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► **To cite this version:**

K. Laroucau, F. Vorimore, R. Aaziz, L. Solmonson, R.C. Hsia, et al.. Chlamydia buteonis, a new Chlamydia species isolated from a red-shouldered hawk. Systematic and Applied Microbiology, 2019, 42, pp.125997 -. 10.1016/j.syapm.2019.06.002 . hal-03487805

HAL Id: hal-03487805

<https://hal.science/hal-03487805v1>

Submitted on 20 Jul 2022

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2 ***Chlamydia buteonis*, a new *Chlamydia* species isolated from a red-shouldered hawk**
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16 # equal contribution

17 18 19 **Abstract**

20 *Chlamydiaceae* are obligate intracellular bacterial pathogens for humans and animals. A recent study
21 highlighted that a *Chlamydiaceae* intermediary between *C. psittaci* and *C. abortus* can infect hawks.
22 Here, an isolate was obtained upon passage of cloacal and conjunctival sac material collected from a
23 female hatch-year red-shouldered hawk (*Buteo lineatus*) in cultured cells. The diseased bird, one of 12
24 birds housed in a rehabilitation center, developed conjunctivitis and later died. Swabs from both sites
25 tested positive for *Chlamydia* using the QuickVue Chlamydia test. The isolate, named RSHA, tested
26 negative in qPCR assays specific for *C. psittaci* and *C. abortus*, respectively. Analysis of the 16S rRNA,
27 23S rRNA and whole genome sequences as well as MLST, ANIb and TETRA values reveal that *C.*
28 *psittaci* and *C. abortus* are the closest relatives of RSHA. However, the overall results strongly suggest
29 a phylogenetic intermediate position between these two species. Therefore, we propose the introduction
30 of a new species designated *Chlamydia buteonis* with RSHA^T as the type strain.

31
32 **Keywords:** *Chlamydiaceae*, red-shouldered hawk, MLST, WGS, electron microscopy.

33 34 35 **Introduction**

36 The family *Chlamydiaceae* currently comprises 11 validly published species that are pathogenic to
37 humans and/or animals: *Chlamydia* (*C.*) *abortus*, *C. avium*, *C. caviae*, *C. felis*, *C. gallinacea*, *C.*
38 *muridarum*, *C. pecorum*, *C. pneumoniae*, *C. psittaci*, *C. suis*, and *C. trachomatis* [25].

39 Avian chlamydiosis (ornithosis) and psittacosis, its zoonotically transmitted counterpart in humans, are
40 well-documented diseases caused by the obligate intracellular bacterium *C. psittaci* [26]. It has been
41 reported that more than 467 avian species can be affected by chlamydial infection [13]. In birds, the
42 infection is usually systemic and can be fatal. The severity of clinical signs varies and depends on the
43 species and age of the bird, as well as on the causative *C. psittaci* strain [2]. Genotypes of *C. psittaci*
44 are based on sequences of the gene encoding the major outer membrane protein OmpA and have been
45 tentatively associated with specific hosts, such as ducks, pigeons, psittacines and turkeys [18, 27, 36].
46 In the past decade, the broad use of DNA-based detection tools has revealed the occurrence of
47 chlamydiae other than *C. psittaci* in birds. For example, *C. trachomatis*, *C. abortus* and *C. pecorum*
48 along with non-classified chlamydial organisms have been detected in pigeons [23]. In the past few
49 years, whole-genome sequencing (WGS) analysis of formerly non-classified strains has led to the
50 identification of two new species: *C. avium* and *C. gallinacea* [10, 24]. Atypical strains from wild ibises

51 (*Threskiornis aethiopicus*) were assigned to Candidatus *C. ibidis* [37]. More recently, a group of *C.*
52 *abortus* strains that are distinct from ruminant strains were isolated from wild swans and ducks [32].
53 Overall, this suggests that the spectrum of chlamydial lineages occurring in wild birds is wider than
54 current knowledge indicates.

