxobacterial predators
63 secrete antimicrobial substances, causing the lysis of prey organisms and release of their

64 nutrients into the environment, which has led to the controversial assumption that
65 predation, like fruiting, is also cooperative (Marshall and Whitworth, 2019).

66 Little work has been published that associates myxobacterial taxa with particular
67 ecological roles/niches beyond labelling them as terrestrial or marine, or defining whether
68 or not they degrade cellulose. It has become apparent that individual myxobacterial species
69 can exhibit a great deal of phenotypic variation even within a very small geographical area
70 (Vos and Velicer, 2008; Vos and Velicer, 2009), which may explain our current lack of
71 ecological understanding.

72 Such phenotypic diversity, which often does not correlate with taxonomy, has also
73 hampered traditional taxonomic approaches to classify the myxobacteria, leading to the
74 adoption of polyphasic approaches for taxonomic assignment (Mohr et al., 2018). Over
75 recent decades myxobacterial classification approaches have focussed on morphological
76 features (including the architecture of colonies and fruiting bodies), biochemical properties
77 and the sequence of conserved genes (particularly the 16S gene). With the advent of whole
78 genome sequencing, it has also become possible to undertake genome-based assessments
79 of bacterial taxonomy and evolution (Chun et al., 2018).

80 The genus *Coralloccoccus* was validly described in 2007 as a member of suborder
81 Cystobacterineae within family Myxococcaceae and included three species: *C. coralloides*, *C.*
82 *exiguus* and *C. macrosporus* (Euzéby, 2007). Subsequently, Lang and Stackebrandt (2009)
83 published an emended description of the genera *Coralloccoccus* and *Myxococcus*, reassigning
84 *C. macrosporus* to the *Myxococcus* genus as *Myxococcus macrosporus*.

85 *Coralloccoccus* spp. cells are Gram-negative bacilli when growing vegetatively, but
86 produce coral-shaped orange/peach coloured fruiting bodies upon starvation (Garcia et al.,
87 2010). It is one of the myxobacterial genera most easily isolated from soil and exhibits a
88 wide range of predatory activity against diverse microbes (Mohr et al., 2016; Livingstone et
89 al., 2017). This is largely attributable to the secondary metabolites they produce, which
90 possess a range of antimicrobial properties (Xiao et al., 2011; Landwehr et al., 2016).

91 We have recently completed a comparative genome analysis of 23 *Coralloccoccus*
92 spp. strains which suggested the sequenced organisms belonged to ten discrete
93 genomospecies, of which eight were likely to be novel (Livingstone et al., 2018). In the
94 current study we undertook a traditional polyphasic characterisation of representatives
95 from each of the seven *Coralloccoccus* genomospecies. Biochemical and physiological

96 measurements confirmed that they belong to distinct species and we therefore propose
97 eight novel *Corallococcus* species.

98

99 **Methods and Materials**

100 Bacterial strains

101 Strains AB043A, AB047A, AB050A, CA031B, CA040B, CA043D, CA051B and CA054A
102 were originally isolated from soil and identified as *Corallococcus* spp. in a previous study
103 (Livingstone et al., 2017). The type strains of *C. coralloides* (DSM 2259^T) and *C. exiguus* (DSM
104 14696^T) were obtained from the DSMZ (German Collection of Microorganisms and Cell
105 Cultures). All ten strains were cultured on VY-2 agar (0.5% dried baker's yeast, 0.1%
106 CaCl₂·2H₂O, 1.5% agar) for further characterisation.

107 Phenotypic characterisation

108 Growth properties were assessed at various temperatures (at pH 7.8) and pH values
109 (at 30 °C) on VY-2 agar. The biochemical properties of strains were characterised using the
110 API 20E kit (BioMérieux) according to the manufacturer's kit instructions. Stokes' method
111 for antibiotic susceptibility testing was used, with results compared against those for
112 *Escherichia coli* ATCC 25922 and interpreted as 'resistant' or 'susceptible' according to
113 standard rules (BSAC, 1991).

114 FAME analysis

115 Saponification of cellular fatty acids was achieved by incubating in 1.875 M NaOH at
116 100 °C for 30 minutes. For methylation 2 volumes of 3.25 M HCl in methanol were added
117 and incubated at 80 °C for 10 minutes. Fatty acid methyl esters (FAMES) were extracted in
118 1:1 hexane: methyl tert-butyl ether and washed in 0.3 M NaOH (Sasser, 2006). Analysis of
119 FAMES was performed using an Agilent 7890B gas chromatograph with a Leco Pegasus BT
120 time-of-flight mass spectrometer. The GC was equipped with a CP-Sil 88 capillary column
121 (Agilent CP7489, 100 m x 0.25 mm x 0.2 µm). The carrier gas was helium at a constant
122 pressure of 20.7 psi and flow rate of 0.7 ml/min. The GC oven start temperature was 70 °C,
123 ramping at 8 °C/min to 100 °C, then at 5 °C/min up to 170 °C for 10 minutes before a final
124 ramp at 4° C/min to 240 °C for 30 minutes. The inlet and transfer line to the MS were both
125 240 °C. A split injection (1:50) of 1 µl sample was used.

126 Data were analysed using the ChromaTOF software from Leco. Samples were
127 compared to standard solutions run under the same conditions and peaks identified by both

128 retention time and mass spectra. The standards used were: 37 component FAME mix
129 (Supelco, CRM47885), Linoleic acid, conjugated methyl ester (Supelco, O5362), Mixture
130 ME93 (Larodan, 90-1093) and Bacterial Acid Methyl Esters CP Mixture (Matreya, 1114). The
131 data presented are mean values derived from biological replicates (prepared on at least two
132 occasions from at least two cultures).

133 Predation assays

134 The predatory activity of the eight candidate strains has been previously reported
135 (Livingstone et al., 2017). For comparison, here the predatory profile of strains *C. coralloides*
136 DSM 2259^T and *C. exiguus* DSM 14696^T were assayed using the same protocol, which
137 involved inoculation onto lawns of ten prey organisms (see Livingstone et al., 2017 for
138 details of prey strains). The diameter of the predatory zone on the prey lawn was measured
139 after seven days' incubation at 30 °C.

