

1 **On the ecology of *Acinetobacter baumannii* – jet stream rider and opportunist by nature**

2
3 Gottfried Wilharm^{1,*}, Evelyn Skiebe¹, Andżelina Łopińska^{1,2}, Paul G. Higgins^{3,4}, Kristin Weber¹, Christoph
4 Schaudinn⁵, Christof Neugebauer¹, Katharina Görlitz¹, Gideon Meimers¹, Yana Rizova⁶, Ulrike Blaschke¹,
5 Christine Heider¹, Christiane Cuny¹, Stephan Drewes⁷, Elisa Heuser⁷, Kathrin Jeske⁷, Jens Jacob⁸, Rainer
6 G. Ulrich^{7,9}, Marcin Bochenski^{2,10}, Mariusz Kasprzak^{2,11}, Ewa Burda², Mateusz Ciepliński², Ireneusz
7 Kaługa¹², Łukasz Jankowiak¹³, José I. Aguirre¹⁴, Alejandro López-García¹⁴, Ursula Höfle¹⁵, Zuzanna
8 Jagiello^{16,17}, Marcin Tobółka¹⁶, Bartosz Janic¹⁸, Piotr Zieliński¹⁸, Maciej Kamiński¹⁹, Johannes Frisch²⁰,
9 Joachim Siekiera²¹, Andreas F. Wendel^{22,23}, Paul Brauner²⁴, Udo Jäckel²⁴, Michael Kaatz²⁵, Stefanie
10 Müller²⁶, Antina Lübke-Becker²⁶, Lothar H. Wieler^{27,28}, Johanna von Wachsmann²⁷, Lakshmi Priya
11 Thrukonda²⁷, Mustafa Helal²⁷, Lennard Epping²⁷, Silver A. Wolf²⁷, Torsten Semmler²⁷, and Leszek Jerzak²

13 ¹ Robert Koch Institute, Wernigerode Branch, Burgstr. 37, D-38855 Wernigerode, Germany

14 ² Institute of Biological Sciences, University of Zielona Góra, Prof. Z. Szafrana Street 1, 65-561 Zielona
15 Góra, Poland

16 ³ Institute for Medical Microbiology, Immunology and Hygiene, Faculty of Medicine and University Hospital
17 Cologne, University of Cologne, D-50935 Cologne, Germany

18 ⁴ German Centre for Infection Research (DZIF), Partner site Bonn-Cologne, Germany

19 ⁵ Robert Koch Institute, Seestr. 10, D-13353 Berlin, Germany

20 ⁶ Trepetlika 7, Lozenets, Sofia, Bulgaria

21 ⁷ Institute of Novel and Emerging Infectious Diseases, Friedrich-Loeffler-Institut, Federal Research Institute for
22 Animal Health, Südufer 10, D-17493 Greifswald-Insel Riems, Germany

23 ⁸ Julius Kühn-Institute, Federal Research Centre for Cultivated Plants, Institute for Epidemiology and Pathogen
24 Diagnostics, Rodent Research, Toppeideweg 88, D-48161 Münster, Germany

25 ⁹ German Centre for Infection Research (DZIF), Partner site Hamburg-Lübeck-Borstel-Riems, Germany

26 ¹⁰ EndoNature s.c., Drzonków - Jastrzębia 4 Str., 66-004 Zielona Góra, Poland

27 ¹¹ Institute of Sport, Tourism and Nutrition, University of Zielona Góra, Prof. Z. Szafrana Street 1, 65-561

28 Zielona Góra, Poland

- 29 ¹² EcoLogical Group, Brzozów 19, PL-08–125 Suchożebry, Poland
- 30 ¹³ Institute of Biology, University of Szczecin, Wąska 13, 71-415, Szczecin, Poland
- 31 ¹⁴ Department of Biodiversity, Ecology and Evolution Universidad Complutense de Madrid, Madrid, Spain
- 32 ¹⁵ Health and Biotechnology (SaBio) Research Group, National Wildlife Research Institute, IREC (CSIC-UCLM),
33 Ciudad Real, Spain
- 34 ¹⁶ Department of Zoology, Poznań University of Life Sciences, ul. Wojska Polskiego 71C, 60-625 Poznań, Poland
- 35 ¹⁷ Department of Zoology, Faculty of Sciences, University of Granada, 18071 Granada, Spain
- 36 ¹⁸ Department of Ecology and Vertebrate Zoology, Faculty of Biology and Environmental Protection, University of
37 Łódź, Banacha 12/16, 90-237, Łódź, Poland
- 38 ¹⁹ Department of Biodiversity Studies and Bioeducation, Faculty of Biology and Environmental Protection,
39 University of Lodz, Banacha 1/3, 90-237, Lodz, Poland
- 40 ²⁰ Museum für Naturkunde, Invalidenstraße 43, 10115 Berlin, Germany
- 41 ²¹ Ul. Rzeczna 17, 47-300 Żywoćice, Poland
- 42 ²² Institute of Hygiene, Cologne Merheim Medical Center, University Hospital of Witten/Herdecke, Cologne,
43 Germany
- 44 ²³ Division of Hygiene and Environmental Medicine, Department of Human Medicine, Faculty of Health,
45 Witten/Herdecke University, Witten, Germany
- 46 ²⁴ Unit for Biological Agents, Federal Institute for Occupational Safety and Health, Nöldnerstr. 40-42, 10317 Berlin,
47 Germany
- 48 ²⁵ Vogelschutzwarte Storchenhof Loburg e.V, Chausseestr. 18, Loburg, D-39279 Germany
- 49 ²⁶ Institute of Microbiology and Epizootics, Veterinary Faculty, Freie Universität Berlin, Robert-von-Ostertag Str. 7-
50 13, 14163 Berlin, Germany
- 51 ²⁷ Robert Koch Institute, Nordufer 20, D-13353 Berlin, Germany
- 52 ²⁸ Digital Global Public Health, Digital Health Cluster, Hasso Plattner Institute, University Potsdam, Potsdam,
53 Germany
- 54 *Correspondence to: Gottfried Wilharm, Robert Koch-Institut, Projektgruppe P2, Bereich Wernigerode, Burgstr. 37,
55 D-38855 Wernigerode, Germany, e-mail: wilharm@rki.de, Phone: +49 30 18754 4282; Fax: +49 30 18754 4207
- 56

57 **RUNNING TITLE:** *Acinetobacter baumannii* ecology

58

ORIGINALITY - SIGNIFICANCE

59

60 The ecology of the nosocomial pathogen *Acinetobacter baumannii* remains poorly understood
61 outside the hospital. Here, we present the most comprehensive study on its environmental biology
62 to date, after having collected more than 1,450 independent isolates of which around 400 were
63 whole genome-sequenced. This study more than doubles the size of the pan-genome of the species,
64 illustrating both the diversity of our collection and the bias of previous work, but also the bottleneck
65 for the establishment of lineages within the hospital environment. We reached isolation rates of
66 about 30% both in white stork (*Ciconia ciconia*) nestlings and in soil samples when considering
67 for sampling all preferences of *A. baumannii* we uncovered. Thus, it is now possible to study the
68 ecology and evolution of *A. baumannii* in nature at an unprecedented temporal and spatial
69 resolution. We describe the worldwide spread of *A. baumannii* lineages in nature as an ancient
70 phenomenon that even surpasses that of human-associated bacteria in magnitude. This is likely due
71 to airborne spread, putatively facilitated by association with fungal spores. We propose that
72 *A. baumannii* is an opportunist by nature, using airborne patrolling to rapidly enter new suitable
73 habitats consisting of organic matter in early stages of decomposition. Our collective data suggest
74 that *A. baumannii*, early after its speciation, went through massive radiation during the Neolithic,
75 likely due to deforestation, settlement and farming producing numerous favorable habitats. Their
76 natural lifestyle, which requires rapid adaptability to various habitats as well as tolerance to
77 desiccation, radiation and antibiotic stress, perfectly predispose these opportunistic pathogens to
78 establish within the hospital setting. Comparison of genomes from environmental and clinical
79 isolates will now enable studies of the adaptive evolution of environmental bacteria towards
80 multidrug-resistant opportunistic pathogens.

81

82

SUMMARY

83

84 The natural reservoirs of the nosocomial pathogen *Acinetobacter baumannii* are not well defined.

85 We previously identified white storks as a model system to study the ecology of *A. baumannii*.

86 Having screened more than 1,300 white stork nestlings over a period of six years across different

87 regions of Poland and Germany (overall isolation rate of ~29.5%), including food chain analyses

88 and environmental samplings, we come up with a detailed picture of the dynamics and diversity of

89 *A. baumannii* in their natural habitats. Adult storks, rather than being stably colonized with strains

90 of *A. baumannii* which are successively transferred to their offspring, instead initially encounter

91 these bacteria while foraging. Among their common food sources, consisting of earthworms, small

92 mammals, and insects, we identified earthworms as a potential source of *A. baumannii*, but more

93 so the associated soil as well as plant roots. Through this, hotspot soil and compost habitats were

94 identified which enable population dynamics to be studied over the course of the year. We

95 demonstrate that sterilized plant material is rapidly colonized by airborne *A. baumannii* suggesting

96 they patrol to search for novel habitats, being opportunist by nature. The prevalence of

97 *A. baumannii* exhibited a strong seasonality and peaked during summer. The strains we collected

98 in Poland and Germany represent more than 50% of the worldwide known diversity in terms of the

99 intrinsic OXA-51-like β -lactamase. A set of ~400 genomes was determined and compared to a

100 diverse set of publicly available genomes. Our pan-genome estimate of the species (~51,000 unique

101 genes) more than doubles the amount proposed by previous studies. Core-genome based

102 phylogenetic analyses illustrated numerous links between wildlife isolates and hospital strains,

103 including ancient as well as recent intercontinental transfer. Our data further suggest massive

104 radiation within the species early after its emergence, matching with human activity during the

105 Neolithic. Deforestation in particular seemed to set the stage for this bloom as we found that forests

106 do not provide conducive conditions for the proliferation of *A. baumannii*. In contrast, wet and
107 nutrient-rich soil alongside rivers sampled during the summer can yield an isolation rate of ~30%.
108 Linking published work on the interaction between *A. baumannii* and fungi and on aspergillosis as
109 a major cause of mortality in white stork nestlings to our findings, we hypothesized that fungi and
110 *A. baumannii* share a long history of coevolution. Interaction studies revealed the capability of
111 *A. baumannii* to adhere to fungal spores and to suppress spore germination. Taken together, the
112 intrinsic resistance endowment and potential to acquire antibiotic resistance can be explained by
113 coevolution with antibiotic-producing fungi and other microorganisms within soil, and resistance
114 to desiccation stress and radiation can be interpreted in the light of intercontinental hitchhiking
115 through fungal spores.

116

117

KEYWORDS

118 *Acinetobacter baumannii* – nosocomial pathogen – antibiotic resistance – *bla*_{OXA-51-like} – whole
119 genome sequencing – white stork – *Ciconia ciconia* – phylogenomics – pan-genome – ecology –
120 compost – soil – forest – seasonality – evolution – Neolithic – airborne – fungi

121

122

INTRODUCTION

123

124 The Gram-negative *Acinetobacter baumannii* is notorious for its potential to act as an opportunistic
125 pathogen in hospitals, facilitated by an exceptional resistance to desiccation stress and intrinsic as
126 well as acquired resistance to antibiotics and disinfectants. The genus *Acinetobacter* currently
127 comprises of around 100 described or tentative species (80, 83), the majority of which consist of
128 environmental species, or commensals of human and animals that rarely cause any disease. Some
129 species like *A. lwoffii* and *A. johnsonii*, which are regularly found on human skin, mucosa and

130 within the gut of humans and animals, appear to play an essential role in the development of
131 immune tolerance (29, 37, 98, 99). In contrast, the species most frequently involved in hospital
132 infections, e.g. *A. baumannii*, *A. pittii*, *A. nosocomialis*, and *A. seifertii* do not represent
133 commensals of humans and animals, and their natural habitats are still poorly described (9, 81,
134 102). Although the zoonotic potential of *A. baumannii* is evident from previous work (25, 56, 68,
135 95, 129), the pathogen is not generally accepted as zoonotic, e.g. not listed as zoonotic pathogen
136 by public health agencies such as the Centers for Disease Control and Prevention (CDC), Public
137 Health England (PHE) or the European Centre for Disease Prevention and Control (ECDC)
138 (<https://www.cdc.gov/media/releases/2019/s0506-zoonotic-diseases-shared.html>;
139 <https://www.gov.uk/government/publications/list-of-zoonotic-diseases/list-of-zoonotic-diseases>;
140 <https://www.ecdc.europa.eu/sites/default/files/documents/j-efsa-2021-6971.pdf>). As a hallmark,
141 the killing of more than 400 individuals of a flock of sheep by a multidrug-resistant (MDR) and
142 hypervirulent strain related to international clone 2 (IC2) illustrates the threat of the bacterium
143 shuttling between human and animal host systems (63). The relevancy to One-Health is further
144 underlined by the reservoir of antibiotic resistance genes found in environmental *Acinetobacter*
145 spp., as well as other bacteria, that can be mobilized into pathogenic *Acinetobacter* spp. via
146 horizontal gene transfer (33, 41, 133). Moreover, the release of MDR *A. baumannii* from
147 wastewater into the environment has been well-described (42, 51).

148 Here, starting from the association of *A. baumannii* with white stork nestlings as recently
149 described (129), we intended to unravel the ecology of these bacteria in their natural habitats.

150

151

152

RESULTS

153

154

Update on the prevalence of *A. baumannii* in white stork nestlings. Previously, we had

155

presented data from 661 white stork nestlings sampled between 2013 and 2016 in Poland which

156

were found to be colonized with *A. baumannii* in the choana region at an average rate of 25% (129).

157

We continued the systematic study of this environment and, based on 1,319 white stork nestlings

158

sampled between 2013 and 2018 across multiple regions of Poland, the average colonization rate

159

was identified as 29.5% (Fig. 1; Suppl. Table S1). White stork nestlings were also sampled on a

160

smaller scale in Germany in 2015 and the positive rate of choana samples reached 34.5% (n=29).

161

Choana samplings in Spain near Ciudad Real in 2015 revealed no positives from 57 white stork

162

nestlings, but a positive rate of 7.8% (n=64) was detected among white stork nestlings sampled in

163

2019 near Madrid (Suppl. Table S1). Interestingly, this included for the first time the isolation of

164

A. nosocomialis (n=2) from white stork samples, indicating differences in the ecology of bacteria

165

and/or storks in Spain compared to Poland and Germany.

166

Rectal sampling of white stork nestlings was conducted on 747 individuals in different

167

regions of Poland throughout the study period and revealed an overall positive rate of 8%, however

168

with great variability depending on the region and year of sampling (Suppl. Table S1). Rectal

169

sampling of 64 white stork nestlings in Spain in 2019 yielded no *A. baumannii* isolates. Thus,

170

choana sampling yielded higher isolation rates of *A. baumannii* compared to rectal sampling.

171

Notably, colonization of white stork nestlings by *A. baumannii* was apparently not

172

associated with increased mortality of the chicks. However, significantly increased white blood

173

cell counts in colonized nestlings argue for an infection by *A. baumannii* rather than mere

174

colonization (Suppl. Table S2).

175 **Pellets from white storks.** We had previously described that white stork spit pellets,
176 consisting of indigestible remains of their food, are occasionally contaminated with *A. baumannii*
177 and might therefore be of interest for studying the ecology of both bacteria and storks (129). We
178 collected pellets from selected nests in Loburg and neighbouring villages (Germany/state of
179 Saxony-Anhalt) during March to August throughout the years 2015 and 2016. Interestingly, pellet
180 samples proved positive for *A. baumannii* not earlier than the end of May in 2015 and the end of
181 April in 2016, respectively (Suppl. Fig. S1). In 2015, positive samples were identified until
182 migratory departure of the storks in August, with an overall rate of 14.8% positive pellets (13 out
183 of 88), while in 2016 only a few positive samples were found from end of April until June (overall
184 6.9% positive pellets, 6 out of 87). Sporadically collected egg shells and feathers were also a source
185 of *A. baumannii* in few cases, and a stork chick found dead was also sampled positive in 2016.
186 Pellets collected from stork colonies in Spain during the winter season of 2015 were negative
187 irrespective of their particular feeding grounds (landfills or nature, Suppl. Fig. S2). Overall, our
188 data suggest that white storks arriving from their wintering grounds do not appear to be stably
189 colonized by *A. baumannii*. Rather, they seem to acquire these bacteria after arrival in the summer
190 quarters depending on the progression of the season, likely via the food chain.

191 It is worth mentioning, that pH values in pellets contaminated with *A. baumannii* were
192 found to be as low as pH 2 in some cases and it was proven that the bacteria were not only localized
193 at the surface of the pellets but also inside (Suppl. Fig. S3). Consequently, although under
194 laboratory conditions *A. baumannii* cannot thrive at pH 2, it can survive such harsh conditions in a
195 natural setting.

196 **Diversity of strains in individual nests.** To challenge our hypothesis on an only transient
197 carriage/colonization of parental white storks with *A. baumannii* we analyzed the diversity of
198 strains isolated from nestlings within individual nests. As a proxy of diversity, we made use of the

199 intrinsic *bla*_{OXA-51-like} gene of *A. baumannii* encoding the class D oxacillinase OXA-51, the protein
200 variants of which are indexed and previously proven useful as phylogenetic marker (95, 121, 129,
201 135). We sequenced the *bla*_{OXA-51-like} gene of all isolates collected from white stork nestlings within
202 a single year in a selected region of Poland and visualized the diversity on a map (Fig. 2). The
203 diversity found within individual nests was striking, with up to 5 nestlings each carrying a
204 distinguishable strain. These findings are inconsistent with a vertical transmission from stably
205 colonized parental storks and support our hypothesis of a transient colonization/carriage via food
206 intake from a diverse *A. baumannii* population.