55 Avian chlamydiosis has been repeatedly diagnosed in raptors, including red-tailed hawks, Swainson's
56 hawks and ferruginous hawks [4, 11, 16, 28]. Detailed whole-genome sequence (WGS) characterization
57 of strain RTH, isolated from a red-tailed hawk, putatively identified a new species separate from other
58 members of the *Chlamydiaceae*, and with *C. psittaci* as its closest relative [12, 21].

59 Here, we describe the isolation and molecular characterization of a new chlamydial strain from a red-
60 shouldered hawk (*Buteo lineatus*).

61

62 **Materials and Methods**

63 **Case description**

64 In August 2016, a female hatch-year red-shouldered hawk (id 16-066) developed conjunctivitis and died
65 within a week. It was the second fatal case among a group of 12 hawks kept in a flight room. The animal
66 was in a good nutritional state based on significant internal adipose tissue stores. At necropsy, a thick
67 beige exudate covered the conjunctival sac of one eye. The liver was slightly swollen and discolored
68 brown. One small beige nodule, approximately 1 mm in diameter, was present in one lung lobe and the
69 spleen was moderately enlarged. Histopathological analysis revealed ulcerations on conjunctival tissues
70 with numerous coccobacilli and non-specific mononuclear hepatitis and splenitis.

71 *Enterococcus faecalis* and *Pseudomonas aeruginosa* were isolated from conjunctival tissue. Following a
72 positive test obtained for a swab collected from the diseased bird using a rapid Chlamydia test, a
73 duplicate swab was used to inoculate Vero cells and a suspected *Chlamydia* strain, designated RSHA,
74 was isolated.

75

76 **Sampling, first diagnosis and isolation procedure**

77 Conjunctival tissue and cloaca were swabbed in duplicate from the dead bird. One swab was tested with
78 the QuickVue Chlamydia test (Quidel) whereas the second one was inoculated onto fresh monolayers of
79 Vero cells, with four dilutions of the inoculum tested. After inoculation, vials were centrifuged at 2,000
80 rpm for 1 h at 30°C. Monolayers were then washed three times with the Chlamydia Hank's solution and
81 1 mL of fresh medium was added to each vial. The vials were then incubated at 37°C for 7 days and
82 examined daily. Each dilution was passed once after 7 days of inoculation. Infected monolayers on
83 coverslips were then fixed with acetone, and monolayers were stained with the 601-RDV *C. psittaci*
84 fluorescent antibody conjugate (National Veterinary Service Laboratories, USA). When inclusions of
85 typical chlamydial morphology were observed as bright apple-green spots, the sample was considered
86 positive. The isolate was kept frozen at -80°C until further processing.

87

88 **DNA-based characterization**

89 Species-specific real-time PCR

90 PCR assays targeting *C. psittaci*, *C. abortus*, *C. avium* and *C. gallinacea* species were conducted as
91 previously described [17, 19, 38, 39].

92

93 Multi Locus Sequence Typing (MLST) analysis

94 Genotyping by MLST was carried out according to the scheme developed by Pannekoek *et al* [18]
95 targeting seven housekeeping genes: *gatA*, *oppA*, *hflX*, *gidA*, *enoA*, *hemN* and *fumC*. Target genes
96 were amplified and sequenced using primers and conditions described on the Chlamydiales MLST web-
97 site (<http://pubmlst.org/chlamydiales/>). Sequencing of both strands was done by Eurofins (Germany).
98 Sequences for each locus were queried against the online Chlamydiales MLST Databases to determine
99 allelic designations and a subsequent allelic profile was used to determine the sequence type (ST). New
100 allele sequences are accessible via the Chlamydiales MLST web-site.

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Preparation of genomic DNA for WGS

Genomic DNA was prepared from 14 mL of a BGM cell culture infected with the RSHA isolate. The suspension was centrifuged at 20,000 *g* at 8°C for 45 min, and the supernatant was discarded. The pellet was resuspended in 40 mL of PBS buffer and centrifuged at 500 *g* for 15 min to remove cell debris. The supernatant was transferred to a fresh tube and high-speed centrifuged as above. The pellet was resuspended in 200 µL of PBS. Prior to DNA extraction, a DNase I (NEB, France) treatment was performed to remove potential contaminating DNA from cells. Genomic DNA was extracted using the Qiamp DNA minikit (Qiagen, France), with an additional RNase A (Roche) treatment, following the cell protocol. DNA was eluted in 50 µL of water and re-purified using the NEBNext Microbiome DNA enrichment kit (NEB, France).