140 Genome analysis

141 Draft genome sequences of the eight candidate strains were published previously
142 (Livingstone et al., 2018) while the *C. coralloides* DSM 2259^T genome was downloaded from
143 the NCBI database. *C. exiguus* DSM 14696^T was sequenced in this study using 2 × 250 bp
144 paired-end reads on the Illumina Hiseq 2500 platform by MicrobesNG (Birmingham, United
145 Kingdom). The raw reads were subjected to Kraken 2 for read mapping, BWA-MEM for
146 quality control and SPAdes 3.7 for *de novo* assembly (Li and Durbin, 2009; Bankevich et al.,
147 2012; Wood and Salzberg, 2014). The DSM 14696^T genome sequence is available from the
148 NCBI nucleotides database under BioProject accession PRJNA547735.

149 Complete 16S rRNA gene sequences were extracted from the genomes for
150 phylogenetic analysis and similarity searches. Neighbour-joining trees were constructed in
151 MEGA-7.0 (Kumar et al., 2016), using the Kimura 2-parameter model with 500 bootstraps.
152 Phylogenomic relationships were analysed using AMPHORA2 based on 31 concatenated
153 marker genes and visualised as a maximum likelihood tree with 500 bootstraps generated
154 using a Jones-Taylor-Thornton model in MEGA 7.0 (Kerepesi et al 2014; Kumar et al., 2016).
155 The average nucleotide identity (ANI) and digital-DNA/DNA hybridization (dDDH) were
156 calculated using the genome-to-genome distance calculator (Meier-Kolthoff, 2013). The
157 comprehensive antibiotic resistance database (CARD) was used to identify antibiotic
158 resistance genes in the genomes and to correlate them with the phenotypic antibiotic
159 susceptibility tests (Jia et al., 2017).

160

161 **Results**

162 The eight candidate strains represent eight novel genomospecies.

163 The genome sequence of *C. coralloides* DSM 2259^T has previously been shown to lie
164 within a different genomospecies to the eight candidate strains, whether considering ANI or
165 dDDH values (Livingstone et al., 2018). However, the lack of a *C. exiguus* genome sequence
166 meant that it was possible that one of the candidate genomospecies could have been *C.*
167 *exiguus*.

168 A draft genome sequence of *C. exiguus* DSM 14696^T was therefore generated.
169 Similarly to other *Coralloccoccus* spp. draft genomes, the DSM 14696^T assembly had a total
170 size of 10,463,210 bp spread over 880 contigs with 9122 coding sequences and a GC content
171 of 69.5%. The N50 and L50 values for the genome sequence were 24,436 bp and 136
172 respectively (ie. the largest 136 contigs together constituted more than half of the genome
173 sequence, and the 136th contig was 24.4 Kbp long).

174 The genome sequences of DSM 14696^T, DSM 2259^T and the eight candidate strains
175 were compared in every pair-wise combination and ANI and dDDH scores calculated (Table
176 1). In all pair-wise comparisons the ten strains had ANI scores between 84% and 92% with
177 dDDH scores of 50% or less. Based on the currently accepted boundaries for defining same-
178 species membership at 95% for ANI and 70% for dDDH (Chun et al., 2018) this indicates they
179 belong to ten separate species within the same genus.

180 Previous genome sequence comparisons (Livingstone et al., 2018) have
181 demonstrated that *Coralloccoccus* spp. genomospecies lay in two large phylogenomic groups
182 (A and B), with *C. coralloides* found within Group A. Performing comparisons of the *C.*
183 *exiguus* DSM 14696^T genome with other published *Coralloccoccus* spp. genomes revealed
184 that it also lies within Group A, within the genomospecies composed of strains AB004,
185 AB018, AB030, AB38B and CA041A described by Livingstone et al. (2018), which can
186 therefore now be identified as strains of *C. exiguus*.

187 Phylogenetic relationships between the ten genomospecies

188 Evolutionary relationships between the ten strains were visualised by generating
189 phylogenetic trees based on 16S rRNA gene sequences (Figure 1A), concatenated sequences
190 of 31 conserved genes (Figure 1B), and ANI values (Figure 1C). The 16S rRNA tree suggests
191 four groupings, which is mirrored with ANI and dDDH values. *C. exiguus* and *C. coralloides* lie

192 within the same group, alongside AB047A. The four Group B strains are found together as a
193 pair of pairs (CA031B/CA054A with CA040B/CA051B) and the remaining three Group A
194 strains clustering together (AB043A/AB050A/CA043D).

195 Surprisingly, strains CA031B and CA054A show little difference in 16S sequence
196 (Figure 1A) yet the Amphora tree based on 31 conserved genes, demonstrated substantial
197 differences between strains (Figure 1B) as did the ANI-derived tree (Figure 1C).

198 Physiology and biochemical characterisation

199 The cells of all strains were Gram-negative bacilli measuring approximately 0.5-1.0
200 μm by 3.0-7.0 μm , which looked morphologically similar in scanning electron micrographs to
201 the representative strains shown; CA051B and AB043A (Figure 2). Colonies exhibited
202 swarming growth on VY-2 and were of a pale orange/peach colour, with darker fruiting
203 bodies. Testing for growth at different temperatures (at pH 7.8) demonstrated all strains
204 grew at a temperature of 30 °C, no growth of strains at 37 °C or above, while strain growth
205 at 35 °C was strain dependent (Table 2). Of note were strains AB043A and CA043 which
206 grew unusually well at 35 °C for myxobacteria. The pH-dependence of strain growth was
207 also tested (at 30 °C). The optimum pH was 7 or higher for all strains with only four of the
208 strains exhibiting growth at pH 5 (Table 2). AB050A exhibited an exceptionally restricted pH
209 tolerance, only growing at pH 7-7.8. Only strains CA040B and CA054A exhibited the same
210 profile of pH and temperature-dependent growth (Table 2).

211 The ability to metabolise a variety of carbon sources was tested and all strains found
212 to be incapable of metabolising adipate, arabinose, arginine, caprate, gluconate, mannitol,
213 mannose, N-acetyl glucosamine or urea. However some strains were able to metabolise
214 citrate, esculin, gelatin, glucose, malate, maltose, *o*-nitrophenyl- β -D galactopyranoside and
215 phenyl acetate (Table 3). Only strains CA040B and DSM 2259^T exhibited the same profile of
216 substrate utilisation (Table 3). Fatty acid methyl ester (FAME) analysis was also employed to
217 characterise the fatty acids of each strain (Table 4). The profile of fatty acid derivatives
218 detected was unique to each strain, with CA040B possessing a particularly diverse set of
219 lipids.

220 Predatory activity and antibiotic resistance profiling

221 Myxobacteria are known to possess predatory activity against a broad range of prey
222 organisms. The predatory activity of the candidate strains and DSM 2259^T have already been
223 described (Livingstone et al., 2018), but for this study we assessed the activity of DSM

224 14696^T for comparison (Table 5). DSM 14696^T is on average the best predator of the ten
225 strains, out-predating all other predator strains on seven of the ten prey organisms, while
226 DSM 2259^T demonstrated the lowest average predatory activity.