207 **Tracing the food sources.** The predominant prey of white storks consists of small
208 vertebrates, especially rodents and shrews, as well as arthropods and earthworms (11, 58). In line
209 with the literature, the dominant contribution of rodents and arthropods to the diet of white storks
210 could be directly estimated from pellets of white storks collected in Poland and Germany (Suppl.
211 Fig. 4), although analysis of the remains of earthworms from pellets, while possible (87), is time-
212 consuming. To assess the potential role of beetles and other insects as sources of *A. baumannii*, we
213 compared the content of pellets tested positive for *A. baumannii* with that of pellets tested negative
214 and found no difference in the fraction of insect matter (Suppl. Fig. S5). Moreover, dominant
215 arthropods found in pellets such as the ground beetles *Zabrus tenebrioides* and *Pterostichus*
216 *melanarius* (Suppl. Fig. 6) collected from nature, albeit at low numbers (n=13), were also found
217 negative for *A. baumannii*. We also had the opportunity to sample grasshoppers collected in great
218 quantities by an individual, deceased white stork, which was dissected and found gorged with
219 grasshoppers, however all of the swallowed grasshoppers (>50) tested negative for *A. baumannii*.
220 Moreover, pellets from Spanish storks, containing high amounts of crab and grasshopper remains
221 (Suppl. Fig. S2), also tested negative. Altogether, we found no evidence of a contribution of
222 arthropods captured by white storks to the acquisition of *A. baumannii*.

223 Next, we examined the potential role of rodents and shrews as a source of *A. baumannii*.
224 We collected cat-captured rodents and shrews throughout Germany (states of Saxony-Anhalt,
225 Hesse and Thuringia) in the period from 2014 to 2017 and took samples from the trachea and
226 rectum. We found an average colonization rate of 2% for rodents (n=154) and 4.7% for shrews
227 (n=64). Interestingly, all individuals colonized with *A. baumannii* were captured between August
228 and September (Suppl. Fig. S7). Next, we sampled wild, captive and laboratory rats (*Rattus*
229 *norvegicus*) from Germany (75, 94, 109), as well as other rodents of the genera *Microtus*, *Myodes*,
230 and *Apodemus* captured in Germany (48, 49) in the period 2007 to 2017. No rats and other rodents
231 were found positive (n_{rats}=491 and n_{other rodents}=532).

232 Earthworms were collected in Germany in the state of Saxony-Anhalt between August 2016
233 and September 2020. Out of 618 individual earthworms in total, we isolated *A. baumannii* from 22
234 earthworms (3.6%) provisionally assigned to the genera *Lumbricus*, *Octolasion*, *Dendrobaena* and
235 *Eisenia* (Suppl. Tab. 1). Of these positive samples, 19 were collected from May to September and
236 only three isolates dated from March, April and November, respectively (1% positive of n=75
237 earthworms collected between October 21st and March 21st). The overall positive rate of *A.*
238 *baumannii* isolated from garden compost earthworms collected in Wernigerode (Germany) was
239 4.2% (14/331), and 4.3% (4/94) for a specific site at the bank of the river Holtemme (Germany),
240 where we had recently also isolated *A. nosocomialis* from soil (128).

241 **Other birds and their prey.** We reasoned that studying other birds with an overlapping
242 prey spectrum compared to white storks could help to indicate specificities of the relationship to
243 *A. baumannii*. Consequently, we collected pellets, feathers and egg shells from a breeding colony
244 of grey heron (*Ardea cinerea*) in Germany. With the exception of one egg shell sample collected
245 in June from which we could isolate *A. baumannii* (Suppl. Fig. S8), all samples (n=35) were
246 negative. The detailed analysis of the pellets indicated their diet to consist of a significant portion

247 of small mammals and insects (Suppl. Fig. S8). Further, we collected pellets (n=101) from kestrel
248 (*Falco tinnunculus*) between March and October 2015 and 2016, and found three isolates (3%) of
249 *A. baumannii*, each collected between August and September (Suppl. Fig. S9). Occasionally
250 discovered owls' pellets (n=6), putatively from *Tyto alba* and *Asio otus*, collected in August 2015,
251 were also positive for *A. baumannii* in two cases. Moreover, we took rectal samples from nestlings
252 of the black stork (*Ciconia nigra*), a species which, in contrast to white stork, is not synanthropic
253 and is preferentially breeding and foraging in forests. Notwithstanding, anthropogenic waste was
254 found in 26% of occupied nests (45). The diet of black stork nestlings in Poland is known to be
255 dominated by fish and amphibians (53). Not a single one of 64 rectal samples collected in Poland
256 from black stork nestlings over a period of four years was found positive for *A. baumannii*. Taken
257 together, grey heron, kestrel and black stork differ significantly from white stork regarding carriage
258 with *A. baumannii*.

259 **Compost, soil, rhizosphere and the forest paradox.** Following up on a possible role of
260 earthworms in the transmission of *A. baumannii* to white storks, we started collecting soil samples.
261 Initially, we selected compost soil which is wet and rich in decomposing material, providing an
262 environment from which earthworms could be easily collected. As we realized early on that
263 compost soil represented an excellent source for *A. baumannii*, we utilized a boring rod to study
264 the profile within one meter depth of the compost (Suppl. Fig. S10). Continued sampling of the
265 soil originating from a single compost across a period of seven months yielded 86 isolates
266 containing no less than 20 different variants of the OXA-51 family (60/91 samples positive, 66%).
267 Concomitant sampling of earthworms within the same compost yielded 10 different variants of
268 OXA-51 from 7/44 (16%) positive earthworms. We observed a remarkable dynamic of isolated
269 lineages and of the depth-dependent colonization over time. The compost, which was continuously
270 used for the deposition of vegetable waste and egg shells during this period, was not permanently

271 colonized throughout all layers and there was a shift of the dominant lineages isolated over time.
272 Continued sampling in subsequent years revealed that isolation rates declined (i) during winter and
273 (ii) within 8-10 weeks after stopping to replenish the compost with fresh material.

274 Due to the anthropogenic influence on the compost and the ambiguity of the origin of
275 *A. baumannii* throughout this setting, we next attempted to identify soil habitats in more pristine
276 environments. Searching for wet habitats rich in decomposing material where earthworms can
277 thrive, we identified a site at the bank of the river Holtemme near Wernigerode, Germany, where
278 we successfully isolated *A. baumannii* from earthworms, soil samples and the rhizosphere of
279 different plants (*Urtica* spp., *Impatiens* spp., different grass species etc.). This site at the river bank
280 with an area of only approx. 0.1 m² turned out to be a “hot spot” for the isolation of *A. baumannii*
281 and yielded 22 isolates within 3 months representing 18 different variants of OXA-51 (Suppl. Fig.
282 S11). Moreover, samples collected at this specific site yielded 10 isolates on a single day, each
283 harbouring a different OXA-51 variant. Strikingly, this site has remained a “hot spot” over the
284 years even though the river bank has been remodeled several times due to flooding. None of the
285 many additional sites we repeatedly sampled over the years along the river Holtemme showed any
286 comparably high isolation rate.

287 Concomitantly, we had collected soil samples from a forest area south of Wernigerode,
288 representing both deciduous and coniferous forests of various compositions at an altitude between
289 300 and 450 m above sea level. Again, we chose wet habitats with decomposing plant material,
290 mostly alongside creeks and ponds, however, of 269 samples only two were positive for
291 *A. baumannii* (0.7%) (Suppl. Fig. S12). To prove the deduced principle that *A. baumannii*
292 preferentially colonize alongside creeks but not within forest areas, we selected a creek not
293 previously sampled which has its source within the forest and which, after leaving the forest, flows
294 through grassland before reaching the first village. We were unable to isolate *A. baumannii* from

295 any sample collected inside or along the edge of the forest although the creek's banks were rich in
296 decomposing material. The first positive sample was instead collected at a distance of approx. 300
297 m to the edge of the woods, but positive samples remained rare until the creek had passed the first
298 village (Suppl. Fig. S13). After passage of this village, we discovered two “hot spots”, which
299 repeatedly collected positive samples (6/12 positive samples (50%) and 7/12 positive samples
300 (58%), respectively). Collectively, forests do not offer soil habitats supportive of *A. baumannii*, not
301 even alongside creeks, whereas *A. baumannii* can thrive alongside creeks and rivers outside of
302 forests even if they are lined with trees. There are “hot spots” of *A. baumannii* where they can occur
303 in striking diversity outside forests.

304 **Diversity in terms of OXA-51 variants collected from Poland and Germany.** Currently,
305 there exist 380 assigned variants of the β -lactamase OXA-51 protein encoded by the intrinsic
306 *bla*_{OXA-51-like} gene of *A. baumannii* ((79) <http://www.bldb.eu/>, accessed October 31st, 2023). Our
307 collection of strains encompasses 209 variants, thus about 55% of the presently known worldwide
308 diversity. Of the 209 variants representing our collection, 125 were previously undescribed variants
309 that were deposited in the course of this study (Suppl. Table S3). Given that some of these OXA-
310 variants have been shown to be useful as indicators of phylogenetic relationships, our findings
311 suggested that our collection might represent a considerable portion of the worldwide known
312 diversity of lineages. To substantiate this hypothesis, we performed extensive sequencing and
313 phylogenomic analyses.

314 **Phylogenomics-based representation of the diversity of our collection.** From our
315 collection of more than 1,450 non-redundant *A. baumannii* isolates collected outside the hospital
316 context (Suppl. Table S1), we chose at least one strain representing each OXA-variant for whole
317 genome sequencing. Further, we selected few OXA-variants for the sequencing of larger sets of
318 representative strains, in order to illustrate the diversity within these supposed lineages (e.g. OXA-

319 104, -106, -126, 343, -374, -378, -431), and in addition, selected several strains representing each
320 of the OXA-variants associated with the international clones 1 to 8 (OXA-51, -64, -65, -66, -68, -
321 69, -71, -90) (135). Moreover, due to the higher diversity of carbapenem-susceptible clinical
322 isolates compared to carbapenem-resistant ones (102), 15 carbapenem-susceptible human clinical
323 isolates from Germany were selected according to their encoding OXA-variant, some of the
324 previously described (126). Finally, the collection was supplemented by a diverse set of 21 isolates
325 covering veterinarian und human clinical isolates from a previous study (77). Altogether, our study
326 provides 401 novel genomes, of which 229 originated from white stork nestling isolates, 77 from
327 soil and plant root samples, 2 from air samples above compost, 59 from diverse animal materials
328 including earthworms, rodents and shrews, pellets from diverse bird species, egg shells, feathers
329 and nesting materials, 7 from veterinarian samples, and 27 from human clinical samples. For
330 comparison to the previously available diversity within the species *A. baumannii*, a generic
331 protocol selected 413 additional genomes available within public databases (Suppl. Table S4).

332 The pan-genome of this collection includes 50,989 unique genes, given a threshold of 90%
333 sequence identity on the protein level (Table 1). The phylogenomic tree based on the core genome
334 set of 1,728 conserved genes representing 1.328 megabasepairs (Mbp) of *A. baumannii* genomic
335 sequences is illustrated in Fig. 3. Especially remarkable is the share of deeply branching lineages,
336 suggesting massive radiation early in evolution of the species. Most of the isolates differ by 18,000
337 to 23,000 single nucleotide polymorphisms (SNPs) between each other (Suppl. Table S5). While
338 only a few OXA-variants represented multiple times in this study are apparently monophyletic,
339 such as OXA-431 or OXA-68, most OXA-variants show phylogenetic clustering (see interactive
340 microreact project at [https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-
341 acinetobacternobaps12dec23](https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-acinetobacternobaps12dec23) and Suppl. Fig. S14). In contrast, few OXA-variants show broad
342 scattering, in particular the prototypic OXA-51 and some other OXA-variants (OXA-65, OXA-69,

343 OXA-71) found associated with international clones (ICs) (135) (Suppl. Fig. S14). Another
344 remarkable observation is that the collection of wildlife and environmental strains from Poland
345 (n=235) and Germany (n=159) respectively, each covers a considerable portion of the worldwide
346 known diversity (Fig. 4), pointing to an efficient mechanism of global spread. Moreover, human,
347 animal and environmental isolates likewise spread all-over the phylogenetic tree (Fig. 5). Of
348 particular interest are the many clades represented by environmental, animal and human clinical
349 isolates, underpinning the relevancy of the One-Health concept in regards to *A. baumannii*. This
350 also includes representatives of international clones, namely IC8 (Suppl. Fig. S15). Additionally,
351 IC4, IC5, IC6 and IC7 are now also represented by at least one isolate from wild animals, livestock
352 or the environment. Distances between human clinical isolates and their related isolates from
353 environmental or wildlife sources cover a broad range, approaching distances of 27 SNPs within
354 the core genome in the case of a human clinical isolate from Canada related to a white stork isolate
355 from Poland (both OXA-64), 35 SNPs between a white stork isolate from Poland and a human
356 clinical isolate from Thailand (both OXA-433), or 48 SNPs between a human clinical isolate from
357 Japan and another white stork isolate from Poland (both OXA-762) (Suppl. Tab. S4-S6). These
358 results called for a molecular clock analysis to allow for temporal placement of the genetic and
359 geographical distances. Accordingly, we performed BEAST analyses (43) on the OXA-126 clade
360 (n=34), revealing a mutation rate of 1.1345×10^{-6} ($\pm 3.2 \times 10^{-7}$) per site per year corresponding
361 to approx. 1.5 SNPs per year within the core genome (range 1,08-1,93 SNPs per year), slightly
362 lower than the 1.5 substitutions per site per year reported for IC1 (43) (Suppl. Tab. S7). The most
363 distant isolates within the OXA-126 clade, 13-291-1C and 19-Pos71-1, differ by 12,354 SNPs
364 corresponding to 8,236 years (range ~6,400-11,440 years), pointing to a strong and constant
365 selection pressure stabilizing the OXA-126 variant within the natural context. Applying this
366 molecular clock on the species level, the most recent common ancestor of all members of the

367 species *A. baumannii* likely existed only around 15,000 years ago. Accordingly when applied to
368 the closest relatives found between clinical and environmental/wildlife isolates in our study, those
369 intercontinental pairs of isolates mentioned above share their most recent common ancestor only
370 18-32 years before present. Further relationships of particular interest are listed in Suppl. Table S6.

371 **Natural endowment with resistance genes and IS elements.** Altogether, intercontinental
372 spread between North America, Europe and Asia within a few years cannot be explained by the
373 migratory activity of white storks which migrate between Europe and Africa. Rather, human
374 activity, or natural mechanisms of airborne spread, need to be considered. Hence, we analyzed the
375 genomes regarding their endowment with antibiotic resistance genes and insertion sequences (IS
376 elements) as indicators of anthropogenic selection pressure (Suppl. Tab. S4; Suppl. Fig. S16-S17).
377 Globally, the newly sequenced isolates harbour an intrinsic *bla*_{OXA-51-like} gene (96% of the
378 collection), a majority of which also harbour the *bla*_{ADC} gene in one of 43 variants. Nickel
379 resistance gene *nreB* and efflux pump gene *amvA* are also highly abundant. Moreover, most isolates
380 also harbour the *ant(3'')-IIa* aminoglycoside and the *abaF* fosfomycin resistance genes, suggesting
381 these also to be part of the intrinsic genomic endowment of the species. Additionally acquired
382 resistance genes are limited to a few isolates, mostly collected with a veterinary or human clinical
383 contexts, or within the context of livestock production. Environmental and wildlife-associated
384 isolates do not harbour these acquired resistance genes known from the clinical isolates indicating
385 the comparably pristine habitats they originate from. Similarly, while IS elements are rarely
386 enriched in environmental and wildlife-associated isolates, clinically related strains harbour an
387 increased amount of IS elements (Suppl. Table S4, Suppl. Fig. S17). Moreover, few of our
388 environmental or wild animal isolates harbored an interrupted *comM* gene, a configuration
389 typically found in multidrug-resistant lineages firmly established in the hospital (36). Altogether,

390 this suggests that our environmental and wildlife-associated isolates show little signs of
391 anthropogenic selection pressure and indeed originate from pristine environments.

392 **Colonization of compost material and linkages to the fungal world.** As our
393 phylogenomic analyses suggested global spread of clonal lineages long before globalization of
394 modern times, we considered various modes of dispersion independent of human activity. Our
395 samplings in garden compost suggest that colonization of *A. baumannii* is associated with
396 decomposition of fresh plant material, as *A. baumannii* vanishes after the feed of the compost is
397 stopped. This points to attraction of *A. baumannii* throughout the early steps of decomposition,
398 during which fungi are key players. We thus reasoned that *A. baumannii* might start colonization
399 together with fungal spores that could serve as a vehicle for local as well as global spread of *A.*
400 *baumannii*. To prove an airborne spread of *A. baumannii* in a local setting we mounted open tubes
401 in a distance of 50 cm above an active compost with the opening positioned downwards or the tube
402 positioned vertically for 24 hours. Then the tubes were closed, transported to the laboratory, filled
403 with liquid medium and processed to cultivate *A. baumannii*. As this *ad hoc* setting instantly
404 yielded several isolates of *A. baumannii*, we next designed experiments to study the colonization
405 of sterilized fresh plant material deposited in the garden. The autoclaved plant material was
406 deposited either directly in the garden in a distance of 5 to 10 m from the compost, or it was
407 deposited in a sterilized plastic bag either open top and shielded from the soil or shielded from the
408 top and accessible from the soil. We found that every setting was colonized within 2-3 weeks,
409 indicating that colonization can occur not only via soil contact but also via the air.

410 Next, we tested if *A. baumannii* is capable of attaching to fungal spores using *Aspergillus*
411 spp., which are known to play a key role during the first steps of plant decomposition and dominate
412 within the compost setting (38). We incubated spores from different *Aspergillus* spp. isolates with
413 different strains of *A. baumannii* and observed a marked adherence of the bacteria to fungal spores

414 (Fig. 6). Similarly, adherence to spores from different *Penicillium* spp. isolates was observed.
415 Interestingly, adherence was not an *ad hoc* phenomenon but required 2 to 3 hours of incubation to
416 manifest and resulted in an inhibition of spore germination, a process that typically became
417 observable after 5-6 hours of incubation in our setting. Taken together, these experiments
418 demonstrate that *A. baumannii* has the capacity to interact with fungal spores and to colonize new
419 habitats via the air.