Genome sequencing, assembly and draft annotation

Libraries were prepared using the Nextera XT kit (Illumina). Whole-genome sequencing was performed using an Illumina MiSeq platform (Illumina) according to the manufacturer's instructions. The MiSeq run was carried out on the DNA preparation, with paired-end reads of 150 bp using MiSeq V2 reagents. The raw reads were trimmed with a quality value of 20 and a window size of 5 using Trimmomatic [5] and assembled *de novo* using SPAdes v3.11.1 with the careful parameter and the automatic determination of the k-mer values [3]. To remove residual mammalian sequences from cell culture constituents, scaffolds from SPAdes were subsequently run on the nucleotide database of NCBI. The draft genome was evaluated using Quast v4.6.3 [8] and annotated using Prokka v1.13 [29]. The genome sequence of strain RSHA has been deposited at the European Nucleotide Archive (ENA) under accession number PRJEB30277.

Phylogenetic and genome analysis

The parameters of the tetranucleotide signature frequency correlation coefficient (tetranucleotide regression) and average nucleotide identity (ANIb) were determined as described previously [22] using the program JSpecies v1.2.1 with default parameters.

Nine phylogenetical markers previously described [20] were extracted from 12 *Chlamydiaceae* reference sequences and one outgroup. Amino acid sequences were aligned with mafft v7 [14] and were concatenated to build a reference phylogeny using RAxML v8 [30], with the LG+G+I model and 1000 bootstrap replicates. Pairwise amino acid sequence identities were calculated based on the mafft alignment by Geneious v10 (www.geneious.com).

Electron microscopy

BGM cells were infected with strain RSHA. Infected cells were harvested at 24, 48, 72 and 96 hours post-infection. After washing, cells were fixed in 2% paraformaldehyde and 2.5% glutaraldehyde, scrapped off the culture plate and enrobed in gelatin. Gelatin containing infected cells was trimmed into ~1 mm³ cubes, post-fixed with 1% osmium tetroxide, washed and en-bloc stained with 1% uranyl acetate in water. Specimens were then washed and dehydrated using 30%, 50%, 70%, 90% and 100% ethanol in series, 10 minutes each. This was followed by two more 100% ethanol washes and infiltration with increasing concentrations of Spurr resin (Electron Microscopy Sciences, PA). After two exchanges of pure resin, specimens were embedded in Spurr resin and polymerized at 60°C overnight. Silver colored ultrathin (~70 nm) sections were cut and collected using a Leica UC6 ultramicrotome (Leica Microsystems, Inc., Bannockburn, IL), counterstained with uranyl acetate and lead, and examined in a transmission electron microscope (Tecnai T12, FEI) operated at 80 kV. Digital images were acquired using an AMT bottom mount CCD camera and AMT600 software (Advanced Microscopy Techniques, MA).

Real-time PCR for detection of the new species

151 Specific primers RSHA-F (5'-ATTTCCAACACGCACTGCAT-3') and RSHA-R (5'-
152 TGGGACTAGGTGTTTCTCCCT-3') as well as a specific probe RSHA-P (5'-FAM-
153 GGACAACATGCCTAGATGAAGA -TAMRA 3') were designed using the primer3 software and
154 synthesised by Eurofins MWG Operon. Amplification was performed using the 2X TaqMan Universal
155 PCR Master Mix (Applied Biosystems, Courtaboeuf, France). The final volume of the reaction mixture
156 was 20 µL including 10 µL of master mix, 2 µL of DNA sample, 0.6 µM of each primer, 0.1 µM of the
157 probe and sterile PCR water. Amplification was carried out at a Vii7 thermocycler (Applied Biosystems)
158 using the following cycling parameters: heating at 95 °C for 10 min, 50 cycles of 95 °C for 15 s and 56
159 °C for 1 min. For all PCR reactions, DNA of the isolate RSHA, arbitrarily defined as the reference strain
160 for *C. buteonis*, was used as a positive control, while sterile water was used as negative control. The
161 specificity of the new real-time PCR was evaluated on 32 *Chlamydiaceae* DNA samples (**Table S1**),
162 diluted to a Ct value around 30 when tested with the 23S rRNA-based *Chlamydiaceae*-specific real-time
163 PCR (*Chlamydiaceae* 23S-rtPCR) [7].
164
165