227 Myxobacterial predation is thought to involve, at least partly, the secretion of
228 cocktails of antibiotic secondary metabolites encoded by large biosynthetic gene clusters
229 (BGCs). The BGCs which direct antibiotic production, and their associated resistance genes,
230 are members of the accessory pan-genome and each strain/taxon possesses a distinctive set
231 of BGCs. This is presumably responsible for the individuality of predatory activities against
232 diverse prey (Livingstone et al., 2018). We therefore characterised the antibiotic resistance
233 profile of the ten *Coralloccoccus* spp. strains to investigate the individuality of antibiotic
234 production by each strains.

235 All isolates were resistant to Ampicillin, Ceftazidime, Ertapenem and
236 Piperacillin/Tazobactam and all were susceptible to Amikacin, Ciprofloxacin and
237 Trimethoprim/Sulfamethoxazole (Table 6). CA031B was unique in being sensitive to
238 Imipenem, while CA043D was uniquely sensitive to Gentamicin and Cefotaxime. CA031B,
239 CA040B and CA054A were sensitive to Augmentin whereas all other strains were resistant
240 (Table 6). The Resfinder tool of the comprehensive antibiotic resistance database (CARD)
241 demonstrated the presence of the multidrug resistance efflux gene *adeF* within the
242 genomes of each strain. In addition, CA031B, CA040B and CA051B were found to possess
243 the AAC(3)-IIIb gene for aminoglycoside resistance, and AB043A possesses the gene for the
244 MsbA multidrug resistance transporter (Table 6).

245 *Proposal of eight novel Coralloccoccus species.*

246 On the basis of genomic and phylogenetic differences, distinct growth
247 characteristics, biochemical activities, fatty acid profiles and antibiotic resistance profiles,
248 we propose that the eight candidate strains described here each belong to and typify novel
249 *Coralloccoccus*: *Coralloccoccus exercitus* sp. nov. (AB043A^T), *Coralloccoccus interemptor* sp.
250 nov. (AB047A^T), *Coralloccoccus aberystwythensis* sp. nov. (AB050A^T), *Coralloccoccus praedator*
251 sp. nov. (CA031B^T), *Coralloccoccus sicarius* sp. nov. (CA040B^T), *Coralloccoccus carmarthensis*
252 sp. nov. (CA043D^T), *Coralloccoccus llansteffanensis* sp. nov. (CA051B^T) and *Coralloccoccus*
253 *terminator* sp. nov. (CA054A^T).

254 This proposal also allows to define species membership for additional *Coralloccoccus*
255 spp. isolates described previously (Livingstone et al., 2018), on the basis of ANI values $\geq 95\%$.

256 Specifically, AB011P, AB045, CA049B and CA054B are classified as *C. coralloides*, AB004,
257 AB018, AB030, AB032C, AB038B and CA041A as *C. exiguus*, AB049A and AB050B as *C.*
258 *interemptor*, and CA031C and CA047B as *C. praedator*.

259

260 **Discussion**

261 The genus *Corallocooccus*

262 The Myxococcaceae family currently contains five validly described genera;
263 *Aggregicooccus*, *Corallocooccus*, *Myxococcus*, *Pyxidicooccus* and *Simulacricoccus*. When
264 compared to the genus *Myxococcus*, the remaining four genera are relatively poorly
265 understood with *Corallocooccus* being the second best characterised. Indeed, *Myxococcus*
266 *xanthus* is the single best studied myxobacterium, being the model organism for the whole
267 Myxococcales order. In June 2019, a Pubmed search for '*Myxococcus xanthus*' gave 1,469
268 hits, while the search term '*Corallocooccus*' gave a mere 45. Compared to the five valid
269 *Myxococcus* species (*Myxococcus fulvus*, *Myxococcus macrosporus*, *Myxococcus stipitatus*,
270 *Myxococcus virescens* and *M. xanthus*), only two have been described in *Corallocooccus* (*C.*
271 *coralloides* and *C. exiguus*).

272 *Corallocooccus* spp. members are nevertheless important organisms in their own right
273 and deserve to emerge from under the shadow of *Myxococcus* spp. They are amongst the
274 most abundant myxobacterial genera isolated from soils (Mohr et al., 2016; Livingstone et
275 al., 2017), and are proven producers of antimicrobial metabolites (Xiao et al., 2011;
276 Landwehr et al., 2016). Genome sequencing of 23 *Corallocooccus* isolates revealed an open
277 pan-genome with strains having highly individual complements of BGCs, suggesting that the
278 few compounds isolated from *Corallocooccus* spp. to date represent just the tip of an iceberg
279 of novel *Corallocooccus* metabolites (Livingstone et al., 2018; Gregory et al., 2019).

280 Diversity within the *Corallocooccus* genus

281 When originally isolated, and subjected to 16S rRNA gene sequencing, the eight
282 candidate *Corallocooccus* spp. strains described here exhibited greatest 16S sequence
283 similarity to *Corallocooccus coralloides/exiguus*, with similarities of at least 98.7 %. 16S rRNA
284 phylogenetic analysis demonstrated that the strains belonged to a clade distinct from the
285 other Myxococcaceae genera, encompassing *C. coralloides* and *C. exiguus* (Livingstone et al.,
286 2017). This mirrored the results of a study in 2005, which concluded that 'the genus

287 *Corallococcus* may embrace a broad range of yet-to-be described novel species.’
288 (Stackebrandt and Päuker, 2005).

289 In recent years, it has become increasingly appreciated that 16S rRNA phylogenetic
290 taxonomic assignment has limitations, which can be overcome by considering more genes,
291 ultimately considering every gene in an organism’s genome (phylogenomics). The gold
292 standard for sequence-based taxonomic assignment has therefore shifted from 16S rRNA to
293 genome-based methods (Richter and Rosselló-Móra, 2009), and has recently culminated in
294 the proposal of new standards for genome-based taxonomy based on ‘overall genome
295 relatedness indices’ (OGRIs) such as ANI (Chun et al., 2018).

296 Following assessment of the genomic diversity of our *Corallococcus* spp. culture
297 collection, OGRIs indicated that our 23 sequenced strains belonged to at least ten discrete
298 genomospecies, one of which included the *C. coralloides* type strain (Livingstone et al.,
299 2018). Sequencing the *C. exiguus* type strain genome in this study has now allowed us to
300 identify a second genomospecies as being *C. exiguus*, confirming that *C. exiguus* and *C.*
301 *coralloides* are discrete species despite their virtually identical 16S rRNA gene sequences
302 (Stackebrandt and Päuker, 2005).