420 **The “where” and “when” of sampling.** Finally, we challenged our current model of the
421 prevalence of *A. baumannii* in natural habitats. We chose to collect samples during late summer
422 when positive rates at our hotspot sites peaked. We collected 20 samples from river banks within
423 forests and 20 samples from river banks outside of forests across the Harz district, Germany. For
424 both groups we chose sites we had never sampled previously and with indicators of nutrient-rich
425 soil, such as deposition of decomposing plant material and growth of nettles (*Urtica* spp.),
426 *Impatiens* spp. or *Aegopodium podagraria*. While 1 out of 20 (5%) forest samples was positive for
427 *A. baumannii*, 6 out of 20 (30%) samples were positive from river banks outside of forests. The
428 positive rate of 30% in selected soil samples thus is in the same range as that yielded from choana
429 sampling of white stork nestlings.

430

DISCUSSION

431

432 Here, we present the most comprehensive study on the ecology of *A. baumannii* to date.
433 Today, representatives of this species can be isolated from specific natural habitats at an
434 unprecedented scale, and we hope that this will stimulate the scientific community to collect and
435 characterize *A. baumannii* from natural habitats worldwide. Although our sample setting,
436 essentially restricted to samples from Poland and Germany, represents a significant portion of the
437 worldwide known diversity, evidently, our picture remains incomplete. In particular, we have not
438 yet collected representatives of the international clones IC1 - IC3 from natural environments,
439 including the clinically dominant IC2, suggesting that their relatives either prefer completely
440 different habitats or are geographically restricted. We focus the discussion on the interpretation of
441 our data in light of understanding the evolution behind this species and in particular adaptation to
442 the hospital environment.

443 **Comparison of the *A. baumannii* population structure to *Pseudomonas aeruginosa*.** It
444 is interesting to compare the population structure of *A. baumannii* with that of another
445 cosmopolitan opportunistic pathogen within the order of *Pseudomonadales*, *Pseudomonas*
446 *aeruginosa*. Likewise, *A. baumannii* and *P. aeruginosa* are found worldwide across various
447 habitats, including soil. Similarly, a local study setting also captured a significant fraction of the
448 global diversity within the species *P. aeruginosa* (93, 100). Possibly, the two species share similar
449 modes of global spread and future studies should compare their velocities of spread to challenge
450 this hypothesis (67).

451 However, in striking contrast to *A. baumannii*, the global diversity of *P. aeruginosa* consists
452 of only five groups, two of which dominate the scene both as human opportunistic pathogens and
453 environmental bacteria (27). In *P. aeruginosa*, the dominant clones characterized within the context

454 of human infection are also found in the environment, albeit at a skewed abundance (127), while
455 the dominant clone of *A. baumannii* in hospitals (IC2) has not been isolated from pristine
456 environments in our study or elsewhere. It is also interesting to note that the pan-genome of
457 *A. baumannii* determined in our study is in the same order of magnitude as that of *P. aeruginosa*
458 (50,989 versus 54,272), while the core gene sets consist of 1,728 and 665 genes, respectively, and
459 the average genome size of *A. baumannii* is also considerably smaller compared to that of
460 *P. aeruginosa* (4 Mbp versus 6-7 Mbp) (27).

461 Altogether, these findings not only indicate a significantly different evolution of both
462 species in the environment but also differently selecting bottlenecks for entry and establishment of
463 environmental isolates in the hospital setting.

464 **Evidence for interrelatedness of *A. baumannii* life cycle with the fungal world.** The
465 linkages between the worlds of fungi and *A. baumannii* found in the literature are manifold and
466 require a review for full appraisal. To justify our claims, we will discuss selected aspects and
467 provide a more detailed list of published evidence in the Supplements (Suppl. Table S8). Tan et al.
468 (116) found airway colonization with *Candida* spp. yeasts to be an independent risk factor for
469 *A. baumannii* ventilator-associated pneumonia. This finding was consolidated in an infection
470 model of the rat lung (115). In a pioneering paper, Smith et al. (108) described the synergistic
471 interaction between the yeast *Saccharomyces cerevisiae* and *A. baumannii*, with ethanol produced
472 by the fungi stimulating the virulence of *A. baumannii* in the nematode host *Caenorhabditis*
473 *elegans*. Seminal work by Peleg et al. (90, 91) applying a co-infection model of *A. baumannii*
474 together with the yeast *Candida albicans* in *C. elegans* revealed a complex interplay between
475 bacteria and fungi. While *A. baumannii* suppressed filamentation of the fungus, the latter arranged
476 counteroffensive via the quorum sensing molecule farnesol. Farnesol was later demonstrated to
477 disrupt cell membrane integrity in *A. baumannii* and to impair biofilm formation and motility (59).

478 The virulence potential of *A. baumannii* against *C. albicans* has been further characterized by
479 others (30, 74, 78). Moreover, several isolates of *A. baumannii* have been described to suppress
480 phytopathogenic fungi (64, 113). The microbiome analysis of household dust revealed a significant
481 positive correlation of *Acinetobacter* with several fungal genera such as *Alternaria*, *Aspergillus*
482 and *Fusarium* (20). Further, it is worthwhile to note that 1,3-diaminopropane, the dominant
483 polyamine of *Acinetobacter* with a known role in virulence of *A. baumannii* (107), upregulates
484 secondary metabolism in fungi such as *Aspergillus* and *Penicillium*, including the biosynthesis of
485 β -lactams (73, 139). In this light, we speculate that as a result of co-evolution with fungi producing
486 differing β -lactam variants, a multitude of OXA-51 variants have evolved in *A. baumannii*.

487 *Aspergillus* is a major cause of morbidity and mortality in a wide range of birds including
488 specific lineages of poultry (117) and particularly so in white stork nestlings (86). It is important
489 to keep in mind that azole antifungal drugs are not only used in the hospital setting but also in
490 agriculture (15). This may influence the *Aspergillus-Acinetobacter* relationship with a possible
491 impact on the abundance of *A. baumannii*. Consistently, our data indicate that *A. baumannii*
492 prevalence in white stork samples is positively correlated with heterogeneous agricultural use
493 (Suppl. Fig. S18 and Suppl. Material S1).

494 Sporadically, *A. baumannii* infection has been reported following *Aspergillus* infection in
495 humans (69), but metagenomics-based analyses suggest that fungal and bacterial co-infections of
496 the lung are common, with *A. baumannii* being one of the dominant pathogens (138). Concerning
497 our hypothesis that *A. baumannii* could use *Aspergillus* and other fungal spores for hitchhiking, it
498 is important to emphasize that both *Acinetobacter* and *Aspergillus* readily aerosolize (38). In the
499 light of all this groundwork, our findings about the interaction between fungal spores and
500 *A. baumannii* are far from surprising. It is however important to consider these linkages in the
501 context of hygiene and nosocomial infections. For instance, mold growth on moist surfaces, a

502 common problem in tropical regions, may also contribute to the spread of *Acinetobacter* in the
503 hospital. Municipal composting plants should be also assessed carefully (38).

504 **Forest as a ‘no-go’ area for *A. baumannii*.** Our data indicate that forests do not provide
505 supportive habitats for *A. baumannii*. Particularly, we documented low isolation rates from forest
506 soil samples and from samples collected in the vicinity of forests, and we found no association of
507 *A. baumannii* with sylvan black storks. Measured pH values from soils supportive of *A. baumannii*
508 were not significantly different from those of forest soil samples (data not shown). We therefore
509 propose that *A. baumannii* is kept away from forests either via direct inhibition of *A. baumannii* by
510 the fungi of the forests’ mycorrhizae or via suppression of those fungi supportive of *A. baumannii*
511 colonization. In line with the latter hypothesis, fungi of the division *Basidiomycota* for example
512 are known to produce antifungal compounds (61). If the former explanation should hold, forest
513 microbiota should be intensively screened for potential antibiotic producers. Interestingly, a study
514 from China on microbial emission levels depending on land use did not reveal a negative effect of
515 forests on *Acinetobacter* abundance (62). Possibly, the situation in Europe differs from that in
516 China or the general trend for the genus *Acinetobacter* does not represent the situation for
517 *A. baumannii*. In line with the latter explanation, several *Acinetobacter* species such as *A. silvestris*
518 (83) and *A. bohemicus* (60) have been isolated from forests. Although the microbial communities
519 of forest soils are largely defined by pH (52) and dominant tree species (6), we could not observe
520 a correlation of either of the two parameters with the lack of *A. baumannii* in forests (data not
521 shown). It is evident that metagenomics data already available from forest soils need to be
522 evaluated and complemented by new studies specifically involving *A. baumannii* habitats, such as
523 those uncovered within this study.

524 **Early adaptive radiation within the species *A. baumannii* associated with Neolithic?**
525 Our data suggest a massive radiation within the species *A. baumannii* early after its emergence.

526 The average distance of the numerous unrelated lineages within the species is approx. 20,000 SNPs
527 per genome based on our core set of genes (Suppl. Table S5). According to our molecular clock
528 analyses and those of others (Holt et al., 2016), the substitution rates are in the range of 1.13 - 1.5
529 $\times 10^{-6}$ substitutions per site and per year. Based on our core genome alignment, this corresponds to
530 1.5 SNPs per core genome per year. Accordingly, most of the lineages are about 13,000 years apart
531 from each other (range ~10,400-18,500 years). This is in agreement with global warming during
532 the beginning of the Holocene and early Neolithic when human activities started to change the
533 environment producing a plethora of novel types of habitats, especially due to deforestation and
534 later the development of agriculture and livestock farming. In this context, deforestation is of
535 specific importance given the adverse impact of forests on *A. baumannii* as outlined above. In the
536 European Alps, deforestation on small areas due to human activity has been dated back to about
537 10,000 years before present (32). Moreover, livestock farming may have additionally contributed
538 to this radiation, given the association of *A. baumannii* with cattle, sheep, and poultry (56, 63, 129).
539 All in all, our data suggest that human activity during the beginning of the Holocene and early
540 Neolithic was a key driver of the adaptive radiation within the species. This possibly also applies
541 to radiation within the *A. calcoaceticus*-*A. baumannii* complex in the earliest phase of the Neolithic,
542 in line with the close relationship of species within this clade (21).

543 ***A. baumannii* – jet stream rider.** Our local sample settings in Poland and Germany
544 revealed a significant proportion of the worldwide known diversity of *A. baumannii*, with
545 evolutionary distances to hitherto known genomes, mostly of clinical origin, ranging from very
546 ancient to very recent. Thus, our data illustrate a massive global dispersal on the sub-species level
547 since ancient times, which is consistent with the findings of Louca (67) that most prokaryotes are
548 globally spread even at sub-species resolution. However, the velocity of spread even for human-
549 associated prokaryotes exhibiting the highest diffusivity, was determined at only 580 kilometers

550 per 100 years for individual lineages while for terrestrial bacteria it was only 370 km per 100 years.
551 Intercontinental transmission rates of human-associated bacteria on a per-lineage basis were
552 estimated at around 5.5 events per 10^6 years for the most probable transfer between North America
553 and Europe, i.e. one intercontinental transfer event in every ~182,000 years (67). Evidently, the
554 massive intercontinental spread suggested by our data is exceeding estimates for those most
555 transmissible species, namely human-associated ones (67), by far. If modern human activity would
556 account for the spread observed, a strong association of *A. baumannii* with the human microbiota
557 could possibly explain the data, however such an association has been refuted (9). Alternatively, a
558 strong association of *A. baumannii* with global flow of commodity, in particular livestock and meat
559 which can be heavily contaminated with *A. baumannii* (68), might explain the global spread.
560 However, as outlined above, the origin of our environmental and wildlife isolates from pristine
561 environments is evident from their genomic structure. All in all, there is no evidence that the
562 observed global pattern of distribution of environmental *A. baumannii* is caused by human activity.
563 It is further not explainable by migratory patterns of white storks, which do not cross oceans (26).
564 Based on our data and published work, we propose airborne spread as an original strategy of the
565 species and possibly of other members of the genus *Acinetobacter*, likely facilitated by hitchhiking
566 on fungal spores. In the hospital setting and livestock production facilities, airborne spread of
567 *A. baumannii* has been already demonstrated (72, 132). The prerequisites for an effective long-
568 distance atmospheric spread are tolerance to desiccation and radiation, as well as potential for
569 aerosolization. The tolerance of *A. baumannii* to desiccation is well documented (47, 57, 88, 136).
570 Further, resistance to radiation is not only described for *A. radioresistens*, but also for other
571 *Acinetobacter* species, including *A. baumannii* (16). Moreover, *Acinetobacter* spp. are among the
572 dominant airborne bacteria found in bioaerosols (62, 76). The aerosolization behavior of bacteria
573 and fungi from vegetable waste compost has been studied in detail, revealing efficient

574 aerosolization of both *Acinetobacter* and various fungi including *Aspergillus* (38). In line with these
575 findings, *Acinetobacter* is abundant in rainwater (1, 5). What is more, glacier microbiomes show
576 the highest relative abundance of *A. baumannii* and *A. junii* compared to all other potential
577 pathogens (65). Taken together, there is evidence illustrating that *A. baumannii* is well adapted to
578 survive atmospheric long-distance spread. This scenario may apply to other species of the genus
579 *Acinetobacter* but also to other bacteria with linkages to the fungal world such as other members
580 of the *Pseudomonadales* (90).

581 After future increase of studies focusing on environmental, animal and non-MDR isolates
582 and their corresponding genomes from all-over the globe, it should be possible to challenge (67)
583 the “jet stream rider” hypothesis. It would claim that because of jet streams’ west to east streaming
584 and their hemispheric association, spread between e.g. North America and Europe should be more
585 likely than between North and South America. In line with this hypothesis, the diversity of clinical
586 isolates from South America differs significantly from those observed in the northern hemisphere
587 (85), but at present ecological differences cannot be excluded as a reason for this phenomenon.

588 **Seasonality and entry into the hospital environment.** Seasonality of *Acinetobacter*
589 infections with a global peak in summer has been discussed (97). However, seasonality has not
590 been observed for MDR *Acinetobacter* (28), which show a high degree of clonality and are known
591 to be transmitted from patient to patient and from hospital to hospital in contrast to the diverse
592 group of non-MDR *Acinetobacter* (102, 126). Our data on the occurrence of *A. baumannii* in
593 compost and soil samples as well as birds’ pellets and small mammals approve seasonality with a
594 summer peak. In line, association of *A. baumannii* with cattle also exhibits seasonality, peaking
595 between May and August (56). Noteworthy, aerosolization of bacteria and fungi also peaks in
596 summer (131), as discussed above. In conclusion, we provide further evidence that preferentially
597 during the summer season, when *A. baumannii* thrive in natural habitats, novel lineages of *A.*

598 *baumannii* enter the hospital environment worldwide causing increased infection rates with non-
599 MDR appearance.

600 **Pan-genome and potential for further development of the species.** Previous analyses of
601 the pan-genome of the species *A. baumannii* ranged from 16,000-20,000 genes (31, 70, 123). Here,
602 we present a conservative estimate of 50,989 different genes, more than doubling previous
603 appraisals (Table 1). This drastic increase in the size of the pan-genome of the species illustrates
604 the significant bias due to the focus on MDR isolates (the majority of which belong to a few widely
605 disseminated clonal lineages) within the scientific community, but also indicates that compared to
606 the broad diversity of lineages in nature, only few have managed to establish themselves within the
607 hospital environment. Our data set will now facilitate identification of the critical factors of success
608 owned by international clones. Even though a few established lineages dominate, there is a constant
609 invasion of novel lineages into the hospital, particularly in summer. Given the enormous genomic
610 diversity and fluidity illustrated here, combined with the capacity to recombine excessively (34,
611 130), a huge potential is evident for further development including the adaptation to the hospital
612 environment and humans as hosts. This potential must not be underestimated given the recent
613 development of a hypervirulent sub-lineage of IC2 isolated from sheep (63). Note that as
614 *A. baumannii* is apparently a very recent species, with its radiation starting only around 15,000
615 years ago, its adaptation to humans and livestock might be only in its beginnings. Moreover, we
616 also need to consider the potential interspecies transfer of DNA from other nosocomial pathogens
617 (120).

618 ***A. baumannii* – opportunist by nature.** We have demonstrated that sterilized organic
619 matter deposited under the open sky is colonized by *A. baumannii* within 2-3 weeks during
620 summer. Our data suggest that *A. baumannii* is present in various environmental habitats and in the
621 air, albeit at generally low abundance and with marked seasonality. Consequently, almost all

622 humans have already been exposed to *A. baumannii*. However, only few people suffering from
623 predisposing diseases, mostly in tropical regions, face community-acquired infections from
624 *A. baumannii* (18) suggesting a very low virulence potential and/or high infection doses required
625 to establish an infection. It is only in the hospital context that *A. baumannii* becomes a more
626 pronounced issue, even more in intensive care units (ICUs) and in tropical countries. It appears to
627 be the nature of this species to patrol the environment in search of conducive habitats and it is our
628 challenge to protect the most vulnerable from this opportunistic contact.

629 The transient nature of *A. baumannii* occurrence is not only due to seasonality but also due
630 to succession in its habitats. So far there is no evidence of permanent colonization of any habitat
631 with *A. baumannii*. If compost feeding is stopped, *A. baumannii* vanishes. Likewise, the probability
632 of isolating *A. baumannii* from white stork nestlings decreases with the age of the chicks (Suppl.
633 Fig. S19, Suppl. Material S1). Similarly, samples from commercially reared turkey chicks are
634 heavily loaded with *A. baumannii* at the first day of life, but this load vanishes during life (103).
635 Where permanent establishment and local spread is not possible, patrolling in the air appears as an
636 efficient strategy to identify the next opportunity for colonization. Several studies resolved on the
637 level of the genus *Acinetobacter* illustrate the marked position of *Acinetobacter* species at the
638 beginning of a succession. Aging of cattle and chicken manure correlates with a characteristic burst
639 and decline of *Acinetobacter* (17, 84, 92). In line, *Acinetobacter* has been described to dominate
640 the rice paddy rhizosphere after green manure treatment in comparison to winter fallow treatment
641 (137). Taken together, to be in the right place at the right time is the challenge valid for both the
642 bug and the bug hunter.