166 Results

167 Molecular characterization of the RSHA isolate

168 DNA from the RSHA isolate tested positive using the *C. psittaci incA*-based real-time PCR assay, but
169 negative using *C. psittaci ompA*-based real-time PCR. The same result was obtained with primers
170 targeting *ompA* of *C. abortus* and with species-specific *C. avium* and *C. gallinacea* real-time PCR
171 systems.

172 MLST genes were successfully amplified using primers designed for *C. psittaci* [18]. Nucleotide
173 sequences were obtained for all 7 MLST genes of the RSHA isolate, and their analysis revealed a new
174 sequence type (sequence type number 196), which was not represented in the *Chlamydiales* database
175 (<http://pubmlst.org/chlamydiales/>). Comparative phylogenetic analysis of the concatenated MLST
176 sequences from RSHA and the corresponding MLST sequences of the RTH strain [12] places the
177 RSHA isolate on the same clade as the RTH isolate, *i.e.* at an intermediate phylogenetic position
178 between *C. abortus* and *C. psittaci* (**Figure 1**).

179 In order to ascertain the species identity of the RSHA isolate, its WGS was obtained resulting in two
180 scaffolds with a length of 770,995 and 375,551 bases and an average coverage of 117x and 106x,
181 respectively. The full plasmid sequence of pRSHA was identified with a length of 7681 bases and an
182 average coverage of 82x. The 16S and 23S rRNA gene sequences were extracted and then aligned
183 with representative sequences of all established *Chlamydiaceae spp.* (**Figure 2** and **Supplementary**
184 **Figure S1**). Sequence homology was greater than 95.17% for 16S and greater than 93.08% for 23S
185 rRNA genes, thus confirming the taxonomic position of strain RSHA within the genus *Chlamydia* and its
186 close relatedness to both *C. psittaci* and *C. abortus* (**Table S2**). While the 23S rRNA sequence could
187 not be extracted from the RTH genome sequence (SRA061571), comparison of the 16S rRNA
188 sequences of the RTH and RSHA isolate revealed a single point mutation difference.

189 Basic genomic features of the RSHA isolate were then compared with those of established species of
190 the *Chlamydiaceae*. The RSHA genome size is 1.14 Mbp, with 977 CDS identified and GC% 38.3.
191 These numbers are in the same range as those for the other chlamydial species (**Table 1**). A plasmid
192 similar to that of *C. psittaci* M56 was also identified in RSHA.

193 Pairwise comparisons of the RSHA genome sequence with genomic sequences of the type strains of
194 RSHA's closest relatives were conducted to determine average nucleotide identity (ANIb) and
195 tetranucleotide regressions. The results in **Table 2** show maximal values of 0.98725 (tetranucleotide
196 regression) and 93.67% (ANIb) between RSHA and type strain 6BC of *C. psittaci*. A similar ANI value
197 (93.96%) was previously reported for the RTH isolate [12].

198 Using a classification scheme recently proposed for the order *Chlamydiales* [20], the percentage of
199 sequence identity was calculated for nine conserved taxonomically informative gene products (RpoN,
200 FtsK, PepF, Adk, HemL, Dna, SucA, Hyp325 and FabI) extracted from the RSHA genome sequence

201 and those of the other 11 *Chlamydia* species. Although results presented in **Figure S2** reveal *C. psittaci*
202 as the most closely related species, all values obtained for RSHA are below the accepted cut-off for
203 species assignment.