303 *Corallococcus* Physiology

304 Early taxonomic classification of the myxobacteria relied heavily on fruiting body
305 morphology, colony behaviour and colouration. However, it became clear that such
306 phenotypes were difficult to reproduce, being sensitive to laboratory conditions such as
307 batch variations in media and adaptation of lineages to repeated sub-culturing. Therefore,
308 myxobacterial taxonomists incorporated gene sequence based approaches and polyphasic
309 assessments of physiology and biochemical properties (Garcia et al., 2010; Mohr et al.,
310 2018). Rather than relying solely on genome-based arguments to assess taxonomy, we have
311 instead tried to reconcile a traditional polyphasic approach with genome-based taxonomic
312 approaches in this study.

313 No consistent morphological differences were observed between candidate strains
314 at a colonial or cellular level. Physiological differences were observed, for instance in
315 preferred growth temperatures and pH, but these were often slight (Table 2). All strains
316 were capable predators, as expected given their initial isolation using *E. coli* bait, yet
317 significant variation was observed in their predatory efficiencies and antibiotic resistance
318 profiles. *C. exiguus* was a particularly efficient predator, while *C. coralloides* was particularly

319 poor (Table 6). Differences in antibiotic susceptibility were observed between candidate
320 strains, but with many strains showing identical susceptibility profiles. Phenotypic
321 distinctiveness of candidate strains was most apparent in biochemical tests for compound
322 metabolism (Table 3) and fatty acid profiling (Table 4) with each strain having an absolutely
323 unique profile.

324 Given their similarities to *Coralloccoccus* type strains, and their distinctive
325 biochemical, predatory and genomic characteristics, we are confident in proposing that the
326 eight candidate strains characterised above, each typifies a novel *Coralloccoccus* species,
327 which we describe below. Given that characterising 23 *Coralloccoccus* isolates has here led to
328 the identification of ten novel species, we suggest that the statement of Stackebrandt and
329 Päuker (2005) remains true, that ‘the genus *Coralloccoccus* may [still] embrace a broad range
330 of yet-to-be described novel species.’

331 Summary

332 Here we present morphological, physiological, predatory, biochemical and genomic
333 data which support the designation of eight strains as type strains for novel species within
334 the genus *Coralloccoccus*. As well as being untapped reservoirs of novel metabolites, these
335 species will be extremely useful in investigating the evolution, diversity and physiology of
336 antimicrobial microbes.

337

338

339 **Species Descriptions**

340

341 Description of *Corallococcus aberystwythensis* sp. nov.

342 *Corallococcus aberystwythensis* (ab.e'r.yst.w'yth.en.sis N.L. masc. adj.
343 *aberystwythensis* from Aberystwyth, reflecting the fact that the new species was isolated
344 near Aberystwyth in Wales [52.41°N 4.08°W]).

345 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
346 1.2-1.4 µm x 3.0-7.0 µm under the light microscope. Colonies were swarming and appeared
347 pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O, 1.5% agar).
348 Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic growth observed
349 at 30 °C but not 35 °C and at pH 7.0-7.8. Produces indole, nonanoate, decanoate,
350 undecanoate, tetradecanoate, pentadecanoate, palmitoleate, oleate, iso-C13:0, iso-C15:0
351 and iso-C17:0. Antibiotic resistance/susceptibility profile typical for *Corallococcus* spp. Cells
352 prey upon *Escherichia coli*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, *Proteus*
353 *mirabilis*, *Staphylococcus aureus*, *Staphylococcus epidermidis*, *Staphylococcus saprophyticus*,
354 *Enterococcus faecalis*, *Bacillus subtilis*, and *Candida albicans*. DNA GC content is 70.0 mol%.
355 The draft genome sequence of the organism is available from GenBank (Biosample number
356 SAMN10026036). Phylogenetically most similar to *C. exercitus* and *C. carmarthensis*.

357 The type strain (AB050A^T = DSM 108846^T = NBRC 114019^T) was isolated from soil
358 collected from a field near Aberystwyth, United Kingdom [gridref 52.41°N 4.08°W].

359

360 Description of *Corallococcus carmarthensis* sp. nov.

361 *Corallococcus carmarthensis* (car.ma'r.th.en.sis. N.L. masc. adj. *carmarthensis* from
362 Carmarthen, the fact that the new species was isolated near Carmarthen, Wales [51.86°N
363 4.31°W]).

364 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
365 1.1-1.5 µm x 3.0-5.0 µm under the light microscope. Colonies were swarming and appeared
366 pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O, 1.5% agar).
367 Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic growth observed
368 at 30-35 °C but not at 37 °C, and at pH 5.0-9.0. Assimilates citrate and phenyl-acetate,
369 hydrolyses esculin, gelatine and *o*-nitrophenyl-β-D-galactopyranoside. Produces nonanoate,
370 decanoate, undecanoate, dodecanoate, tetradecanoate, pentadecanoate, hexadecanoic,

371 palmitoleate, iso-C13:0, iso-C15:0, iso-C16:0 and iso-C17:0. Antibiotic
372 resistance/susceptibility profile typical for *Corallocooccus* spp., except sensitive to Cefotaxime
373 and Gentamicin. Cells prey upon *Escherichia coli*, *Pseudomonas aeruginosa*, *Proteus*
374 *mirabilis*, *Staphylococcus aureus*, *Staphylococcus epidermidis*, *Staphylococcus saprophyticus*,
375 *Candida albicans*, and feed particularly well on *Klebsiella pneumoniae*, *Enterococcus faecalis*
376 and *Bacillus subtilis*. DNA GC content is 69.9 mol%. The draft genome sequence of the
377 organism is available from GenBank (Biosample number SAMN10026042). Phylogenetically
378 most similar to *C. exercitus* and *C. aberystwythensis*.

379 The type strain (CA043D^T = DSM 108842^T = NBRC 113891^T) was isolated from soil
380 collected from a field near Carmarthen, United Kingdom [gridref 51.86°N 4.31°W].

381

382 Description of *Corallocooccus exercitus* sp. nov.

383 *Corallocooccus exercitus* (ex.e'r.cit.us. L. nom. n. *exercitus* the army, reflecting
384 concerted killing of prey by a large number of cells).