643 **One-Health perspective.** Given the broad distribution of human clinical isolates, animal
644 and environmental isolates all-over the phylogenetic tree and the linkages between isolates of
645 different sources disclosed, the capability to cause opportunistic infections appears as an ancient

646 skill of the species rather than that of a few recent human-adapted lineages. In line with this,
647 previous studies on avian isolates did not reveal significant differences in virulence compared to
648 human clinical isolates (129). Studies on wastewater discharge and river water indicate spreading
649 of clinical isolates of *A. baumannii* into the environment in Poland and elsewhere (44, 51, 105).
650 However, the IS*Aba1*/*bla*_{OXA-51-like} genetic configuration observed in carbapenem-resistant
651 *A. baumannii* from wastewater and river water in Poland by Hubeny et al. (44) has not been
652 observed in any of our environmental and wildlife isolates indicating their still pristine context.
653 Interestingly, the same is true for the compost setting studied here indicating that the source of
654 compost isolates is from nature rather than from the anthropogenic context. Thus, our sample and
655 data collection can serve to represent the baseline of nativeness to study the evolution of lineages
656 towards adaptation to the hospital environment and multidrug resistance. It will also help to
657 decipher the role of livestock farming as a potential accelerant to the development of some lineages.
658 We emphatically support the call to action recently expressed by others to implement a One-Health
659 perspective on *A. baumannii* (14, 40, 124). This should not only include pet, livestock and wildlife
660 animals as well as environmental sampling, but also genome-based studying of non-MDR clinical
661 isolates as these presumably only recently entered the hospital setting.

662 **Miscellaneous.** Our findings outline that *A. baumannii* can be effectively isolated from wet
663 and nutrient-rich soil alongside waters, which is in line with previous studies (3, 35, 55, 96, 112).
664 The natural resistance endowment of *A. baumannii* indicates evolution in an environment rich in
665 antibiotic producers, such as the soil habitats verified here. Note, however, that also the adaptation
666 to airborne spread is linked to antibiotic resistance. Resistance to UV radiation involves enzymes
667 dedicated to the detoxification of reactive oxygen species (ROS) such as catalases and superoxide
668 dismutases (101, 111), and these enzymes, ROS detoxification and thus redox homeostasis
669 crucially determine deployment of antibiotic activity (2, 23, 39). Moreover, *Aspergillus* spores are

670 coated with antimicrobial peptides (22). Adaptation to this specific niche therefore requires
671 resistance mechanisms, which again may contribute to resistance development of *A. baumannii* in
672 the hospital setting.

673 Stork nests are typically used for several years or even decades with a continuous input of
674 organic matter resulting in soil formation and the settlement of soil organisms as well as plants (10,
675 24). Thus, a stork's nest is the perfect reproduction of a compost-like habitat, so that fungi-*A.*
676 *baumannii* aerosols from the nest should be considered as a potential source of *A. baumannii*
677 colonizing nestlings. In line with this, nest material and egg shells from white storks revealed
678 *A. baumannii* contamination rates of 30-40% (Suppl. Table S1). Future studies should correlate the
679 age of nests with the probability of colonization of nestlings within these environments.

680 A recent study found no *Acinetobacter* in faeces collected from white storks in Spain (46).
681 This is in accordance with the low abundance documented in material from Spanish storks here
682 and more so since the samples for the cited study were collected during winter. Comparing our data
683 on white stork nestlings from Poland and Spain, it is evident that there are significant ecological
684 differences. Of 60 eggs tested in Spain not a single one was positive for *A. baumannii*, while 27
685 out of 68 eggs (40%) tested in Poland (voivodship Greater Poland) were contaminated with
686 *A. baumannii*.

687 Our groundwork now offers the potential to study horizontal gene transfer (HGT) on-site.
688 The diversity found at a specific site reached 20 distinct lineages during a season and up to 10
689 distinct lineages could be isolated from a single sample site on a single day (Suppl. Fig. S11).
690 Extensive HGT was detected between co-colonizing lineages (Suppl. Fig. S20).

691 **Open questions.** Among the most interesting questions is where and how *A. baumannii*
692 survives during the winter season. Given its marked tolerance to desiccation stress, dormancy in
693 dry places might be a simple explanation (57). Alternatively, there might be (micro-)habitats where

694 they are permanently established and from where they spread again at opportunity. Soil-dwelling
695 amoebae should be considered potential hosts (12, 114). Since colonization rates of earthworms
696 were found lower than those of ambient soil we do not consider earthworms as original reservoir
697 although they might contribute to spread. In this regard, it is interesting to note that other bird
698 species partially feeding on earthworms such as the blackbird *Turdus merula* and the European
699 robin *Erithacus rubecula* do not exhibit colonization with *A. baumannii* (66) once again pointing
700 to a very specific ecological setting of the white stork nestling.

701 **Limitations.** Reliable isolation of *A. baumannii* from clinical samples is challenging (71)
702 and so is from environmental material (134). Recently, evidence was presented that CHROMagar
703 Acinetobacter might introduce a bias in isolation so that specific lineages might not be represented
704 (134). Accordingly, alternative enrichment and isolation protocols should be run in parallel to
705 complete our picture. Although we could demonstrate worldwide spread of lineages isolated in
706 Poland and Germany, not all lineages necessarily spread worldwide. Ecology of *A. baumannii* in
707 other climates and geographic regions may differ considerably.

708 **Our current view on the ecology of *A. baumannii*.** In a nutshell, our collective data predict
709 that the primary habitats of *A. baumannii* are associated with soil. Decomposition of plant material
710 by fungi appears to set the stage for proliferation of *A. baumannii*. After the first steps of
711 decomposition they rapidly leave the scene and spread via aerosols, possibly including hitchhiking
712 on fungal spores, to patrol in search of novel conducive habitats. This opportunistic lifestyle
713 requires effective basic equipment to withstand antibiotics produced by fungi and other soil-
714 dwelling organisms, as well as rapid adaptability to novel and changing environments which is
715 facilitated via its notable potential to undergo horizontal gene transfer. More so, the capability to
716 spread via the atmosphere on a global scale co-evolved with adaptation to desiccation and radiation
717 stress. These traits are key to a successful establishment in the hospital environment. The virulence

718 potential of this opportunistic pathogen is low, ancient and currently not specific to humans.
719 However, in terms of evolutionary history the species is still young and has a tremendous potential
720 to further develop into a human and animal pathogen. Key virulence factors such as iron
721 siderophore and capsule biogenesis might have evolved to compete in the soil and to resist
722 phagocytosis by amoebae, respectively. While the mechanism of global dispersal of *A. baumannii*
723 in nature appears to be ancient and not a direct result of human activity, evolution of the species
724 and present-day occurrence is significantly impacted by humans' land use and its influences on
725 habitats favorable to *A. baumannii*.

726

727

EXPERIMENTAL PROCEDURES

728

729 **Sample collection and processing.** Agar gel medium transport swabs (COPAN 108C,
730 HAIN Lifescience, Germany) were used for sampling of white stork nestlings as previously
731 described (129), and COPAN 110C swabs were analogously used to sample dead rodents and
732 shrew (tracheal and rectal sampling). Swabs were immediately transferred to Amies transport
733 medium and stored at 4°C until direct plating on CHROMagar™ Acinetobacter (CHROMagar,
734 France). CHROMagar Acinetobacter was prepared according to the manufacturer's description
735 without addition of the CHROMagar MDR supplement CR102. Pellet and soil samples were
736 preincubated in minimal salt medium supplemented with 0.2% acetate for 5 hours at 37°C as
737 previously described (134) prior to plating on CHROMagar Acinetobacter.

738 **Garden compost.** The compost was fed with plant remains from the garden, vegetable
739 kitchen waste and egg shells which were deposited within a wooden frame (length/width/height:
740 0.8 m/0.8 m/0.5 m), the compost regime was as follows: feeding for twelve months beginning in
741 spring (approx. March), afterwards rest period for 12 months without relocation and without

742 stirring or turning, then spreading into garden, continuous sampling over the complete two years
743 (approx. 10 cm below surface (sampling with metal shovel and disinfection wipes); occasionally,
744 sampling was applied with a boring rod of an effective length of 1 m (Bodenprobentechnik Peters,
745 Germany); samples were taken every 10 cm.

746 **Bacterial species identification.** Species determination of isolates recovered from
747 CHROMagar Acinetobacter was based on PCR detection of *bla*_{OXA-51-like} (122), partial 16S rRNA
748 gene sequencing (125), and partial *rpoB* sequencing using primers Ac696F and Ac1598R as
749 described previously (82). To determine *bla*_{OXA-51-like} variation the coding region was fully
750 sequenced as described previously (135). New OXA-51 variants were assigned and deposited at
751 GenBank (Suppl. Table S3).

752 **Illumina sequencing.** Libraries for Illumina short read sequencing were prepared from 1
753 ng of extracted DNA utilizing the Nextera XT DNA Library Prep Kit according to the
754 manufacturer's recommendations (Illumina Inc., USA). Sequencing was carried out in paired-end
755 (2x300 base pairs) on a MiSeq benchtop instrument. Quality control included the removal of
756 adapter sequences, minor contaminations and short contigs below 700 bp in length through an in-
757 house pipeline. The whole genome shotgun project of 401 isolates has been deposited at GenBank
758 under the BioProject accession PRJNA862736.

759 **Genomic reconstruction and gene-marker analysis.** Short-read DNA fragments were
760 successively utilized to re-construct high-quality genomes of the isolate collection using the *de*
761 *novo* SPAdes assembler (v3.11.1) (7). Re-constructed genomes were then subjected to *in silico*
762 MLST profiling using the mlst tool (v2.23.0) (<https://github.com/tseemann/mlst>) with both the
763 'Oxford' and 'Pasteur' schemas for *A. baumannii*. Novel allele profiles and variants were deposited
764 at PubMLST (<https://pubmlst.org/>). Additional AMR gene profiling was conducted through the
765 AMRFinderPlus pipeline (v3.11.26) (<https://github.com/ncbi/amr>), utilizing the NCBI

766 Antimicrobial Resistance Library for AMR (dated 2023-07-05) with default values of 80% for
767 identity and coverage, respectively. Next, IS element characterization was performed via the
768 ABRicate software (v1.0.1) (<https://github.com/tseemann/abricate>), utilizing a custom database
769 based on the ISfinder collection (106) (dated 2023-07-05) with 90% identity and coverage. Finally,
770 novel *bla*_{ADC} variants and the continuity of the *comM* gene were further investigated through a
771 BLAST-based custom Python script. A total of 32 novel *bla*_{ADC} variants were identified and
772 subsequently submitted to NCBI.

773 **Phylogenetic characterization.** Open reading frames (ORFs) predicted by Prokka (v1.13)
774 (104) were subsequently used as input for Roary (v3.12.0) (89) in order to conduct pan-genome
775 analyses. Computed core genes were subsequently extracted, aligned and concatenated using
776 default settings. The resulting alignment was then utilized to calculate a maximum likelihood-based
777 phylogeny with RAxML (v.8.2.10) (110) using 100 bootstraps under the assumption of the GTR-
778 gamma DNA substitution model. ClonalFrameML (v1.11) (19) was then used to correct for
779 recombination events and phylogenetic groups were identified through Bayesian Analysis of
780 Population Structure (BAPS). Here, we utilized BAPS with hierarchical clustering as implemented
781 in the R package RhierBAPS (v1.0.1) (119). Grouping of the accessory genome was further
782 assessed via t-distributed stochastic neighbor embedding (t-SNE), in order to cluster the data
783 through a range of values for perplexity (p=5,10,20,50), the results of which were visualized using
784 the microreact platform (4). SNP distances between individual samples were computed through the
785 snippy pipeline (v4.6.0) (<https://github.com/tseemann/snippy>).

786 **Molecular clock analysis.** In order to assess the molecular clock of *A. baumannii*, a xml
787 file was configured using BEAUTi and subsequently utilized for BEAST (v2.5.0) (13) analysis.
788 BEAST was run on the OXA-126 group, containing detailed sampling dates of 30 isolates. The run
789 was allowed to continue for 50 million iterations, sampling from the posterior every 1000st

790 iteration. We inferred the temporal phylogeny for OXA-126 under a strict clock setting (i.e.
791 normally distributed rate variation over the tree). The strict clock was set to utilize a log-normal
792 prior on the clock rate, with a mean of -5 and sd of 1.25 (43).

793 **Isolation of fungi and interaction studies with *A. baumannii*.** Fungal isolates were
794 obtained from environmental samples previously tested positive for *A. baumannii* using the
795 following protocol: Samples (e.g. 1 g of soil) were resuspended in 10 ml of minimal salt medium
796 supplemented with 0.2% acetate (see above) and 100 μ l suspension before being spread on Kimmig
797 fungal agar ((54), Becton Dickinson, Heidelberg, Germany) supplemented with 80 mg/l
798 chloramphenicol (“Kimmig agar”). After 2-3 days of incubation at 27°C, fungal colonies were
799 selected and spread on Kimmig agar several times until considered pure cultures after macroscopic
800 and microscopic inspection. The absence of bacterial contamination was verified via colony PCR
801 using global 16S rRNA gene primers (125). Provisional species determination of fungal isolates
802 was performed by sequencing of the rRNA genes and ITS (internal transcribed spacer) (8, 118).
803 *Aspergillus* spores were harvested after growth of fungi on Kimmig agar for 3 days at 34°C. To
804 this end, the plate was flooded with 5 ml of sterile phosphate-buffered saline (PBS) supplemented
805 with 0.1% Triton X-100, followed by soft panning. Subsequently, the suspension was removed
806 with a pipette while avoiding contact with the fungal colonies, aliquoted and frozen at -80°C until
807 further use. For seeding into 24-well plates, frozen spore suspensions were thawed, diluted by a
808 factor of 50 into LB medium and 300 μ l deposited into each well. The *A. baumannii* strains were
809 cultured in LB medium overnight at 37°C, diluted 1:50 into fresh medium and further cultured until
810 an optical density (OD)_{600 nm} of 1 was reached. For the spore adhesion assay, the bacteria were
811 diluted 1:200 into LB medium and 300 μ l were added to the spore seeding of a well. After 2-4
812 hours, the medium was removed from the wells and replaced twice with fresh medium to filter any
813 non-adherent bacteria before inverted microscopy was performed. For the spore germination

814 inhibition assay, bacterial suspensions with an OD_{600 nm} of 1 generated as above were diluted
815 1:2000 into LB medium, of which 300 µl were added to the spore seeding of a well. Microscopic
816 evaluation of spore germination inhibition was conducted after 5-7 hours. For scanning electron
817 microscopy (SEM), Thermanox™ coverslips (ThermoFisher Scientific) were placed in 6-well
818 plates, the incubation volume was reduced to 300 µl with seeding as above and fixed after 2 hours
819 in a solution of 2.5% glutaraldehyde, 1.0% paraformaldehyde in 50 mM HEPES buffer for 24 hrs.
820 All samples were then washed in 50 mM HEPES, dehydrated in 30, 50, 70, 90, 95, 100, 100%
821 ethanol, critical point dried, mounted on aluminum stubs, sputter coated with a 10 nm layer of gold-
822 palladium and finally examined in the SEM (ZEISS 1530 Gemini, Carl Zeiss Microscopy GmbH,
823 Germany) operating at 3 kV using the in-lens electron detector.

824 **Geographic information analysis.** All spatial data were analyzed using geographic
825 information system (GIS) tools (Quantum GIS Software, 2010). Feeding grounds for all white stork
826 nests were set as an area around the nest with a 3.5 and 4 km radius, respectively (11). Habitat
827 structures of all feeding grounds were determined using CORINE Land Cover 2012 types,
828 including arable land, pastures, heterogeneous agricultural areas, forests, total area of water
829 reservoirs and total length of rivers. All results were combined for statistical analysis (Suppl.
830 Material S1)

831 **Legal permissions.** Collection of earthworms and insects was granted by the Landesamt
832 für Umweltschutz, Sachsen-Anhalt, Halle/Saale, Germany (RL-0489-V and RL-0497-V).
833 Collection of stork samples was granted by The Local Ethics Committee and The General
834 Directorate for Environmental Protection in Poland: 21 21/2028, 42/2018, 43/2010, 44/2015,
835 47/2017, 028/2019/P1, 348/2016, DOP-OZGIZ.6401.03.101.2012.km.2, WBA/11/Z/10,
836 WPN.6401.109.2017.AP, WPN.6401.211.2017.MK, DZP-WG.6401.75.2022.WW, DL-
837 III.6713.11.2018.ABR, WPN-II.6401.167.2015.AS.2, DZP-WG.6401.03.98.2016.km, DLP-VIII-

838 6713-21/29762/14/RN. In accordance with the convention on biological diversity (“Nagoya
839 protocol”) a certificate of compliance was issued to collect samples from Spanish storks (ABSCH-
840 IRCC-ES-246587-1; Dirección General de Biodiversidad y Calidad Ambiental del Ministerio para
841 la Transición Ecológica, Madrid, Spain). Trapping small mammals in Thuringia and trapping
842 Norway rats in North Rhine-Westphalia was covered by permits from the districts’ and State’s
843 authorities, respectively (Thuringia: Landratsamt Unstrut-Hainich-Kreis file number 31109-16-
844 301, Landkreis Eichsfeld file number 70.2-6-85/KleinSäuger/ausn.-01, Landratsamt
845 Kyffhäuserkreis file number III.3.3 364.53.1/2016-11-01; North Rhine-Westphalia: LANUV file
846 number 84-02.04.2015.A279).

847 **Collection of rodents, rats and shrews.** Cat-captured rodents and shrews were wrapped
848 into aluminum foil or transferred into 50 ml tubes by the instructed collectors, stored at 4°C and
849 transported to the lab within 24 h. Tracheal and rectal swab samples were taken under the safety
850 cabinet while wearing gloves.