204

205 Phenotypic characterization of the strain RSHA

206 RSHA can be propagated under conditions routinely used for culture of chlamydiae, such as in BGM
207 cells or embryonated chicken eggs (not shown). The electron micrograph in **Figure 3** displays a large
208 inclusion in an infected BGM cell with reticulate bodies (RBs), elementary bodies (EBs) and
209 intermediate bodies (IBs). EBs were small (240–330 nm), round and electron dense. RBs appeared
210 larger (450–1100 nm in diameter), round to oval and more electron lucent. Different stages of division by
211 binary fission were seen in RBs. These observations support a conserved biphasic developmental cycle
212 in RSHA as seen in all chlamydiae.

213

214 Diagnostic tools to detect the new taxon

215 A specific real-time PCR assay for RSHA was designed based on the *oxaA* gene locus (see Materials
216 and Methods). This gene has the particularity to be present in the genome of all *Chlamydiaceae* with
217 specific mutations identified for the hawk strain. RSHA, *C. abortus*, *C. avium*, *C. caviae*, *C. gallinacea*,
218 *C. felis*, *C. pecorum* and *C. psittaci* strains were tested using this protocol. The results confirmed the
219 specificity of the assay (data not shown).

220 Measurements on dilution series of cell culture aliquots with defined numbers of inclusion-forming units
221 (IFUs) indicated detection limits in the range of 10 IFUs. As the target *oxaA* sequence of strain RTH is
222 identical to that of strain RSHA, it is safe to assume that it would be detected by this assay as well.

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224

225 **Discussion**

226 The present report of a new taxon underpins the widely held notion among chlamydia researchers that
227 wildlife, and particularly wild birds, harbor yet unknown or non-classified chlamydial organisms [6, 40].

228 In the past decade, advances in DNA-based diagnostic technology have enabled the discovery of new
229 members of the family *Chlamydiaceae*, including *C. avium* and *C. gallinacea* [24], as well as *Candidati*
230 *C. ibidis* [20, 37], *C. sanzinia* [33], *C. corallus* [34], *C. serpentis*, and *C. poikilothermis* [31].

231 In this study, an isolate, named RSHA, obtained from a dead red-shouldered hawk (*Buteo lineatus*) was
232 not detected using *ompA*-based qPCR assays for *C. psittaci* and *C. abortus*, but was detected using an
233 *incA*-based assay originally developed for *C. psittaci*, which was already known to identify certain *C.*
234 *abortus* strains (unpublished data). Preliminary genotyping of this strain based on 7 MLST target genes
235 identified a new sequence type located at an intermediate position between *C. psittaci* and *C. abortus*
236 (**Figure 1**). Intermediate strains from birds have been previously reported [1, 9, 35]. Recently, some of
237 these strains were assigned to the species of *C. abortus* [32] based on 16S rRNA, *ompA*, and MLST
238 analyses.

239 Analysis of WGS data of the RSHA isolate revealed that the criteria for assignment to a new chlamydial
240 species within the family *Chlamydiaceae* were fulfilled. Indeed, according to the recent classification
241 scheme proposed by Pillonel *et al.* [20], sequence identity values of $\geq 80\%$ for 16S rRNA and 23S
242 rRNA, and of $\geq 92.5\%$ for 16S rRNA, $\geq 91\%$ for 23S rRNA confirm the assignment of strain RSHA to the
243 order *Chlamydiales* and family *Chlamydiaceae*, respectively. Furthermore, comparative analysis of nine
244 taxonomically conserved proteins including a representative strain from each member of the *Chlamydia*
245 genus yields sequence identities (RpoN < 96%, FtsK < 98%, PepF < 96%, Adk < 95%, HemL < 95%,
246 DnA $\geq 70\%$, SucA $\geq 64\%$, Hyp325 $\geq 57\%$ and FabI $\geq 78\%$) that are consistent with RSHA being
247 assigned to a new species with *C. psittaci* as closest neighbor. A similar analysis was previously applied
248 *a posteriori* to *C. avium* and *Candidatus C. ibidis* confirming their assignment to new species [20].
249 Recently, the same method was used for the description of *Candidati C. serpentis* and *C. poikilothermis*