385 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
386 0.4-0.5 µm x 2.8-5.6 µm under the scanning electron microscope. Colonies were swarming
387 and appeared pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂.2H₂O,
388 1.5% agar). Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic
389 growth observed at 30 °C but not 35 °C and at pH 5.0-9.0. Hydrolyses gelatine and
390 assimilates glucose. Produces indole, decanoate, undecanoate, pentadecanoate,
391 heptadecanoate, palmitoleate, 7,10-hexadecenoate, linolenate, iso-C13:0, iso-C15:0, iso-
392 C16:0 and iso-C17:0. Antibiotic resistance/susceptibility profile typical for *Corallocooccus* spp.
393 Cells prey upon *Escherichia coli*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, *Proteus*
394 *mirabilis*, *Staphylococcus aureus*, *Staphylococcus epidermidis*, *Staphylococcus saprophyticus*,
395 *Enterococcus faecalis*, *Bacillus subtilis*, and *Candida albicans*. DNA GC content is 70.3 mol%.
396 The draft genome sequence of the organism is available from GenBank (Biosample number
397 SAMN10026050). Phylogenetically most similar to *C. aberystwythensis* and *C. carmarthensis*.

398 The type strain (AB043A^T = DSM 108849^T = NBRC 113887^T) was isolated from soil
399 collected from a field near the village of Goginan, United Kingdom [gridref 52.41°N 3.93°W].

400

401 Description of *Corallocooccus interemptor* sp. nov.

402 *Coralloccoccus interemptor* (int.er.e'mpt.or. L. nom. n. *interemptor* the destroyer,
403 reflecting the destruction of neighbouring prey cells).

404 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
405 1.2-1.3 µm x 3.0-6.0 µm under the light microscope. Colonies were swarming and appeared
406 pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O, 1.5% agar).
407 Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic growth observed
408 at 30 °C but not 35 °C and at pH 5.0-9.0. Reduces nitrate and hydrolyses esculin, gelatine
409 and *o*-nitrophenyl-β-D-galactopyranoside. Produces indole, nonanoate, decanoate,
410 undecanoate, tridecanoate, pentadecanoate, palmitoleate, 2-hexyl-cyclopropaneoctanoate,
411 iso-C13:0, iso-C15:0, iso-C16:0 and iso-C17:0. Antibiotic resistance/susceptibility profile
412 typical for *Coralloccoccus* spp. Cells prey upon *Escherichia coli*, *Klebsiella pneumoniae*,
413 *Pseudomonas aeruginosa*, *Proteus mirabilis*, *Staphylococcus aureus*, *Staphylococcus*
414 *epidermidis*, *Staphylococcus saprophyticus*, *Enterococcus faecalis*, *Candida albicans*, and
415 grows particularly well on *Bacillus subtilis*. DNA GC content is 69.8 mol%. The draft genome
416 sequence of the organism is available from GenBank (Biosample number SAMN10026034).
417 Phylogenetically most similar to *C. coralloides* and *C. exiguus*.

418 The type strain (AB047A^T = DSM 108843^T = NBRC 113888^T) was isolated from soil
419 collected from a field near the village of Goginan, United Kingdom [gridref 52.41°N 3.93°W].

420

421 Description of *Coralloccoccus llansteffanensis* sp. nov.

422 *Coralloccoccus llansteffanensis* (llan.stef.an.en.sis. N.L. masc. adj. *llansteffanensis*
423 from Llansteffan, reflecting the fact that the new species was isolated near the village of
424 Llansteffan in Wales [51.77°N 4.39°W]).

425 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, measuring
426 0.4-0.9 µm x 2.0-4.0 µm under the scanning electron microscope. Colonies were swarming
427 and appeared pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O,
428 1.5% agar). Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic
429 growth observed at 30 °C but not 35 °C and at pH 6.0-9.0. Hydrolyses esculin. Produces
430 indole, nonanoate, undecanoate, decanoate, dodecanoate, tridecanoate, pentadecanoate,
431 palmitoleate, oleate, linoleate, linolenate, 2-hexyl-cyclopropaneoctanoate, iso-C13:0, iso-
432 C15:0, iso-C16:0 and iso-C17:0. Antibiotic resistance/susceptibility profile typical for
433 *Coralloccoccus* spp. Cells prey upon *Escherichia coli*, *Bacillus subtilis*, *Klebsiella pneumoniae*,

434 *Pseudomonas aeruginosa*, *Proteus mirabilis*, *Staphylococcus aureus*, *Staphylococcus*
435 *epidermidis*, *Staphylococcus saprophyticus*, *Enterococcus faecalis*, and *Candida albicans*.
436 DNA GC content is 70.3 mol%. The draft genome sequence of the organism is available from
437 GenBank (Biosample number SAMN10026045). Phylogenetically most similar to *C. sicarius*.

438 The type strain (CA051B^T = DSM 108844^T = NBRC 114100^T) was isolated from soil
439 collected from the edge of a stream near the village of Llansteffan, United Kingdom [gridref
440 51.77°N 4.39°W].

441

442 Description of *Corallocooccus praedator* sp. nov.

443 *Corallocooccus praedator* (prae.da't.or. L. nom. n. *praedator* the plunderer, reflecting
444 the acquisition of nutrients from prey cells).

445 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
446 1.2-1.4 µm x 3.0-6.0 µm under the light microscope. Colonies were swarming and appeared
447 pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O, 1.5% agar).
448 Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic growth observed
449 at 30 °C but not 35 °C and at pH 6.0-7.8. Assimilates malate and hydrolyses esculin.
450 Produces indole, nonanoate, decanoate, undecanoate, pentadecanoate, palmitoleate, 2-
451 hexyl-cyclopropaneoctanoate, iso-C13:0, iso-C15:0, iso-C16:0, and iso-C17:0. Antibiotic
452 resistance/susceptibility profile typical for *Corallocooccus* spp., except sensitive to Augmentin
453 and Imipenem. Cells prey upon *Escherichia coli*, *Bacillus subtilis*, *Klebsiella pneumoniae*,
454 *Proteus mirabilis*, *Staphylococcus aureus*, *Staphylococcus epidermidis*, *Staphylococcus*
455 *saprophyticus*, *Enterococcus faecalis*, *Candida albicans*, but grow poorly on *Pseudomonas*
456 *aeruginosa*. DNA GC content is 69.6 mol%. The draft genome sequence of the organism is
457 available from GenBank (Biosample number SAMN10026038). Phylogenetically most similar
458 to *C. terminator*.

459 The type strain (CA031B^T = DSM 108841^T = NBRC 113889^T) was isolated from soil
460 collected from woodland near Tanerdy, United Kingdom [gridref 51.87°N 4.29°W].