851

852 ACKNOWLEDGEMENTS

853

854 We would like to thank our colleagues at the central DNA sequencing lab of the Robert Koch
855 Institute for excellent technical assistance. G.W. & P.G.H. acknowledge financial support from the
856 Deutsche Forschungsgemeinschaft (DFG-FOR 2251). A. Ł. acknowledges financial support from
857 a traineeship within the ERASMUS+ Programme (agreement no. 20/
858 SMP/2015/16). The collection of rats was funded by Deutsches Zentrum für Infektionsforschung
859 (DZIF), thematic translational Uni (TTU) “Emerging Infections” to RGU; the collection of other
860 rodents was commissioned and funded by the Federal Environment Agency (UBA) within the
861 Environment Research Plan of the German Federal Ministry for the Environment, Nature

862 Conservation, Building and Nuclear Safety (JJ, grant numbers 3716484310 and 3714674070). This
863 publication made use of the *Acinetobacter baumannii* MLST website
864 (<http://pubmlst.org/abaumannii/>) hosted at the University of Oxford (50). The development of this
865 site has been funded by the Wellcome Trust. We would also like to thank numerous colleagues,
866 friends and extramural partners supporting collection of sample material: Wolfgang Witte, Steffi
867 Walter, Christina Lang, Christa Cuny, Ulrich Brandt, Alexander Riess, Magdalena Heindorf,
868 Christian Schumacher, Andreas Tille, Emil Friedrich, Christian Imholt, Mechthild Budde,
869 Engelbert Kampling, Angela Langbein-Lorf, Denise Kreuzmann, Christian Fritsch, Reinhard
870 Kappe, Bernd Nicolai. We are indebted to Mechthild and Christoph Kaatz (Storchenhof Loburg)
871 for various support in obtaining stork samples, and to Volker Rickerts for support with fungal
872 taxonomy. We would like to apologize to all those whose work could not be cited due to the
873 extensive linkage of issues to the existing literature. We will try to acknowledge this in a review
874 article.

875

876

LEGENDS TO FIGURES

877

878 **Fig. 1: Map of the sampling sites of white stork nestlings in the years 2013-2018 in Poland.**

879 The overall positive rate for isolation of *A. baumannii* from choana swabs of nestlings was 29.5%
880 (n=1,319). Nestlings tested positive for *A. baumannii* are represented by red circles, nestlings tested
881 negative are indicated black.

882

883 **Fig. 2: Diversity of *A. baumannii* isolates within individual nests.** Cartographic presentation of
884 individual nests with nestlings tested positive for *A. baumannii* within a region of Opole in the year
885 2016. Nests with more than one nestling tested positive are represented by a central red-filled circle.

886 The numbers represent OXA-51 variant numbers. Nestlings tested negative have not been
887 visualized for the sake of clarity.

888
889 **Fig. 3: Phylogenomic tree of *A. baumannii* based on the core genome of a set of 826 genomes.**

890 Colors by OXA-51 variant types. See microreact project at
891 <https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-acinetobacternobaps12dec23> for
892 further analysis and illustration of the dataset.

893
894 **Fig. 4: Isolates from Poland and Germany represent a significant part of the global diversity.**

895 Isolates from Poland and Germany, respectively, indicated by grey blue circles. See microreact
896 project at [https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-](https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-acinetobacternobaps12dec23)
897 [acinetobacternobaps12dec23](https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-acinetobacternobaps12dec23) for further analysis and illustration of the dataset; perplexity
898 clustering to the left ($p=10$).

899
900 **Fig. 5: One-Health perspective: Human, animal and environmental samples are distributed**

901 **all over the tree.** Isolates of human, animal and environmental origin indicated by grey blue
902 circles. See microreact project at [https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-](https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-acinetobacternobaps12dec23)
903 [acinetobacternobaps12dec23](https://microreact.org/project/3ApuGKD61qPLT1ZNmoKcTb-acinetobacternobaps12dec23) for further analysis and illustration of the dataset.

904
905 **Fig. 6: Scanning electron microscopy on *A. baumannii* adhering to *Aspergillus* spores. (A)**

906 *A. baumannii* 31D1 adhering to a spore of *Aspergillus niger* complex isolate U17-Zw-P20. (B)
907 *A. baumannii* 31D1 adhering to a spore of *Aspergillus quadrilineatus* strain Eld3.

908
909

Table 1: Pan-genome analysis: comparison with previous studies.

Pan Genome	Description	90 % Seq. Id.	85% Seq. Id.	Mangas et al. (70) 90% Seq. Id.	Galac et al. (31) 95% Seq. Id.	Urhan & Abeel (123) 95% Seq. Id.
Dataset		826 genomes (ca. 50/50 human vs non-human)	826 genomes (ca. 50/50 human vs non-human)	2467 genomes (non-human host -17)	100 human clinical genomes	70 closed genomes from NCBI
Core genes	(99% <= strains <= 100%)	1,728	1,733	2,221	2,119	1,996
Soft core genes	(95% <= strains < 99%)	548	540	~3,000		429
Shell genes	(15% <= strains < 95%)	1,804	1,832		~13,900	1,912
Cloud genes	(0% <= strains < 15%)	46,909	44,111	~16,000 (<=20%)		14,867
Total genes	(0% <= strains <= 100%)	50,989	48,216	19,272	~16,000	19,204

Seq. Id.; sequence identity on the amino acid level

1 REFERENCES

- 2
- 3 1. **Ahmed, W, Staley, C, Hamilton, KA, Beale, DJ, Sadowsky, MJ, Toze, S, and Haas,**
4 **CN.** 2017. Amplicon-based taxonomic characterization of bacteria in urban and peri-urban
5 roof-harvested rainwater stored in tanks. *Sci Total Environ* **576**:326-334.
- 6 2. **Ajiboye, TO, Skiebe, E, and Wilharm, G.** 2018. Phenolic acids potentiate colistin-
7 mediated killing of *Acinetobacter baumannii* by inducing redox imbalance. *Biomed*
8 *Pharmacother* **101**:737-744.
- 9 3. **Al Atrouni, A, Hamze, M, Rafei, R, Eveillard, M, Joly-Guillou, ML, and Kempf, M.**
10 2016. Diversity of *Acinetobacter* species isolated from different environments in Lebanon:
11 a nationwide study. *Future Microbiol* **11**:1147-1156.
- 12 4. **Argimón, S, Abudahab, K, Goater, RJE, Fedosejev, A, Bhai, J, Glasner, C, Feil, EJ,**
13 **Holden, MTG, Yeats, CA, Grundmann, H, Spratt, BG, and Aanensen, DM.** 2016.
14 Microreact: visualizing and sharing data for genomic epidemiology and phylogeography.
15 *Microb Genom* **2**:e000093.
- 16 5. **Bae, S, Maestre, JP, Kinney, KA, and Kirisits, MJ.** 2019. An examination of the
17 microbial community and occurrence of potential human pathogens in rainwater harvested
18 from different roofing materials. *Water Res* **159**:406-413.
- 19 6. **Baldrian, P, Kolařík, M, Stursová, M, Kopecký, J, Valášková, V, Větrovský, T,**
20 **Zifčáková, L, Snajdr, J, Rídl, J, Vlček, C, and Voříšková, J.** 2012. Active and total
21 microbial communities in forest soil are largely different and highly stratified during
22 decomposition. *Isme j* **6**:248-258.
- 23 7. **Bankevich, A, Nurk, S, Antipov, D, Gurevich, AA, Dvorkin, M, Kulikov, AS, Lesin,**
24 **VM, Nikolenko, SI, Pham, S, Prjibelski, AD, Pyshkin, AV, Sirotkin, AV, Vyahhi, N,**
25 **Tesler, G, Alekseyev, MA, and Pevzner, PA.** 2012. SPAdes: a new genome assembly
26 algorithm and its applications to single-cell sequencing. *J Comput Biol* **19**:455-477.
- 27 8. **Bellemain, E, Carlsen, T, Brochmann, C, Coissac, E, Taberlet, P, and Kauserud, H.**
28 2010. ITS as an environmental DNA barcode for fungi: an in silico approach reveals
29 potential PCR biases. *BMC Microbiol* **10**:189.
- 30 9. **Berlau, J, Aucken, H, Malnick, H, and Pitt, T.** 1999. Distribution of *Acinetobacter*
31 species on skin of healthy humans. *Eur J Clin Microbiol Infect Dis* **18**:179-183.
- 32 10. **Błońska, E, Lasota, J, Jankowiak, R, Michalcewicz, J, Wojas, T, Zbyryt, A, and Ciach,**
33 **M.** 2020. Biological and physicochemical properties of the nests of White Stork *Ciconia*
34 *ciconia* reveal soil entirely formed, modified and maintained by birds. *Sci Total Environ*
35 doi:10.1016/j.scitotenv.2020.143020:143020.
- 36 11. **Böhning-Gaese, K.** 1992. Zur Nahrungsökologie des Weißstorchs (*Ciconia ciconia*) in
37 Oberschwaben: Beobachtungen an zwei Paaren. *Journal für Ornithologie* **133**:61-71.
- 38 12. **Bornier, F, Zas, E, Potheret, D, Laaberki, MH, Coupat-Goutaland, B, and**
39 **Charpentier, X.** 2021. Environmental Free-Living Amoebae Can Predate on Diverse
40 Antibiotic-Resistant Human Pathogens. *Appl Environ Microbiol* **87**:e0074721.
- 41 13. **Bouckaert, R, Vaughan, TG, Barido-Sottani, J, Duchêne, S, Fourment, M,**
42 **Gavryushkina, A, Heled, J, Jones, G, Kühnert, D, De Maio, N, Matschiner, M,**
43 **Mendes, FK, Müller, NF, Ogilvie, HA, du Plessis, L, Popinga, A, Rambaut, A,**
44 **Rasmussen, D, Siveroni, I, Suchard, MA, Wu, C-H, Xie, D, Zhang, C, Stadler, T, and**
45 **Drummond, AJ.** 2019. BEAST 2.5: An advanced software platform for Bayesian
46 evolutionary analysis. *PLOS Computational Biology* **15**:e1006650.

- 47 14. **Castillo-Ramírez, S.** 2022. Zoonotic *Acinetobacter baumannii*: the need for genomic
48 epidemiology in a One Health context. *Lancet Microbe* doi:10.1016/s2666-5247(22)00255-
49 5.
- 50 15. **Chowdhary, A, Kathuria, S, Xu, J, and Meis, JF.** 2013. Emergence of azole-resistant
51 *aspergillus fumigatus* strains due to agricultural azole use creates an increasing threat to
52 human health. *PLoS Pathog* **9**:e1003633.
- 53 16. **Christensen, EA, Gerner-Smith, P, and Kristensen, H.** 1991. Radiation resistance of
54 clinical *Acinetobacter* spp.: a need for concern? *J Hosp Infect* **18**:85-92.
- 55 17. **Deng, W, Zhang, A, Chen, S, He, X, Jin, L, Yu, X, Yang, S, Li, B, Fan, L, Ji, L, Pan,
56 X, and Zou, L.** 2020. Heavy metals, antibiotics and nutrients affect the bacterial
57 community and resistance genes in chicken manure composting and fertilized soil. *J
58 Environ Manage* **257**:109980.
- 59 18. **Dexter, C, Murray, GL, Paulsen, IT, and Peleg, AY.** 2015. Community-acquired
60 *Acinetobacter baumannii*: clinical characteristics, epidemiology and pathogenesis. *Expert
61 Rev Anti Infect Ther* **13**:567-573.
- 62 19. **Didelot, X, and Wilson, DJ.** 2015. ClonalFrameML: efficient inference of recombination
63 in whole bacterial genomes. *PLoS Comput Biol* **11**:e1004041.
- 64 20. **Ding, LJ, Zhou, XY, and Zhu, YG.** 2020. Microbiome and antibiotic resistome in
65 household dust from Beijing, China. *Environ Int* **139**:105702.
- 66 21. **Djahanschiri, B, Di Venanzio, G, Distel, JS, Breisch, J, Dieckmann, MA, Goesmann,
67 A, Averhoff, B, Göttig, S, Wilharm, G, Feldman, MF, and Ebersberger, I.** 2022.
68 Evolutionarily stable gene clusters shed light on the common grounds of pathogenicity in
69 the *Acinetobacter calcoaceticus-baumannii* complex. *PLoS Genet* **18**:e1010020.
- 70 22. **Dümig, M, Binder, J, Gaculenko, A, Daul, F, Winandy, L, Hasenberg, M, Gunzer, M,
71 Fischer, R, Künzler, M, and Krappmann, S.** 2021. The infectious propagules of
72 *Aspergillus fumigatus* are coated with antimicrobial peptides. *Cell Microbiol* **23**:e13301.
- 73 23. **Dwyer, DJ, Belenky, PA, Yang, JH, MacDonald, IC, Martell, JD, Takahashi, N, Chan,
74 CT, Lobritz, MA, Braff, D, Schwarz, EG, Ye, JD, Pati, M, Vercruyse, M, Ralifo, PS,
75 Allison, KR, Khalil, AS, Ting, AY, Walker, GC, and Collins, JJ.** 2014. Antibiotics
76 induce redox-related physiological alterations as part of their lethality. *Proc Natl Acad Sci
77 U S A* **111**:E2100-2109.
- 78 24. **Dylewski, Ł, Dyderski, MK, Maćkowiak, Ł, and Tobolka, M.** 2021. Nests of the white
79 stork as suitable microsites for the colonisation and establishment of ruderal plants in the
80 agricultural landscape. *Plant Ecology* **222**:337-348.
- 81 25. **Ewers, C, Klotz, P, Leidner, U, Stamm, I, Prenger-Berninghoff, E, Göttig, S, Semmler,
82 T, and Scheufen, S.** 2017. OXA-23 and ISAbal-OXA-66 class D β -lactamases in
83 *Acinetobacter baumannii* isolates from companion animals. *Int J Antimicrob Agents* **49**:37-
84 44.
- 85 26. **Flack, A, Fiedler, W, Blas, J, Pokrovsky, I, Kaatz, M, Mitropolsky, M, Aghababyan,
86 K, Fakriadis, I, Makrigianni, E, Jerzak, L, Azafzaf, H, Feltrup-Azafzaf, C, Rotics, S,
87 Mokotjomela, TM, Nathan, R, and Wikelski, M.** 2016. Costs of migratory decisions: A
88 comparison across eight white stork populations. *Sci Adv* **2**:e1500931.
- 89 27. **Freschi, L, Vincent, AT, Jeukens, J, Emond-Rheault, JG, Kukavica-Ibrulj, I, Dupont,
90 MJ, Charette, SJ, Boyle, B, and Levesque, RC.** 2019. The *Pseudomonas aeruginosa* Pan-
91 Genome Provides New Insights on Its Population Structure, Horizontal Gene Transfer, and
92 Pathogenicity. *Genome Biol Evol* **11**:109-120.

- 93 28. **Fukuta, Y, Clarke, LG, Shields, RK, Wagener, MM, Pasculle, AW, and Doi, Y.** 2012.
94 Lack of seasonality in the occurrence of multidrug-resistant *Acinetobacter baumannii*
95 complex. *Infect Control Hosp Epidemiol* **33**:1051-1052.
- 96 29. **Fyhrquist, N, Ruokolainen, L, Suomalainen, A, Lehtimäki, S, Veckman, V, Vendelin,**
97 **J, Karisola, P, Lehto, M, Savinko, T, Jarva, H, Kosunen, TU, Corander, J, Auvinen,**
98 **P, Paulin, L, von Hertzen, L, Laatikainen, T, Mäkelä, M, Haahtela, T, Greco, D,**
99 **Hanski, I, and Alenius, H.** 2014. *Acinetobacter* species in the skin microbiota protect
100 against allergic sensitization and inflammation. *J Allergy Clin Immunol* **134**:1301-
101 1309.e1311.
- 102 30. **Gaddy, JA, Tomaras, AP, and Actis, LA.** 2009. The *Acinetobacter baumannii* 19606
103 *OmpA* protein plays a role in biofilm formation on abiotic surfaces and in the interaction
104 of this pathogen with eukaryotic cells. *Infect Immun* **77**:3150-3160.
- 105 31. **Galac, MR, Snesrud, E, Lebreton, F, Stam, J, Julius, M, Ong, AC, Maybank, R, Jones,**
106 **AR, Kwak, YI, Hinkle, K, Waterman, PE, Lesho, EP, Bennett, JW, and Mc Gann, P.**
107 2020. A Diverse Panel of Clinical *Acinetobacter baumannii* for Research and Development.
108 *Antimicrob Agents Chemother* **64**.
- 109 32. **Garcés-Pastor, S, Coissac, E, Lavergne, S, Schwörer, C, Theurillat, JP, Heintzman,**
110 **PD, Wangensteen, OS, Tinner, W, Rey, F, Heer, M, Rutzer, A, Walsh, K, Lammers,**
111 **Y, Brown, AG, Goslar, T, Rijal, DP, Karger, DN, Pellissier, L, Heiri, O, and Alsos, IG.**
112 2022. High resolution ancient sedimentary DNA shows that alpine plant diversity is
113 associated with human land use and climate change. *Nat Commun* **13**:6559.
- 114 33. **Ghaly, TM, Paulsen, IT, Sajjad, A, Tetu, SG, and Gillings, MR.** 2020. A Novel Family
115 of *Acinetobacter* Mega-Plasmids Are Disseminating Multi-Drug Resistance Across the
116 Globe While Acquiring Location-Specific Accessory Genes. *Front Microbiol* **11**:605952.
- 117 34. **Godeux, AS, Svedholm, E, Barreto, S, Potron, A, Venner, S, Charpentier, X, and**
118 **Laaberki, MH.** 2022. Interbacterial Transfer of Carbapenem Resistance and Large
119 Antibiotic Resistance Islands by Natural Transformation in Pathogenic *Acinetobacter*.
120 *mBio* **13**:e0263121.
- 121 35. **Govender, R, Amoah, ID, Kumari, S, Bux, F, and Stenström, TA.** 2021. Detection of
122 multidrug resistant environmental isolates of *acinetobacter* and *Stenotrophomonas*
123 *maltophilia*: a possible threat for community acquired infections? *J Environ Sci Health A*
124 *Tox Hazard Subst Environ Eng* **56**:213-225.
- 125 36. **Hamidian, M, and Hall, RM.** 2018. The *AbaR* antibiotic resistance islands found in
126 *Acinetobacter baumannii* global clone 1 - Structure, origin and evolution. *Drug Resist*
127 *Updat* **41**:26-39.
- 128 37. **Hanski, I, von Hertzen, L, Fyhrquist, N, Koskinen, K, Torppa, K, Laatikainen, T,**
129 **Karisola, P, Auvinen, P, Paulin, L, Mäkelä, MJ, Vartiainen, E, Kosunen, TU, Alenius,**
130 **H, and Haahtela, T.** 2012. Environmental biodiversity, human microbiota, and allergy are
131 interrelated. *Proc Natl Acad Sci U S A* **109**:8334-8339.
- 132 38. **He, P, Wei, S, Shao, L, and Lü, F.** 2019. Aerosolization behavior of prokaryotes and fungi
133 during composting of vegetable waste. *Waste Manag* **89**:103-113.
- 134 39. **Heindorf, M, Kadari, M, Heider, C, Skiebe, E, and Wilharm, G.** 2014. Impact of
135 *Acinetobacter baumannii* superoxide dismutase on motility, virulence, oxidative stress
136 resistance and susceptibility to antibiotics. *PLoS One* **9**:e101033.
- 137 40. **Hernández-González, IL, and Castillo-Ramírez, S.** 2020. Antibiotic-resistant
138 *Acinetobacter baumannii* is a One Health problem. *Lancet Microbe* **1**:e279.
- 139 41. **Hernández-González, IL, Mateo-Estrada, V, and Castillo-Ramirez, S.** 2022. The
140 promiscuous and highly mobile resistome of *Acinetobacter baumannii*. *Microb Genom* **8**.