250 [31]. The tetra nucleotide regression and ANIb values calculated for RSHA are also below values
251 generally considered for delineating bacterial species [22].
252 In the 1990s, the *C. psittaci*-like strain RTH was isolated from a wild red-tailed hawk (*Buteo jamaicensis*)
253 showing signs of respiratory distress and diarrhea [16]. The genome of this strain was recently
254 sequenced and further analysis suggested that RTH represents a new species in the family
255 *Chlamydiaceae* [12]. Although the 23S rRNA sequence could not be extracted from the RTH genome
256 sequence owing to incomplete assembly and low coverage, comparison of the RTH and RSHA 16S
257 rRNA and MLST sequences revealed complete sequence identity, with the exception of a single
258 nucleotide polymorphism in the 16S rRNA gene sequence, thus strongly suggesting a close
259 evolutionary relationship between these two strains. Unfortunately, none of the nine taxonomically
260 conserved protein sequences could be fully extracted from the published RTH genome sequence data
261 (SRA061571). However, comparison of the incompletely assembled RTH sequences with those of
262 RSHA revealed a strong percentage of identity between these two strains (around 99%; not shown).
263 In consequence, we propose classifying the two hawk strains as members of a new species to be
264 designated as *Chlamydia buteonis* sp. nov., with strain RSHA^T as the type strain.
265 The epidemiological and clinical importance of the proposed new species has yet to be determined.
266 Respiratory distress and diarrhea were reported in the red-tailed hawk (*Buteo jamaicensis*) infected by
267 the RTH isolate [16], while conjunctivitis was observed in the red-shouldered hawk (*Buteo lineatus*)
268 sampled in this study. Few reports have focused on clinical signs associated with chlamydial infections
269 in predatory birds. However, lethargy, weight loss, moderate to severe leukocytosis, and radiographic
270 evidence of splenomegaly were recently reported in a wild bird population [15]. Therefore, future studies
271 of clinical cases in these birds should take the present findings into account. *C. psittaci*-like strains were
272 recently detected in red-tailed and Swainson's hawks from California, with a best sequence alignment of
273 the *ompA* gene, with the *C. psittaci* M56 genotype. It will be important to re-analyze these strains with
274 the new PCR assay specific for *C. buteonis*. Moreover, the assay we have developed for *C. buteonis*
275 should be applied to identify potential pathogens when diseased raptors belonging to the genus *Buteo*
276 are sampled.

277

278 **Description of *Chlamydia buteonis* sp. nov.**

279 *Chlamydia buteonis* (bu.te.o'nis. L. gen. n. buteonis of a buzzard, of a bird of the genus Buteo).

280 *C. buteonis* strains occur in raptor birds called buzzards in Europe and hawks in North America. The
281 agent can be recovered from tissue of the conjunctiva and contents of the cloaca. From the cases seen
282 so far, it seems likely that *C. buteonis* can cause conjunctivitis and/or respiratory signs, or at least be a
283 contributing factor to these clinical manifestations.

284 Natural routes of transmission have yet to be investigated, but, analogous to most other chlamydiae,
285 airborne transmission through aerosolized dry feces and dust particles seems possible. The potential for
286 zoonotic infection of humans is unknown.

287 *C. buteonis* strains can be grown in cell culture or embryonated chicken eggs. Their growth is
288 characterized by a biphasic developmental cycle, which is encountered in the other *Chlamydia* spp. as
289 well. Electron microscopy is the method of choice to visualize the typical vacuole-like intracellular
290 inclusions harboring the various morphological forms, i.e. elementary, reticulate and intermediate
291 bodies.