461

462 Description of *Corallocooccus sicarius* sp. nov.

463 *Corallocooccus sicarius* (si.ca'ri.us. L. nom. n. *sicarius* the killer, reflecting killing of
464 prey during predation).

465 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
466 1.2-1.4 µm x 3.0-6.0 µm under the light microscope. Colonies were swarming and appeared
467 pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O, 1.5% agar).
468 Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic growth observed
469 at 30 °C but not 35 °C and at pH 6.0-9.0. Hydrolyses esculin, gelatine and *o*-nitrophenyl-β-D-
470 galactopyranoside. Produces tridecanoate, pentadecanoate, palmitoleate, iso-C13:0, iso-
471 C15:0, iso-C16:0 and iso-C17:0. Antibiotic resistance/susceptibility profile typical for
472 *Corallocooccus* spp., except sensitive to Augmentin. Cells prey upon *Escherichia coli*, *Bacillus*
473 *subtilis*, *Klebsiella pneumoniae*, *Pseudomonas aeruginosa*, *Proteus mirabilis*, *Staphylococcus*
474 *aureus*, *Staphylococcus epidermidis*, *Staphylococcus saprophyticus*, *Enterococcus faecalis*,
475 and *Candida albicans*. DNA GC content is 70.2 mol%. The draft genome sequence of the
476 organism is available from GenBank (Biosample number SAMN10026040). Phylogenetically
477 most similar to *C. llansteffanensis*.

478 The type strain (CA040B^T = DSM 108850^T = NBRC 113890^T) was isolated from soil
479 collected from woodland near Tanerdy, United Kingdom [gridref 51.87°N 4.29°W].

480

481 Description of *Corallocooccus terminator* sp. nov.

482 *Corallocooccus terminator* (ter.min.a't.or. L. nom. n. *terminator* the ender, reflecting
483 predatory termination of prey viability).

484 Vegetative cells are Gram-negative bacilli tapering slightly at the ends, appearing
485 1.3-1.5 µm x 3.0-7.0 µm under the light microscope. Colonies were swarming and appeared
486 pale orange/peach on VY-2 agar (0.5% dried baker's yeast, 0.1% CaCl₂·2H₂O, 1.5% agar).
487 Fruiting bodies were irregular spheroids, yellow/orange in colour. Aerobic growth observed
488 at 30 °C but not 35 °C and at pH 6.0-9.0. Assimilates maltose and hydrolyses esculin, gelatine
489 and *o*-nitrophenyl-β-D-galactopyranoside. Produces indole, nonanoate, decanoate,
490 tridecanoate, pentadecanoate, palmitoleate, linoleate, linolenate, iso-C13:0, iso-C15:0, iso-
491 C16:0 and iso-C17:0. Antibiotic resistance/susceptibility profile typical for *Corallocooccus* spp.
492 Cells prey upon *Escherichia coli*, *Bacillus subtilis*, *Klebsiella pneumoniae*, *Pseudomonas*
493 *aeruginosa*, *Proteus mirabilis*, *Staphylococcus aureus*, *Staphylococcus epidermidis*,
494 *Staphylococcus saprophyticus*, *Enterococcus faecalis*, and *Candida albicans*. DNA GC content
495 is 69.5 mol%. The draft genome sequence of the organism is available from GenBank
496 (Biosample number SAMN10026047). Phylogenetically most similar to *C. praedator*.

497 The type strain (CA054A^T = DSM 108848^T = NBRC 113892^T) was isolated from soil
498 collected from the edge of a stream near the village of Llansteffan, United Kingdom [gridref
499 51.77°N 4.39°W].

500

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505

506 **Author Contributions**

507 PL undertook phenotypic and bioinformatics characterisation of the strains under
508 the supervision of DW and RM, OL and SG performed FAME analysis and AC captured the
509 EM images. DW and PL drafted the manuscript which was edited by all authors.

510

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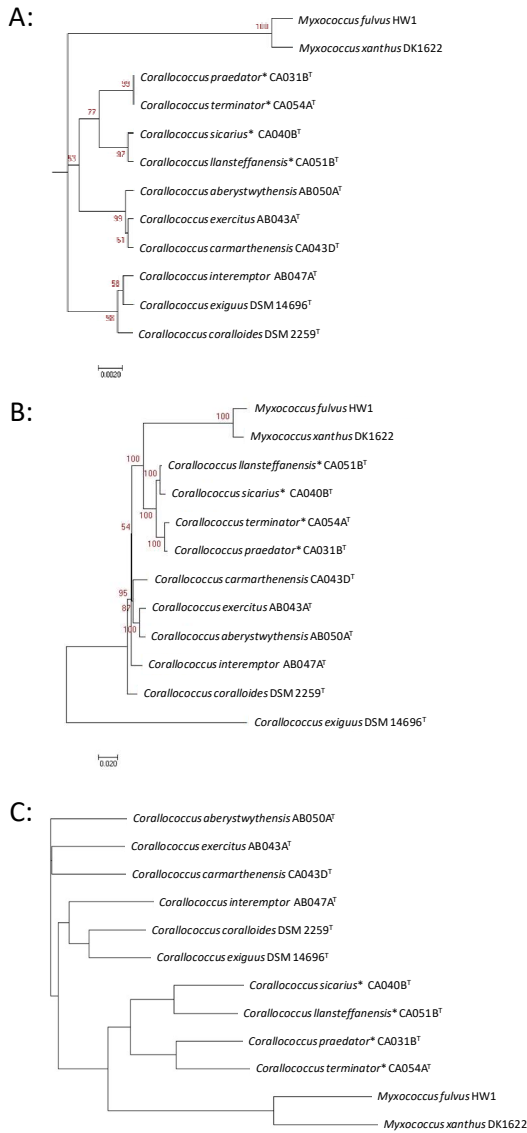
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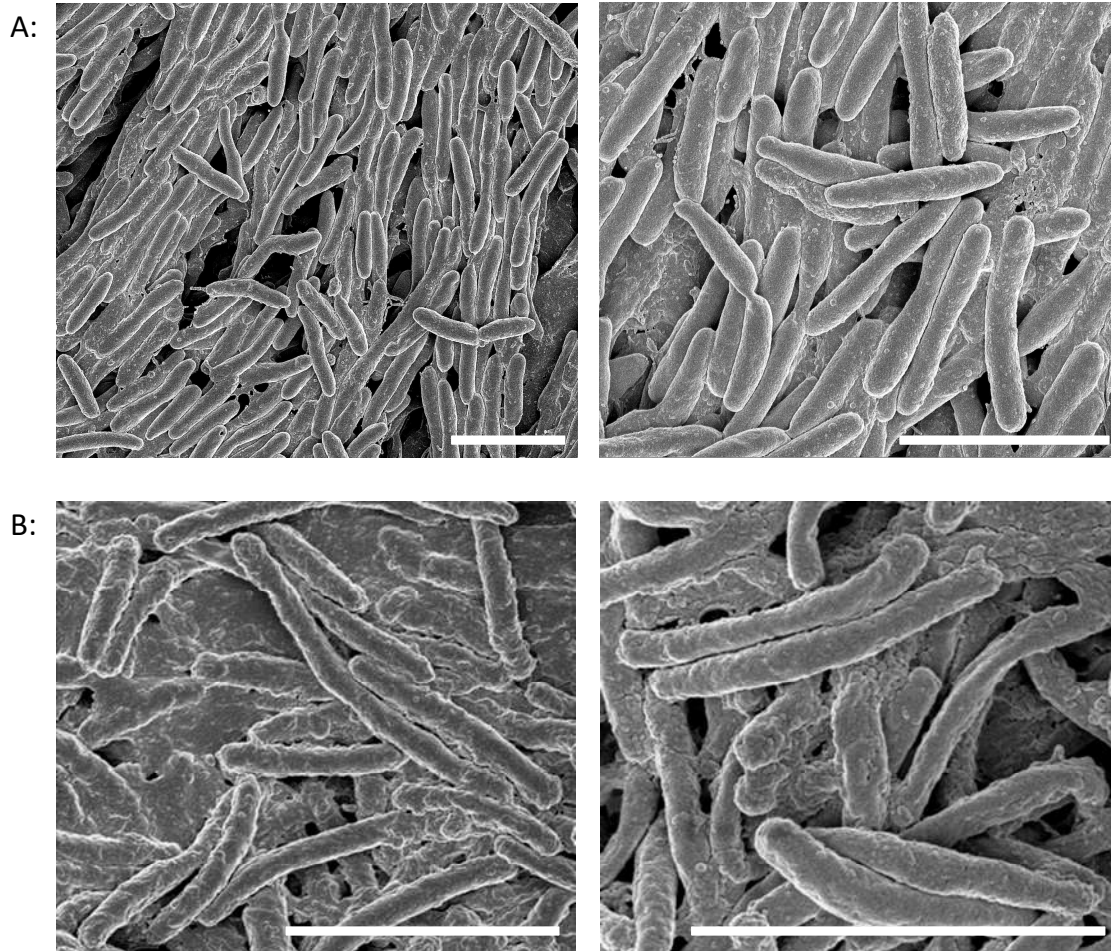
585 **Figures**