- 141 42. **Higgins, PG, Hrenovic, J, Seifert, H, and Dekic, S.** 2018. Characterization of
142 *Acinetobacter baumannii* from water and sludge line of secondary wastewater treatment
143 plant. *Water Res* **140**:261-267.
- 144 43. **Holt, K, Kenyon, JJ, Hamidian, M, Schultz, MB, Pickard, DJ, Dougan, G, and Hall,
145 R.** 2016. Five decades of genome evolution in the globally distributed, extensively
146 antibiotic-resistant *Acinetobacter baumannii* global clone 1. *Microb Genom* **2**:e000052.
- 147 44. **Hubeny, J, Korzeniewska, E, Buta-Hubeny, M, Zieliński, W, Rolbiecki, D, and
148 Harnisz, M.** 2022. Characterization of carbapenem resistance in environmental samples
149 and *Acinetobacter* spp. isolates from wastewater and river water in Poland. *Sci Total*
150 *Environ* **822**:153437.
- 151 45. **Janic, B, Bańbura, J, Gładalski, M, Kaliński, A, Kamiński, M, Marszał, L, Pieniak, D,
152 Wawrzyniak, J, and Zieliński, P.** 2023. Plastic occurrence in nests of a large forest bird.
153 *Ecological Indicators*.
- 154 46. **Jarma, D, Sánchez, MI, Green, AJ, Peralta-Sánchez, JM, Hortas, F, Sánchez-Melsió,
155 A, and Borrego, CM.** 2021. Faecal microbiota and antibiotic resistance genes in migratory
156 waterbirds with contrasting habitat use. *Sci Total Environ* **783**:146872.
- 157 47. **Jawad, A, Seifert, H, Snelling, AM, Heritage, J, and Hawkey, PM.** 1998. Survival of
158 *Acinetobacter baumannii* on dry surfaces: comparison of outbreak and sporadic isolates. *J*
159 *Clin Microbiol* **36**:1938-1941.
- 160 48. **Jeske, K, Hiltbrunner, M, Drewes, S, Ryll, R, Wenk, M, Špakova, A, Petraitytė-
161 Burneikienė, R, Heckel, G, and Ulrich, RG.** 2019. Field vole-associated Traemmersee
162 hantavirus from Germany represents a novel hantavirus species. *Virus Genes* **55**:848-853.
- 163 49. **Jeske, K, Jacob, J, Drewes, S, Pfeffer, M, Heckel, G, Ulrich, RG, and Imholt, C.** 2021.
164 Hantavirus-Leptospira coinfections in small mammals from central Germany. *Epidemiol*
165 *Infect* **149**:e97.
- 166 50. **Jolley, KA, and Maiden, MC.** 2010. BIGSdb: Scalable analysis of bacterial genome
167 variation at the population level. *BMC Bioinformatics* **11**:1-11.
- 168 51. **Jovcic, B, Novovic, K, Dekic, S, and Hrenovic, J.** 2021. Colistin Resistance in
169 Environmental Isolates of *Acinetobacter baumannii*. *Microb Drug Resist* **27**:328-336.
- 170 52. **Kaiser, K, Wemheuer, B, Korolkow, V, Wemheuer, F, Nacke, H, Schöning, I,
171 Schrupf, M, and Daniel, R.** 2016. Driving forces of soil bacterial community structure,
172 diversity, and function in temperate grasslands and forests. *Sci Rep* **6**:33696.
- 173 53. **Kamiński, M, Bańbura, J, Janic, B, Marszał, L, Minias, P, and Zieliński, P.** 2018. Intra-
174 Seasonal and Brood-Size Dependent Variation in the Diet of Black Stork (*Ciconia nigra*)
175 Nestlings. *Waterbirds* **41**:268-275.
- 176 54. **Kimmig, Ju, and Rieth, H.** 1953. * ANTIMYKOTICA IN EXPERIMENT UND KLINIK.
177 ARZNEIMITTEL-FORSCHUNG-DRUG RESEARCH **3**:267-276.
- 178 55. **Kittinger, C, Kirschner, A, Lipp, M, Baumert, R, Mascher, F, Farnleitner, AH, and
179 Zarfel, GE.** 2017. Antibiotic Resistance of *Acinetobacter* spp. Isolates from the River
180 Danube: Susceptibility Stays High. *Int J Environ Res Public Health* **15**.
- 181 56. **Klotz, P, Higgins, PG, Schaubmar, AR, Failing, K, Leidner, U, Seifert, H, Scheufen,
182 S, Semmler, T, and Ewers, C.** 2019. Seasonal Occurrence and Carbapenem Susceptibility
183 of Bovine *Acinetobacter baumannii* in Germany. *Front Microbiol* **10**:272.
- 184 57. **König, P, Wilhelm, A, Schaudinn, C, Poehlein, A, Daniel, R, Widera, M, Averhoff, B,
185 and Müller, V.** 2023. The VBNC state: a fundamental survival strategy of *Acinetobacter*
186 *baumannii*. *mBio* **14**:e0213923.
- 187 58. **Kosicki, JZ, Profus, P, Dolata, PT, and Tobólka, M.** 2006. Food composition and energy
188 demand of the White Stork *Ciconia ciconia* breeding population. Literature survey and

- 189 preliminary results from Poland. *The White Stork in Poland: studies in biology, ecology*
190 *and conservation* Bogucki Wyd Nauk, Poznań:169-183.
- 191 59. **Kostoulias, X, Murray, GL, Cerqueira, GM, Kong, JB, Bantun, F, Mylonakis, E,**
192 **Khoo, CA, and Peleg, AY.** 2016. Impact of a Cross-Kingdom Signaling Molecule of
193 *Candida albicans* on *Acinetobacter baumannii* Physiology. *Antimicrob Agents Chemother*
194 **60**:161-167.
- 195 60. **Krizova, L, Maixnerova, M, Sedo, O, and Nemeč, A.** 2014. *Acinetobacter bohemicus* sp.
196 nov. widespread in natural soil and water ecosystems in the Czech Republic. *Syst Appl*
197 *Microbiol* **37**:467-473.
- 198 61. **Lee, J, Shi, YM, Grün, P, Gube, M, Feldbrügge, M, Bode, H, and Hennicke, F.** 2020.
199 Identification of Feldin, an Antifungal Polyene from the Beefsteak Fungus *Fistulina*
200 *hepatica*. *Biomolecules* **10**.
- 201 62. **Li, X, Chen, H, and Yao, M.** 2020. Microbial emission levels and diversities from different
202 land use types. *Environ Int* **143**:105988.
- 203 63. **Linz, B, Mukhtar, N, Shabbir, MZ, Rivera, I, Ivanov, YV, Tahir, Z, Yaqub, T, and**
204 **Harvill, ET.** 2018. Virulent Epidemic Pneumonia in Sheep Caused by the Human Pathogen
205 *Acinetobacter baumannii*. *Front Microbiol* **9**:2616.
- 206 64. **Liu, CH, Chen, X, Liu, TT, Lian, B, Gu, Y, Caer, V, Xue, YR, and Wang, BT.** 2007.
207 Study of the antifungal activity of *Acinetobacter baumannii* LCH001 in vitro and
208 identification of its antifungal components. *Appl Microbiol Biotechnol* **76**:459-466.
- 209 65. **Liu, Y, Hu, S, Yu, T, Luo, Y, Zhang, Z, Chen, Y, Guo, S, Sun, Q, Fan, G, and Wu, L.**
210 2023. A database of glacier microbiomes for the Three Poles. *Earth System Science Data*
211 *Discussions* **2023**:1-20.
- 212 66. **Lopińska, A, Indykiewicz, P, Skiebe, E, Pfeifer, Y, Trček, J, Jerzak, L, Minias, P,**
213 **Nowakowski, J, Ledwoń, M, Beteleja, J, and Wilharm, G.** 2020. Low Occurrence of
214 *Acinetobacter baumannii* in Gulls and Songbirds. *Pol J Microbiol* **69**:1-6.
- 215 67. **Louca, S.** 2022. The rates of global bacterial and archaeal dispersal. *Isme j* **16**:159-167.
- 216 68. **Lupo, A, Vogt, D, Seiffert, SN, Endimiani, A, and Perreten, V.** 2014. Antibiotic
217 resistance and phylogenetic characterization of *Acinetobacter baumannii* strains isolated
218 from commercial raw meat in Switzerland. *J Food Prot* **77**:1976-1981.
- 219 69. **Mahismita, P, and Dipti, G.** 2020. Pseudomembranous *Aspergillus tracheobronchitis* with
220 secondary *Acinetobacter baumannii* pneumonia. *Indian J Med Res* **152**:S136-s137.
- 221 70. **Mangas, EL, Rubio, A, Álvarez-Marín, R, Labrador-Herrera, G, Pachón, J, Pachón-**
222 **Ibáñez, ME, Divina, F, and Pérez-Pulido, AJ.** 2019. Pangenome of *Acinetobacter*
223 *baumannii* uncovers two groups of genomes, one of them with genes involved in
224 CRISPR/Cas defence systems associated with the absence of plasmids and exclusive genes
225 for biofilm formation. *Microb Genom* **5**.
- 226 71. **Marchaim, D, Navon-Venezia, S, Schwartz, D, Tarabeia, J, Fefer, I, Schwaber, MJ,**
227 **and Carmeli, Y.** 2007. Surveillance cultures and duration of carriage of multidrug-resistant
228 *Acinetobacter baumannii*. *J Clin Microbiol* **45**:1551-1555.
- 229 72. **Martin, E, and Jackel, U.** 2011. Characterization of bacterial contaminants in the air of a
230 duck hatchery by cultivation based and molecular methods. *J Environ Monit* **13**:464-470.
- 231 73. **Martín, J, García-Estrada, C, Rumbero, A, Recio, E, Albillos, SM, Ullán, RV, and**
232 **Martín, JF.** 2011. Characterization of an autoinducer of penicillin biosynthesis in
233 *Penicillium chrysogenum*. *Appl Environ Microbiol* **77**:5688-5696.
- 234 74. **McConnell, MJ, Actis, L, and Pachón, J.** 2013. *Acinetobacter baumannii*: human
235 infections, factors contributing to pathogenesis and animal models. *FEMS Microbiol Rev*
236 **37**:130-155.

- 237 75. **Mehl, C, Mätz-Rensing, K, Linde, J, Struve, B, Ismer, G, van Hümmel, C, Ulrich, RG,**
238 **and Tomaso, H.** 2023. Case report: tularaemia in a white-handed gibbon (*Hylobates lar*),
239 Germany. *International Journal of Veterinary Science and Medicine* **11**:121-125.
- 240 76. **Mu, F, Li, Y, Lu, R, Qi, Y, Xie, W, and Bai, W.** 2020. Source identification of airborne
241 bacteria in the mountainous area and the urban areas. *Atmospheric Research* **231**:104676.
- 242 77. **Müller, S.** 2018. Molecular and functional typing of isolates of the *Acinetobacter*
243 *calcoaceticus*-*Acinetobacter baumannii* complex with emphasis on multi-drug resistant
244 *Acinetobacter baumannii*. Dissertation. doi:188-fudissthesis000000106520-7. Freie
245 Universität Berlin.
- 246 78. **Mussi, MA, Gaddy, JA, Cabruja, M, Arivett, BA, Viale, AM, Rasia, R, and Actis, LA.**
247 2010. The opportunistic human pathogen *Acinetobacter baumannii* senses and responds to
248 light. *J Bacteriol* **192**:6336-6345.
- 249 79. **Naas, T, Oueslati, S, Bonnin, RA, Dabos, ML, Zavala, A, Dortet, L, Retailleau, P, and**
250 **Iorga, BI.** 2017. Beta-lactamase database (BLDB) - structure and function. *J Enzyme Inhib*
251 *Med Chem* **32**:917-919.
- 252 80. **Nemec, A.** *Acinetobacter*, p 1-78, *Bergey's Manual of Systematics of Archaea and Bacteria*
253 doi:<https://doi.org/10.1002/9781118960608.gbm01203.pub2>.
- 254 81. **Nemec, A, Krizova, L, Maixnerova, M, Sedo, O, Brisse, S, and Higgins, PG.** 2015.
255 *Acinetobacter seifertii* sp. nov., a member of the *Acinetobacter calcoaceticus*-*Acinetobacter*
256 *baumannii* complex isolated from human clinical specimens. *Int J Syst Evol Microbiol*
257 **65**:934-942.
- 258 82. **Nemec, A, Musilek, M, Maixnerova, M, De Baere, T, van der Reijden, TJ,**
259 **Vanechoutte, M, and Dijkshoorn, L.** 2009. *Acinetobacter beijerinckii* sp. nov. and
260 *Acinetobacter gyllenbergii* sp. nov., haemolytic organisms isolated from humans. *Int J Syst*
261 *Evol Microbiol* **59**:118-124.
- 262 83. **Nemec, A, Radolfová-Křížová, L, Maixnerová, M, Shestivska, V, Španělová, P, and**
263 **Higgins, PG.** 2022. *Acinetobacter silvestris* sp. nov. discovered in forest ecosystems in
264 Czechia. *Int J Syst Evol Microbiol* **72**.
- 265 84. **Neupane, S, Saski, C, and Nayduch, D.** 2021. House fly larval grazing alters dairy cattle
266 manure microbial communities. *BMC Microbiol* **21**:346.
- 267 85. **Nodari, CS, Cayô, R, Streling, AP, Lei, F, Wille, J, Almeida, MS, de Paula, AI,**
268 **Pignatari, ACC, Seifert, H, Higgins, PG, and Gales, AC.** 2020. Genomic Analysis of
269 Carbapenem-Resistant *Acinetobacter baumannii* Isolates Belonging to Major Endemic
270 Clones in South America. *Front Microbiol* **11**:584603.
- 271 86. **Olias, P, Gruber, AD, Winfried, B, Hafez, HM, and Lierz, M.** 2010. Fungal pneumonia
272 as a major cause of mortality in white stork (*Ciconia ciconia*) chicks. *Avian Dis* **54**:94-98.
- 273 87. **Orłowski, G, Książkiewicz-Parulska, Z, Karg, J, Bocheński, M, Jerzak, L, and Zub,**
274 **K.** 2016. Using soil from pellets of White Storks *Ciconia ciconia* to assess the number of
275 earthworms (*Lumbricidae*) consumed as primary and secondary prey. *Ibis* **158**:587-597.
- 276 88. **Otter, JA, Yezli, S, Salkeld, JA, and French, GL.** 2013. Evidence that contaminated
277 surfaces contribute to the transmission of hospital pathogens and an overview of strategies
278 to address contaminated surfaces in hospital settings. *Am J Infect Control* **41**:S6-11.
- 279 89. **Page, AJ, Cummins, CA, Hunt, M, Wong, VK, Reuter, S, Holden, MT, Fookes, M,**
280 **Falush, D, Keane, JA, and Parkhill, J.** 2015. Roary: rapid large-scale prokaryote pan
281 genome analysis. *Bioinformatics* **31**:3691-3693.
- 282 90. **Peleg, AY, Hogan, DA, and Mylonakis, E.** 2010. Medically important bacterial-fungal
283 interactions. *Nat Rev Microbiol* **8**:340-349.