292 Members of the species can be specifically identified using real-time PCR targeting the *oxaA* gene locus
293 as described in Materials and Methods. In addition, MLST based on 7 housekeeping genes and 16S
294 rRNA gene sequence alignments can be used for identification. Sequence homology of *C. buteonis* 16S
295 genes to those of other *Chlamydia* spp. is greater than 95.17 %, with *C. psittaci* and *C. abortus* being
296 the closest relatives. The size of the circular *C. buteonis* genome is 1.14 Mbp, with a G+C value of 38.3
297 mol-%. The type strain was found to harbor a plasmid sized 7681 bp and similar to that of *C. psittaci*
298 M56. Strain RSHA^T isolated from a red-shouldered hawk (*Buteo lineatus*) is the designated type strain
299 of *C. buteonis*.

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409 **Tables & Figures**

410

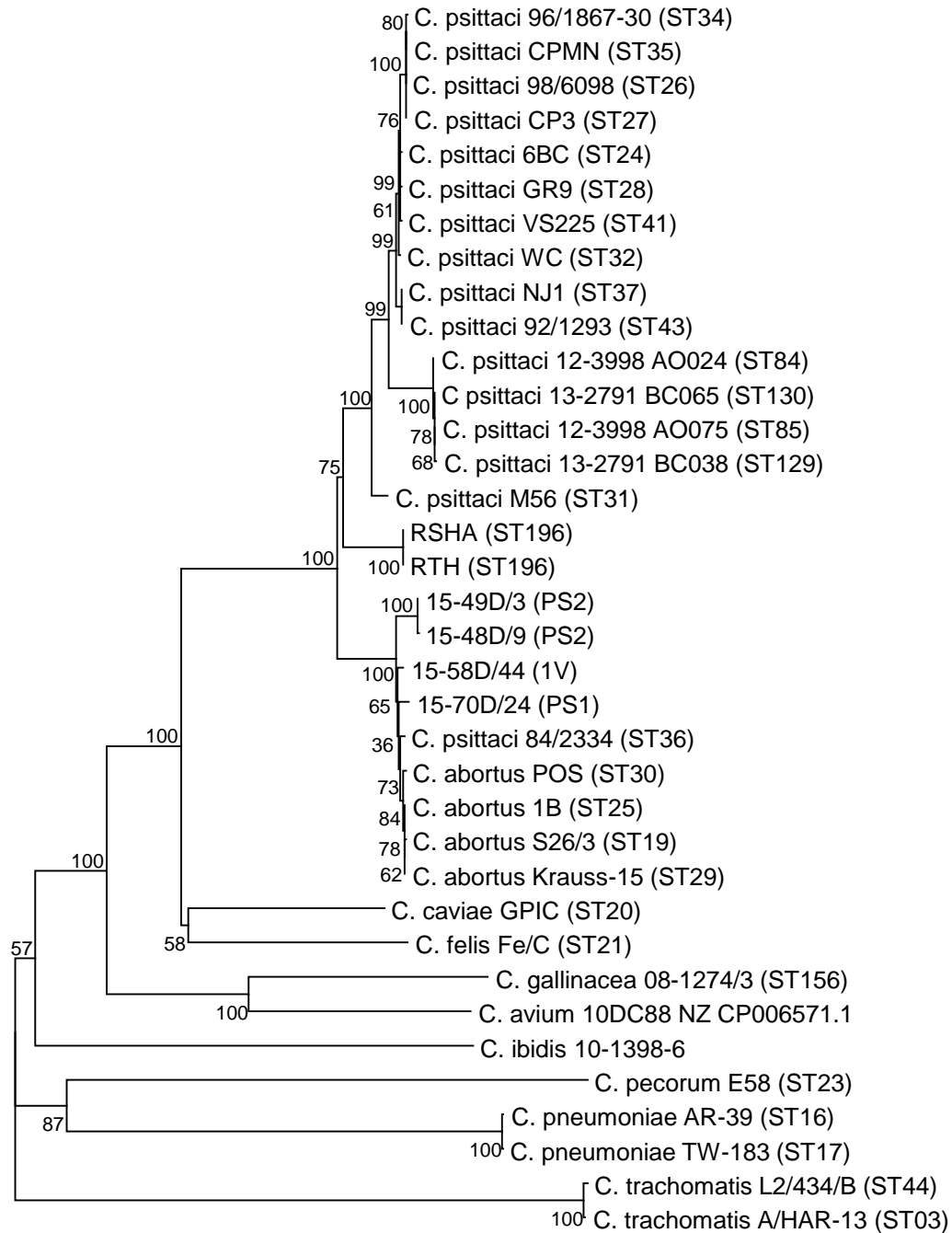
411 **Figure 1.** Phylogenetic analyses of concatenated sequences of 7 MLST housekeeping gene fragments
412 (*enoA*, *fumC*, *gatA*, *gidA*, *hemN*, *hlfX*, and *oppA*) for the RSHA isolate and established *Chlamydiaceae*
413 species, including a larger number of representatives for *C. psittaci* and *C. abortus* species.
414