586

587

588 **Figure 1.** Phylogenetic trees of *Corallocooccus* spp. members, with two strains from the sister
 589 genus *Myxococcus* for comparison. Strains indicated with * belong to Group B while the
 590 others belong to Group A. A: Neighbour-joining 16S rRNA sequence tree. B: Maximum
 591 likelihood Amphora tree based on the sequence of 31 conserved genes. C: Neighbour-
 592 joining tree constructed using ANI values.



593

594

595 **Figure 2.** Scanning electron micrographs of *Corallococcus* spp. A: CA051B cells (*C.*
596 *llansteffanensis*). B: AB043A cells (*C. exercitus*). Bars are 4 μ m long.

597

598

599 **Tables**

600

dDDH \ ANI	DSM 14696 ^T	DSM 2259 ^T	AB047A	AB050A	CA043D	AB043A	CA031B*	CA054A*	CA040B*	CA051B*
DSM 14696 ^T	100	94	92	91	92	92	87	86	86	87
DSM 2259 ^T	34	100	92	91	91	92	86	85	86	86
AB047A	44	46	100	90	90	90	85	84	85	85
AB050A	44	44	43	100	91	91	84	84	85	85
CA043D	44	44	42	48	100	91	84	84	86	85
AB043A	43	44	43	47	48	100	84	84	85	85
CA031B*	30	31	30	31	31	32	100	91	88	87
CA054A*	30	30	30	30	31	31	50	100	88	87
CA040B*	30	30	30	31	31	32	36	35	100	92
CA051B*	31	31	31	32	32	33	37	35	50	100

601

602 **Table 1.** ANI and dDDH values for pair-wise comparisons between the eight candidate
603 strains, *C. exiguus* DSM 14696^T and *C. coralloides* DSM 2259^T. ANI values are shown above
604 the diagonal and dDDH values below the diagonal. ANI values above 90% and dDDH values
605 above 40% are shaded grey. Strains indicated with * belong to phylogenetic Group B while
606 the others belong to Group A.

607

608

Table 2. Growth characteristics of *Corallococcus* spp. Rate of growth is indicated as ‘-’ (no growth), ‘+’ (slow), ‘++’ (moderate) or ‘+++’ (fast). Temperature-dependence was tested at pH 7.8, while pH-dependence was tested at 30 °C.

	AB043A	AB047A	AB050A	CA031B	CA040B	CA043D	CA051B	CA054A	DSM 2259 ^T	DSM 14696 ^T
30 °C	++	++	+	+	++	+++	++	++	++	+++
35 °C	++	+	-	-	-	++	+	-	+	+
37 °C	-	-	-	-	-	-	-	-	-	-
40 °C	-	-	-	-	-	-	-	-	-	-
pH 5.0	+	+	-	-	-	+	-	-	-	+
pH 6.0	++	+	-	+	+	+	+	+	++	++
pH 7.0	+++	++	+	+	++	+++	++	++	++	+++
pH 7.8	++	++	+	+	++	+++	++	++	++	+++
pH 8.0	++	++	-	-	++	+++	++	++	+++	+++
pH 9.0	++	++	-	-	++	+++	++	++	+++	+

Table 3. Metabolic activity of *Corallococcus* spp. Activity is either ‘-’ (inactive) or ‘+’ (active) as tested by the API method (BioMérieux).