- 284 91. **Peleg, AY, Tampakakis, E, Fuchs, BB, Eliopoulos, GM, Moellering, RC, Jr., and**
285 **Mylonakis, E.** 2008. Prokaryote-eukaryote interactions identified by using *Caenorhabditis*
286 *elegans*. *Proc Natl Acad Sci U S A* **105**:14585-14590.
- 287 92. **Pérez-Valera, E, de Melo Rangel, W, and Elhottová, D.** 2022. Cattle manure application
288 triggers short-term dominance of *Acinetobacter* in soil microbial communities. *Applied*
289 *Soil Ecology* **176**:104466.
- 290 93. **Pirnay, JP, Matthijs, S, Colak, H, Chablain, P, Bilocq, F, Van Eldere, J, De Vos, D,**
291 **Zizi, M, Triest, L, and Cornelis, P.** 2005. Global *Pseudomonas aeruginosa* biodiversity
292 as reflected in a Belgian river. *Environ Microbiol* **7**:969-980.
- 293 94. **Raafat, D, Mrochen, DM, Al'Sholui, F, Heuser, E, Ryll, R, Pritchett-Corning, KR,**
294 **Jacob, J, Walther, B, Matuschka, FR, Richter, D, Westerhüs, U, Pikula, J, van den**
295 **Brandt, J, Nicklas, W, Monecke, S, Strommenger, B, van Alen, S, Becker, K, Ulrich,**
296 **RG, and Holtfreter, S.** 2020. Molecular Epidemiology of Methicillin-Susceptible and
297 Methicillin-Resistant *Staphylococcus aureus* in Wild, Captive and Laboratory Rats: Effect
298 of Habitat on the Nasal *S. aureus* Population. *Toxins (Basel)* **12**.
- 299 95. **Rafei, R, Hamze, M, Pailhoriès, H, Eveillard, M, Marsollier, L, Joly-Guillou, ML,**
300 **Dabboussi, F, and Kempf, M.** 2015. Extrahuman epidemiology of *Acinetobacter*
301 *baumannii* in Lebanon. *Appl Environ Microbiol* **81**:2359-2367.
- 302 96. **Repizo, GD, Viale, AM, Borges, V, Cameranesi, MM, Taib, N, Espariz, M, Brochier-**
303 **Armanet, C, Gomes, JP, and Salcedo, SP.** 2017. The Environmental *Acinetobacter*
304 *baumannii* Isolate DSM30011 Reveals Clues into the Preantibiotic Era Genome Diversity,
305 Virulence Potential, and Niche Range of a Predominant Nosocomial Pathogen. *Genome*
306 *Biol Evol* **9**:2292-2307.
- 307 97. **Richet, H.** 2012. Seasonality in Gram-negative and healthcare-associated infections. *Clin*
308 *Microbiol Infect* **18**:934-940.
- 309 98. **Ruokolainen, L, Paalanen, L, Karkman, A, Laatikainen, T, von Hertzen, L, Vlasoff,**
310 **T, Markelova, O, Masyuk, V, Auvinen, P, Paulin, L, Alenius, H, Fyhrquist, N, Hanski,**
311 **I, Mäkelä, MJ, Zilber, E, Jousilahti, P, Vartiainen, E, and Haahtela, T.** 2017.
312 Significant disparities in allergy prevalence and microbiota between the young people in
313 Finnish and Russian Karelia. *Clin Exp Allergy* **47**:665-674.
- 314 99. **Ruokolainen, L, Parkkola, A, Karkman, A, Sinkko, H, Peet, A, Hämäläinen, AM, von**
315 **Hertzen, L, Tillmann, V, Koski, K, Virtanen, SM, Niemelä, O, Haahtela, T, and Knip,**
316 **M.** 2020. Contrasting microbiotas between Finnish and Estonian infants: Exposure to
317 *Acinetobacter* may contribute to the allergy gap. *Allergy* **75**:2342-2351.
- 318 100. **Rutherford, V, Yom, K, Ozer, EA, Pura, O, Hughes, A, Murphy, KR, Cudzilo, L,**
319 **Mitchell, D, and Hauser, AR.** 2018. Environmental reservoirs for *exoS*⁺ and *exoU*⁺
320 strains of *Pseudomonas aeruginosa*. *Environ Microbiol Rep* **10**:485-492.
- 321 101. **Sartorio, MG, Repizo, GD, and Cortez, N.** 2020. Catalases of the polyextremophylic
322 Andean isolate *Acinetobacter* sp. Ver 3 confer adaptive response to H₂ O₂ and UV
323 radiation. *Febs j* doi:10.1111/febs.15244.
- 324 102. **Schleicher, X, Higgins, PG, Wisplinghoff, H, Körber-Irrgang, B, Kresken, M, and**
325 **Seifert, H.** 2013. Molecular epidemiology of *Acinetobacter baumannii* and *Acinetobacter*
326 *nosocomialis* in Germany over a 5-year period (2005-2009). *Clin Microbiol Infect* **19**:737-
327 742.
- 328 103. **Schmitz, A, Hanke, D, Lüscho, D, Schwarz, S, Higgins, PG, and Feßler, AT.** 2023.
329 *Acinetobacter baumannii* from Samples of Commercially Reared Turkeys: Genomic
330 Relationships, Antimicrobial and Biocide Susceptibility. *Microorganisms* **11**:759.

- 331 104. **Seemann, T.** 2014. Prokka: rapid prokaryotic genome annotation. *Bioinformatics* **30**:2068-
332 2069.
- 333 105. **Serwecińska, L, Kiedrzyńska, E, and Kiedrzyński, M.** 2021. A catchment-scale
334 assessment of the sanitary condition of treated wastewater and river water based on fecal
335 indicators and carbapenem-resistant *Acinetobacter* spp. *Sci Total Environ* **750**:142266.
- 336 106. **Siguié, P, Perochon, J, Lestrade, L, Mahillon, J, and Chandler, M.** 2006. ISfinder: the
337 reference centre for bacterial insertion sequences. *Nucleic Acids Res* **34**:D32-36.
- 338 107. **Skiebe, E, de Berardinis, V, Morczinek, P, Kerrinnes, T, Faber, F, Lepka, D, Hammer,
339 B, Zimmermann, O, Ziesing, S, Wichelhaus, TA, Hunfeld, KP, Borgmann, S,
340 Gröbner, S, Higgins, PG, Seifert, H, Busse, HJ, Witte, W, Pfeifer, Y, and Wilharm, G.**
341 2012. Surface-associated motility, a common trait of clinical isolates of *Acinetobacter*
342 *baumannii*, depends on 1,3-diaminopropane. *Int J Med Microbiol* **302**:117-128.
- 343 108. **Smith, MG, Des Etages, SG, and Snyder, M.** 2004. Microbial synergy via an ethanol-
344 triggered pathway. *Mol Cell Biol* **24**:3874-3884.
- 345 109. **Spahr, C, Ryll, R, Knauf-Witzens, T, Vahlenkamp, TW, Ulrich, RG, and Johne, R.**
346 2017. Serological evidence of hepatitis E virus infection in zoo animals and identification
347 of a rodent-borne strain in a Syrian brown bear. *Vet Microbiol* **212**:87-92.
- 348 110. **Stamatakis, A.** 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis
349 of large phylogenies. *Bioinformatics* **30**:1312-1313.
- 350 111. **Steimbruch, BA, Sartorio, MG, Cortez, N, Albanesi, D, Lisa, MN, and Repizo, GD.**
351 2022. The distinctive roles played by the superoxide dismutases of the extremophile
352 *Acinetobacter* sp. Ver3. *Sci Rep* **12**:4321.
- 353 112. **Suresh, S, Aditya, V, Deekshit, VK, Manipura, R, and Premanath, R.** 2022. A rare
354 occurrence of multidrug-resistant environmental *Acinetobacter baumannii* strains from the
355 soil of Mangaluru, India. *Arch Microbiol* **204**:422.
- 356 113. **Syed, S, Tollamadugu, N, and Lian, B.** 2020. *Aspergillus* and *Fusarium* control in the
357 early stages of *Arachis hypogaea* (groundnut crop) by plant growth-promoting
358 rhizobacteria (PGPR) consortium. *Microbiol Res* **240**:126562.
- 359 114. **Tamang, MD, Kim, S, Kim, SM, Kong, HH, and Kim, J.** 2011. Interaction of
360 *Acinetobacter baumannii* 19606 and 1656-2 with *Acanthamoeba castellanii*. *J Microbiol*
361 **49**:841-846.
- 362 115. **Tan, X, Chen, R, Zhu, S, Wang, H, Yan, D, Zhang, X, Farmakiotis, D, and Mylonakis,
363 E.** 2016. *Candida albicans* Airway Colonization Facilitates Subsequent *Acinetobacter*
364 *baumannii* Pneumonia in a Rat Model. *Antimicrob Agents Chemother* **60**:3348-3354.
- 365 116. **Tan, X, Zhu, S, Yan, D, Chen, W, Chen, R, Zou, J, Yan, J, Zhang, X, Farmakiotis, D,
366 and Mylonakis, E.** 2016. *Candida* spp. airway colonization: A potential risk factor for
367 *Acinetobacter baumannii* ventilator-associated pneumonia. *Med Mycol* **54**:557-566.
- 368 117. **Thierry, S, Durand, B, Melloul, E, Tafani, JP, Wang, DY, Deville, M, Cordonnier, N,
369 Chermette, R, Guillot, J, and Arné, P.** 2013. Assessment of *Aspergillus fumigatus*
370 pathogenicity in aerosol-challenged chickens (*Gallus gallus*) belonging to two lineages.
371 *Comp Immunol Microbiol Infect Dis* **36**:379-385.
- 372 118. **Toju, H, Tanabe, AS, Yamamoto, S, and Sato, H.** 2012. High-coverage ITS primers for
373 the DNA-based identification of ascomycetes and basidiomycetes in environmental
374 samples. *PLoS One* **7**:e40863.
- 375 119. **Tonkin-Hill, G, Lees, JA, Bentley, SD, Frost, SDW, and Corander, J.** 2018.
376 RhierBAPS: An R implementation of the population clustering algorithm hierBAPS.
377 *Wellcome Open Res* **3**:93.

- 378 120. **Traglia, GM, Place, K, Dotto, C, Fernandez, JS, Montaña, S, Bahiense, CDS, Soler-**
379 **Bistue, A, Iriarte, A, Perez, F, Tolmasky, ME, Bonomo, RA, Melano, RG, and**
380 **Ramírez, MS.** 2019. Interspecies DNA acquisition by a naturally competent *Acinetobacter*
381 *baumannii* strain. *Int J Antimicrob Agents* **53**:483-490.
- 382 121. **Turton, JF, Gabriel, SN, Valderrey, C, Kaufmann, ME, and Pitt, TL.** 2007. Use of
383 sequence-based typing and multiplex PCR to identify clonal lineages of outbreak strains of
384 *Acinetobacter baumannii*. *Clin Microbiol Infect* **13**:807-815.
- 385 122. **Turton, JF, Woodford, N, Glover, J, Yarde, S, Kaufmann, ME, and Pitt, TL.** 2006.
386 Identification of *Acinetobacter baumannii* by detection of the blaOXA-51-like
387 carbapenemase gene intrinsic to this species. *J Clin Microbiol* **44**:2974-2976.
- 388 123. **Urhan, A, and Abeel, T.** 2021. A comparative study of pan-genome methods for microbial
389 organisms: *Acinetobacter baumannii* pan-genome reveals structural variation in
390 antimicrobial resistance-carrying plasmids. *Microb Genom* **7**.
- 391 124. **Wareth, G, Neubauer, H, and Sprague, LD.** 2019. *Acinetobacter baumannii* - a neglected
392 pathogen in veterinary and environmental health in Germany. *Vet Res Commun* **43**:1-6.
- 393 125. **Weisburg, WG, Barns, SM, Pelletier, DA, and Lane, DJ.** 1991. 16S ribosomal DNA
394 amplification for phylogenetic study. *J Bacteriol* **173**:697-703.
- 395 126. **Wendel, AF, Malecki, M, Otchwemah, R, Tellez-Castillo, CJ, Sakka, SG, and**
396 **Mattner, F.** 2018. One-year molecular surveillance of carbapenem-susceptible *A.*
397 *baumannii* on a German intensive care unit: diversity or clonality. *Antimicrob Resist Infect*
398 *Control* **7**:145.
- 399 127. **Wiehlmann, L, Cramer, N, and Tümmler, B.** 2015. Habitat-associated skew of clone
400 abundance in the *Pseudomonas aeruginosa* population. *Environ Microbiol Rep* **7**:955-960.
- 401 128. **Wilharm, G.** 2021. Draft Genome Sequence of Environmental Isolate *Acinetobacter*
402 *nosocomialis* U20-HoPe-S34-3 from Germany. *Microbiol Resour Announc* **10**:e0028621.
- 403 129. **Wilharm, G, Skiebe, E, Higgins, PG, Poppel, MT, Blaschke, U, Leser, S, Heider, C,**
404 **Heindorf, M, Brauner, P, Jäckel, U, Böhlend, K, Cuny, C, Łopińska, A, Kaminski, P,**
405 **Kasprzak, M, Bochenski, M, Ciebiera, O, Tobółka, M, Żołnierowicz, KM, Siekiera, J,**
406 **Seifert, H, Gagné, S, Salcedo, SP, Kaatz, M, Layer, F, Bender, JK, Fuchs, S, Semmler,**
407 **T, Pfeifer, Y, and Jerzak, L.** 2017. Relatedness of wildlife and livestock avian isolates of
408 the nosocomial pathogen *Acinetobacter baumannii* to lineages spread in hospitals
409 worldwide. *Environ Microbiol* **19**:4349-4364.
- 410 130. **Wright, MS, Haft, DH, Harkins, DM, Perez, F, Hujer, KM, Bajaksouzian, S, Benard,**
411 **MF, Jacobs, MR, Bonomo, RA, and Adams, MD.** 2014. New insights into dissemination
412 and variation of the health care-associated pathogen *Acinetobacter baumannii* from
413 genomic analysis. *mBio* **5**:e00963-00913.
- 414 131. **Xue, F, Yang, Y, Zou, S, Zhang, Y, Yue, D, Zhao, Y, and Lai, S.** 2022. Characterization
415 of airborne bacteria and fungi at a land-sea transition site in Southern China. *Sci Total*
416 *Environ* **849**:157786.
- 417 132. **Yakupogullari, Y, Otlu, B, Ersoy, Y, Kuzucu, C, Bayindir, Y, Kayabas, U, Togal, T,**
418 **and Kizilkaya, C.** 2016. Is airborne transmission of *Acinetobacter baumannii* possible: A
419 prospective molecular epidemiologic study in a tertiary care hospital. *Am J Infect Control*
420 **44**:1595-1599.
- 421 133. **Yoon, EJ, Goussard, S, Nemeč, A, Lambert, T, Courvalin, P, and Grillot-Courvalin,**
422 **C.** 2016. Origin in *Acinetobacter gyllenbergii* and dissemination of aminoglycoside-
423 modifying enzyme AAC(6)-Ih. *J Antimicrob Chemother* **71**:601-606.

- 424 134. **Yusuf, I, Skiebe, E, and Wilharm, G.** 2022. Evaluation of CHROMagar Acinetobacter
425 and MacConkey media for the recovery of Acinetobacter baumannii from soil samples. Lett
426 Appl Microbiol doi:10.1093/lambio/ovac051.
- 427 135. **Zander, E, Nemeč, A, Seifert, H, and Higgins, PG.** 2012. Association between β -
428 lactamase-encoding bla(OXA-51) variants and DiversiLab rep-PCR-based typing of
429 Acinetobacter baumannii isolates. J Clin Microbiol **50**:1900-1904.
- 430 136. **Zeidler, S, and Müller, V.** 2019. Coping with low water activities and osmotic stress in
431 Acinetobacter baumannii: significance, current status and perspectives. Environ Microbiol
432 **21**:2212-2230.
- 433 137. **Zhang, X, Zhang, R, Gao, J, Wang, X, Fan, F, Ma, X, Yin, H, Zhang, C, Feng, K, and**
434 **Deng, Y.** 2017. Thirty-one years of rice-rice-green manure rotations shape the rhizosphere
435 microbial community and enrich beneficial bacteria. Soil Biology and Biochemistry
436 **104**:208-217.
- 437 138. **Zhao, Z, Song, J, Yang, C, Yang, L, Chen, J, Li, X, Wang, Y, and Feng, J.** 2021.
438 Prevalence of Fungal and Bacterial Co-Infection in Pulmonary Fungal Infections: A
439 Metagenomic Next Generation Sequencing-Based Study. Front Cell Infect Microbiol
440 **11**:749905.
- 441 139. **Zhgun, A, Nuraeva, G, Dumina, M, Voinova, T, Dzhavakhiya, V, and Eldarov, M.**
442 2019. 1, 3-Diaminopropane and spermidine upregulate lovastatin production and
443 expression of lovastatin biosynthetic genes in *Aspergillus terreus* via LaeA regulation.
444 Applied Biochemistry and Microbiology **55**:243-254.
445

Fig. 1



Lubusz

- Culture-negative nestling [321]
- Culture-positive nestling [101]

Greater Poland

- Culture-negative nestling [350]
- Culture-positive nestling [146]

Masovia

- Culture-negative nestling [68]
- Culture-positive nestling [12]

Opole

- Culture-negative nestling [191]
- Culture-positive nestling [130]