	AB043A	AB047A	AB050A	CA031B	CA040B	CA043D	CA051B	CA054A	DSM 2259 ^T	DSM 14696 ^T
Citrate assimilation	-	-	-	-	-	+	-	-	-	+
Esculin hydrolysis	-	+	-	+	+	+	+	+	+	-
Gelatine hydrolysis	+	+	-	-	+	+	-	+	+	+
Glucose assimilation	+	-	-	-	-	-	-	-	-	-
Indole production	+	+	+	+	-	-	+	+	-	+
Malate assimilation	-	-	-	+	-	-	-	-	-	-
Maltose assimilation	-	-	-	-	-	-	-	+	-	+
Nitrate reduction	-	+	-	-	-	-	-	-	-	-
Phenyl-acetate assimilation	-	-	-	-	-	+	-	-	-	-
<i>o</i> -Nitrophenyl-β-D galactopyranoside hydrolysis	-	+	-	-	+	+	-	+	+	+

Table 4. Fatty acids methyl esters detected in *Corallocooccus* spp. A ‘-’ denotes a relative abundance of less than 1 % of total FAMES, and a ‘+’ denotes presence (at least 1 % of total FAMES) in each strain. FAMES are shaded light grey if they represent more than 5 % of a strain’s FAMES and dark grey if more than 10 %.

	AB043A	AB047A	AB050A	CA031B	CA040B	CA043D	CA051B	CA054A	DSM 2259 ^T	DSM 14696 ^T
Nonanoic acid, methyl ester (C9:0)	-	+	+	+	-	+	+	+	+	+
Decanoic acid, methyl ester (C10:0)	+	+	+	+	-	+	+	+	+	+
Undecanoic acid, methyl ester (C11:0)	+	+	+	+	-	+	+	-	+	+
Dodecanoic acid, methyl ester (C12:0)	-	-	-	-	-	-	+	-	+	+
Tridecanoic acid, methyl ester (C13:0)	-	+	-	-	+	-	+	+	+	+
11-Methyl-dodecanoic acid, methyl ester (iso-tridecanoic) (iso C13:0)	+	+	+	+	+	+	+	+	+	+
Tetradecanoic acid, methyl ester (Myristic) (C14:0)	-	-	+	-	-	+	-	-	-	-
12-Methyl-tridecanoic acid, methyl ester (iso-tetradecanoic) (iso C14:0)	-	-	-	-	-	-	-	-	-	+
Pentadecanoic acid, methyl ester (C15:0)	+	+	+	+	+	+	+	+	+	+
13-Methyl-tetradecanoic acid, methyl ester (iso-C15:0)	+	+	+	+	+	+	+	+	+	+
Hexadecanoic acid, methyl ester (C16:0)	-	-	-	-	-	+	-	-	+	+
14-Methyl-pentadecanoic acid, methyl ester (iso-C16:0)	+	+	-	+	+	+	+	+	+	+
9-Hexadecenoic acid (Z), methyl ester (Palmitoleic) (C16:1)	+	+	+	+	+	+	+	+	+	+
7,10-Hexadecadienoic acid, methyl ester (C16:2)	+	-	-	-	-	-	-	+	+	+
Heptadecanoic acid, methyl ester (C17:0)	+	-	-	-	-	-	-	-	+	+
2-Hexyl-cyclopropanoic acid, methyl ester	-	+	-	+	-	-	+	-	-	+

methyl ester (C17:0)										
15-Methyl-hexadecanoic acid, methyl ester (Isomargaric) (iso-C17:0)	+	+	+	+	+	+	+	+	+	+
Octadecanoic acid, methyl ester (Stearic) (C18:0)	-	-	-	-	-	-	-	-	-	+
9-Octadecenoic acid (Z), methyl ester (Oleic) (C18:1)	-	-	+	-	-	-	+	-	-	-
9,12-Octadecadienoic acid (E,E), methyl ester (C18:2)	-	-	-	-	-	-	-	-	-	-
9,12-Octadecadienoic acid (Z,Z), methyl ester (Linoleic) (C18:2)	-	-	-	-	-	-	+	+	-	+
Octadecatrienoic acid, methyl ester (Linolenic) (C18:3)	+	-	-	-	-	-	+	+	+	+
Tetracosanoic acid, methyl ester (C24:0)	-	-	-	-	-	-	-	-	-	+

Table 5. Predatory activity of *Corallocooccus* spp. Values denote the diameter (mm) of zones of killing against ten prey organisms after seven days' growth at 30 °C.

	AB043A	AB047A	AB050A	CA031B	CA040B	CA043D	CA051B	CA054A	DSM 2259 ^T	DSM 14696 ^T
<i>Escherichia coli</i>	30	30	20	31	25	33	26	23	25	54
<i>Pseudomonas aeruginosa</i>	20	19	22	9	25	30	20	17	30	43
<i>Klebsiella pneumoniae</i>	43	35	31	36	35	45	30	29	6	40
<i>Proteus mirabilis</i>	34	31	29	28	33	35	29	23	19	46
<i>Staphylococcus aureus</i>	20	22	16	23	19	35	25	23	27	62
<i>Staphylococcus epidermidis</i>	26	32	20	38	24	38	28	24	12	48
<i>Staphylococcus saprophyticus</i>	20	23	17	25	22	22	28	16	15	46
<i>Enterococcus faecalis</i>	19	25	17	19	22	29	21	18	15	27
<i>Bacillus subtilis</i>	31	40	24	31	28	43	35	24	6	21
<i>Candida albicans</i>	33	36	28	45	42	44	38	26	6	49

Table 6. Antibiotic resistance profiles of *Corallococcus* spp. A: observed resistance to antibiotics in plate assays ('+' denotes resistant, '-' denotes sensitive). B: Presence of resistance genes in the genome ('+' denotes presence, '-' denotes absence).

A:	AB043A	AB047A	AB050A	CA031B	CA040B	CA043D	CA051B	CA054A	DSM 2259 ^T	DSM 14696 ^T
Amikacin	-	-	-	-	-	-	-	-	-	-
Ampicillin	+	+	+	+	+	+	+	+	+	+
Augmentin	+	+	+	-	-	+	+	-	+	+
Cefotaxime	+	+	+	+	+	-	+	+	+	+
Ceftazidime	+	+	+	+	+	+	+	+	+	+
Ciprofloxacin	-	-	-	-	-	-	-	-	-	-
Ertapenem	+	+	+	+	+	+	+	+	+	+
Gentamicin	+	+	+	+	+	-	+	+	+	+
Imipenem	+	+	+	-	+	+	+	+	+	+
Trimethoprim/Sulfamethoxazole	-	-	-	-	-	-	-	-	-	-
Piperacillin/Tazobactam	+	+	+	+	+	+	+	+	+	+
B:	AB043A	AB047A	AB050A	CA031B	CA040B	CA043D	CA051B	CA054A	DSM 2259 ^T	DSM 14696 ^T
<i>adeF</i>	+	+	+	+	+	+	+	+	+	+
AAC(3)-IIIb	-	-	-	+	+	-	+	-	-	-
<i>msbA</i>	+	-	-	-	-	-	-	-	-	-