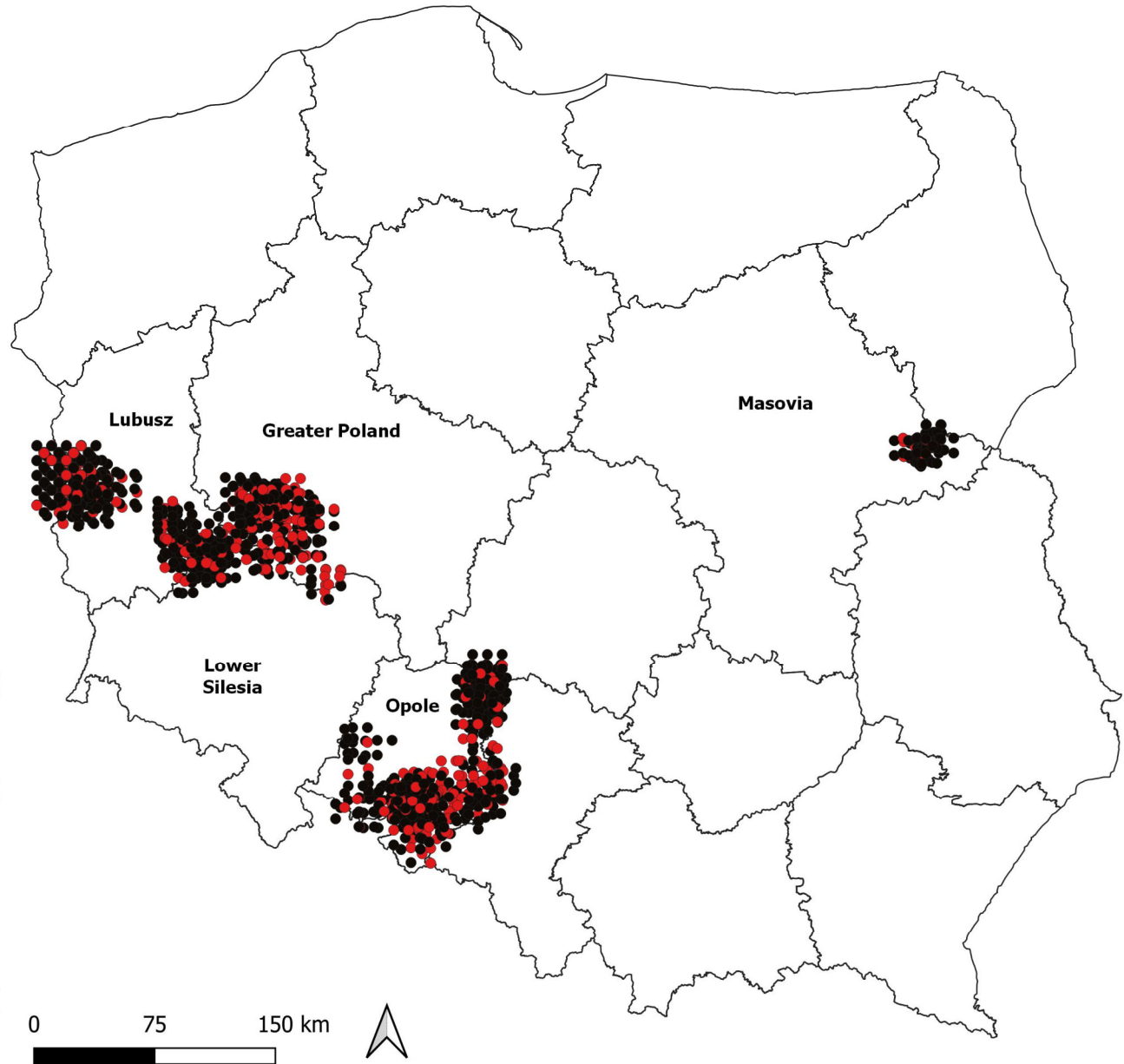
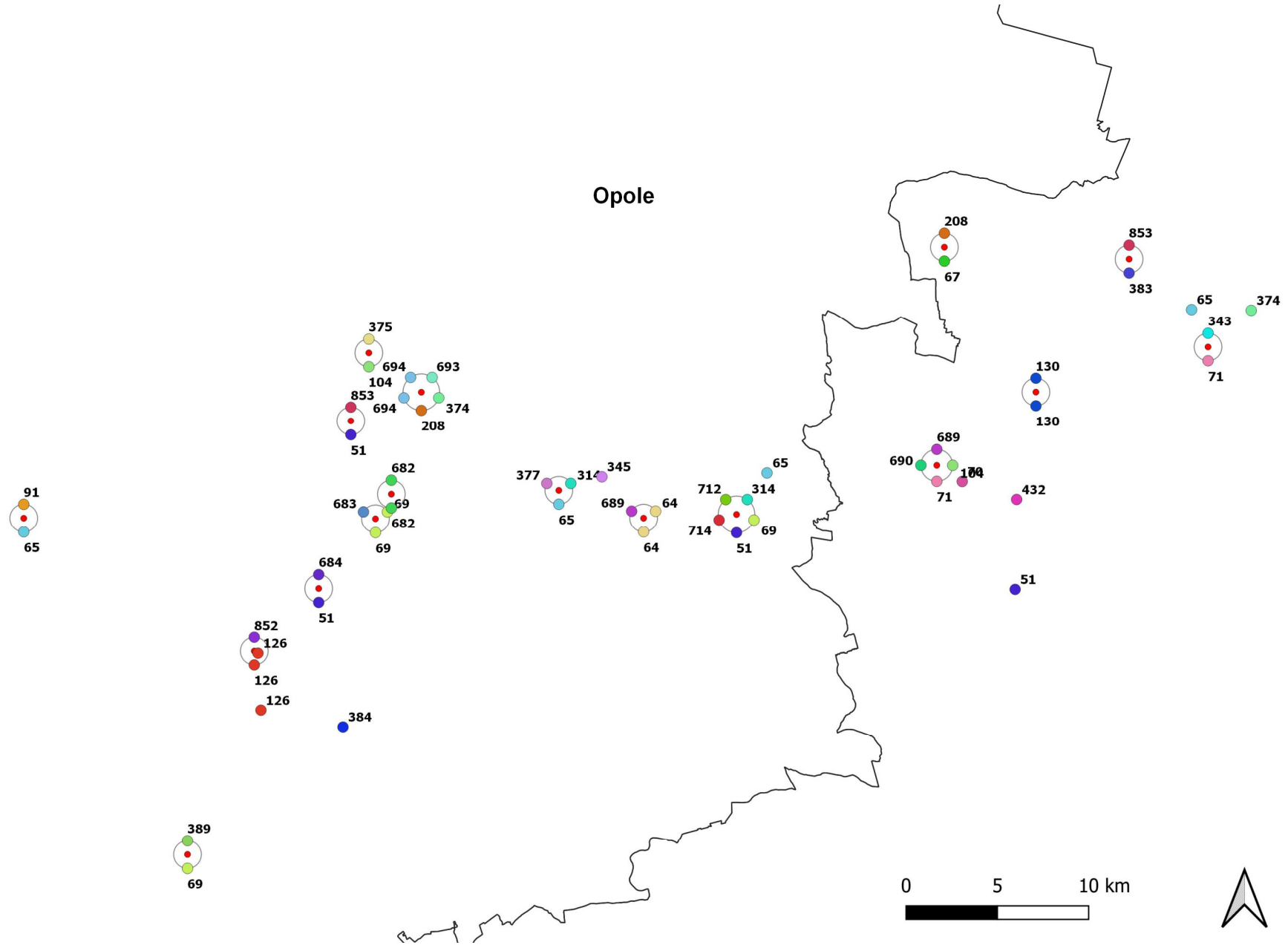


Fig. 2



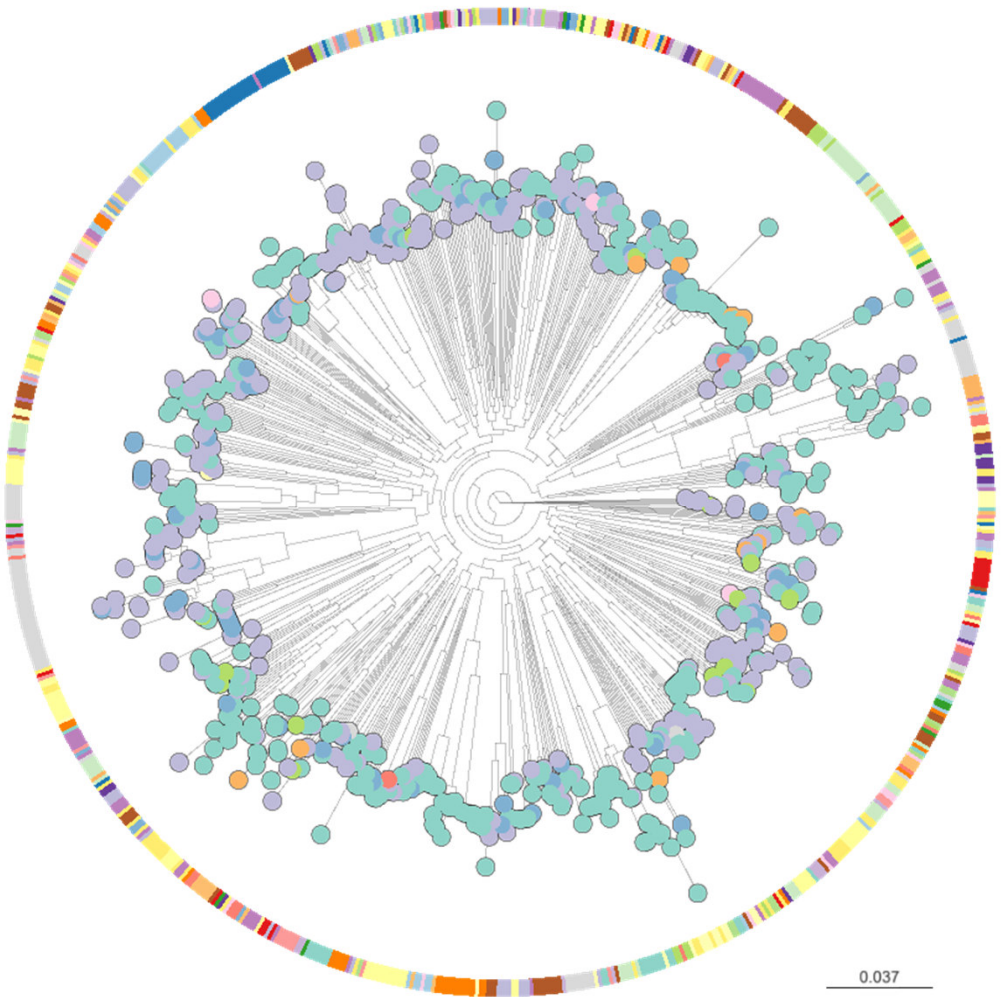


Fig. 3

Fig. 4

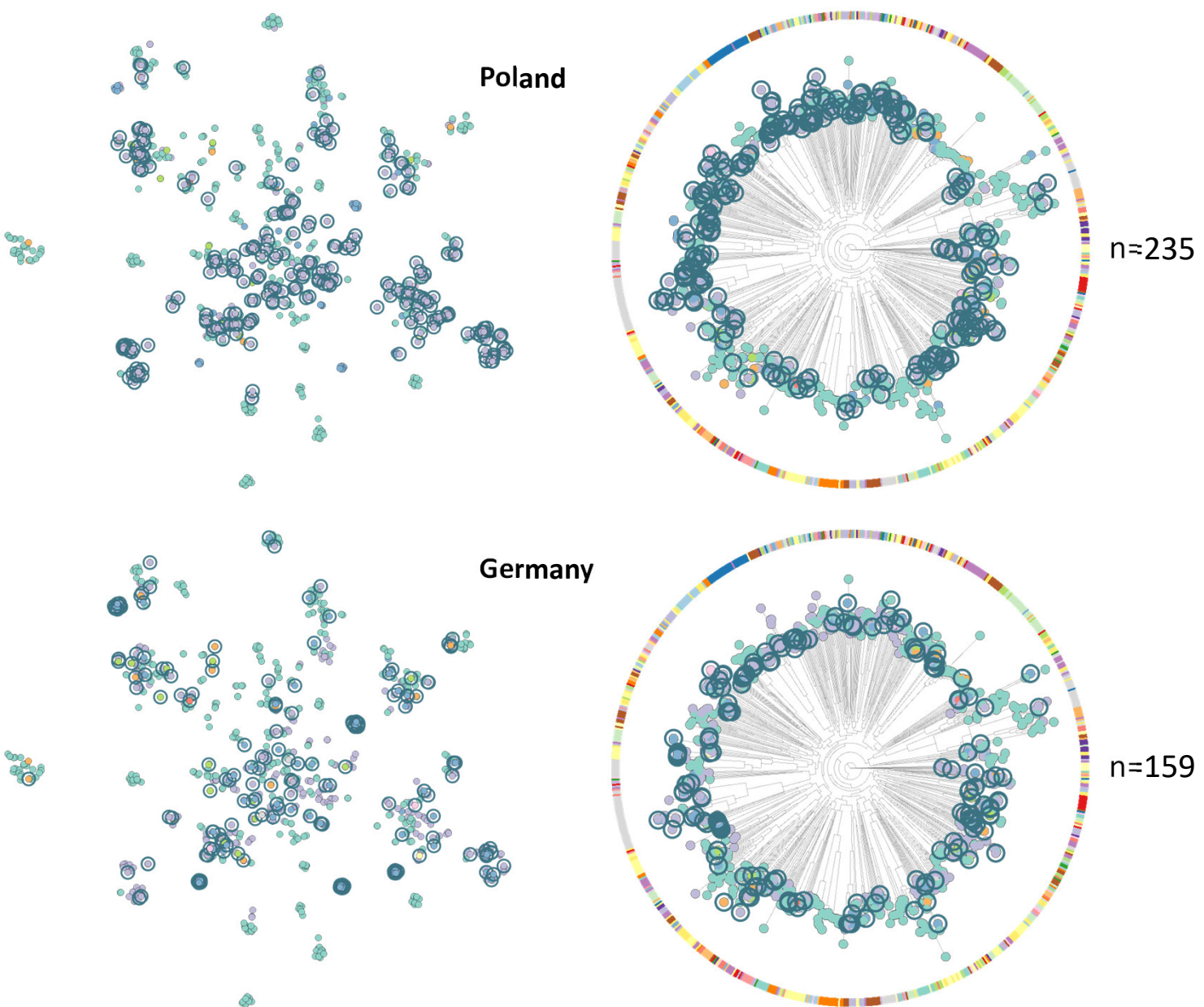
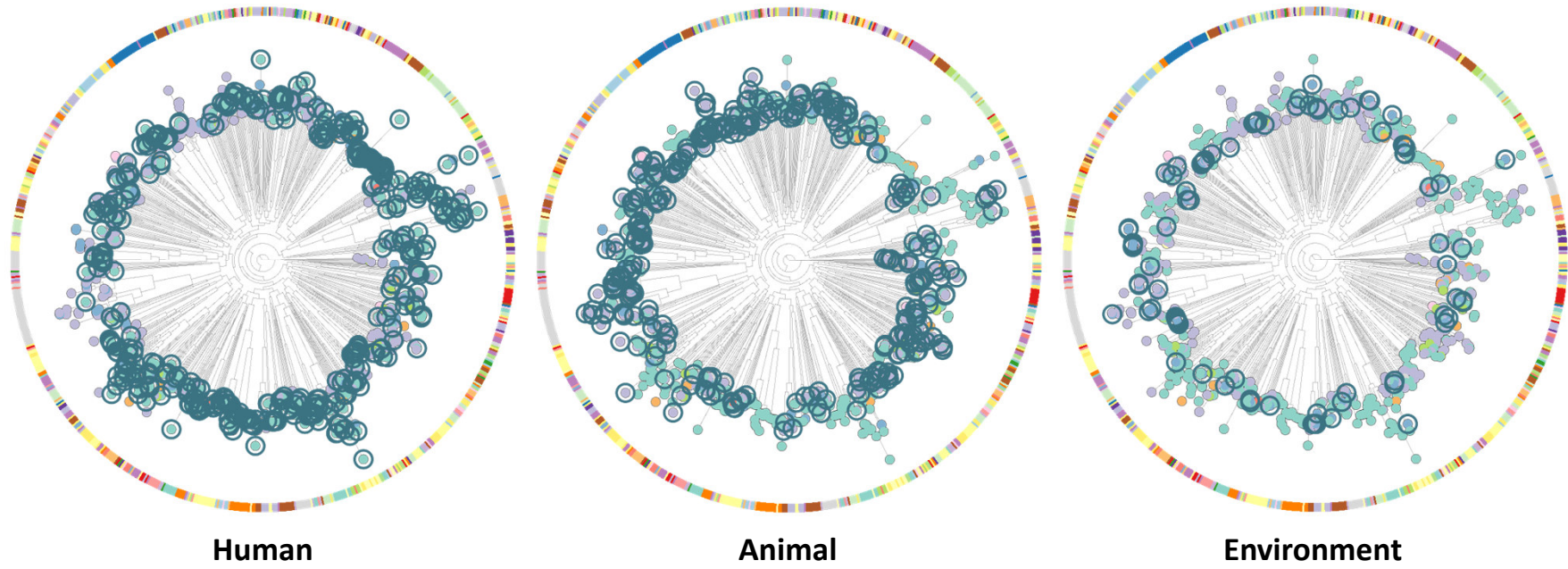


Fig. 5

Phylogenetic distribution of human, animal and environmental isolates



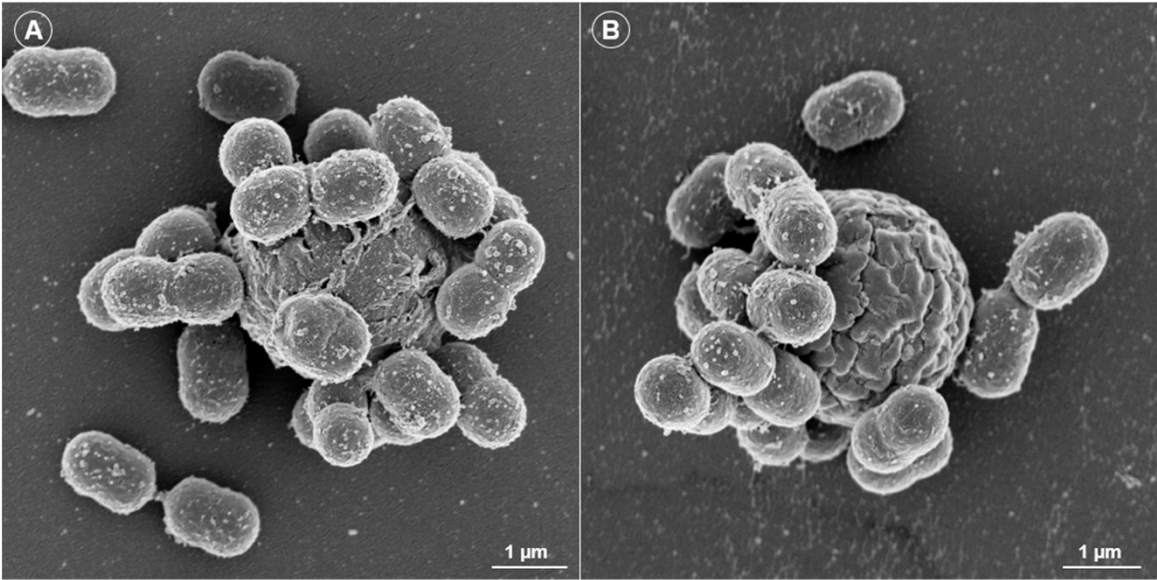


Fig. 6