415 **Figure 2.** Dendrogram based on the analysis of the complete 16S rRNA sequences from the RSHA
416 isolate and from the type strains of twelve *Chlamydiaceae*, including the candidatus *C. ibidis*
417 representative. The dendrogram was constructed by UPGMA method from a similarity matrix calculated
418 by pairwise alignment. Branch quality was calculated by cophenetic correlation. Horizontal distances
419 correspond to genetic distances expressed in percentage of sequence similarity.
420

421 **Figure 3.** Electron microscopic images of BGM cell culture infected with RSHA, after 72h. One inclusion
422 is depicted with a mixture of RBs and EBs.
423

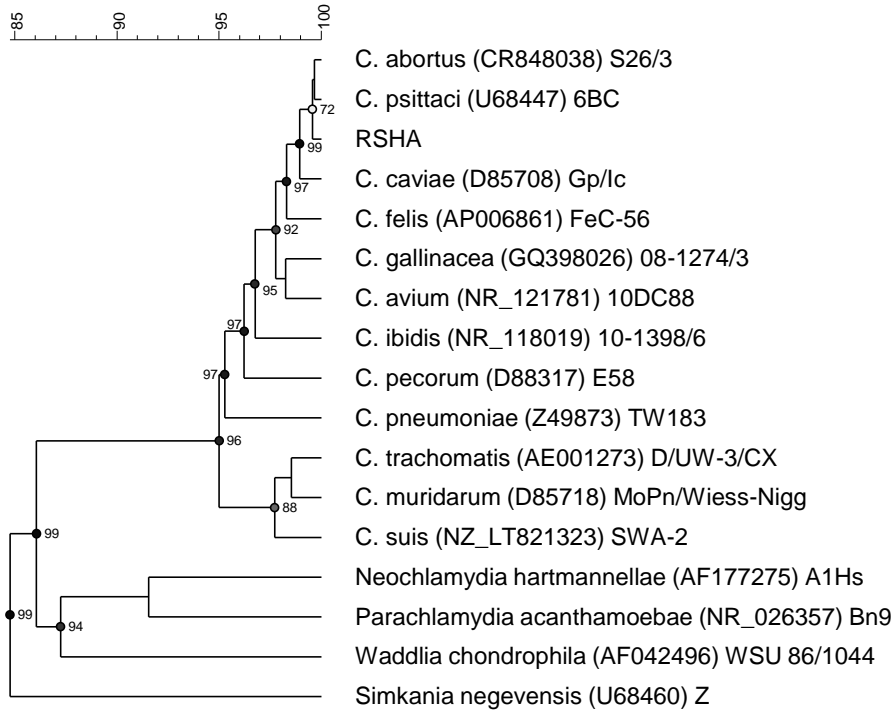
424 **Table 1.** Comparison of basic genomic features of RSHA with those of established species of
425 *Chlamydiaceae*.
426

427 **Table 2.** Pairwise comparison of the available genome sequences of the type strains of *Chlamydiaceae*
428 species based on average nucleotide identity (ANI_b; lower triangle) and tetranucleotide signature
429 correlation index (upper triangle).
430

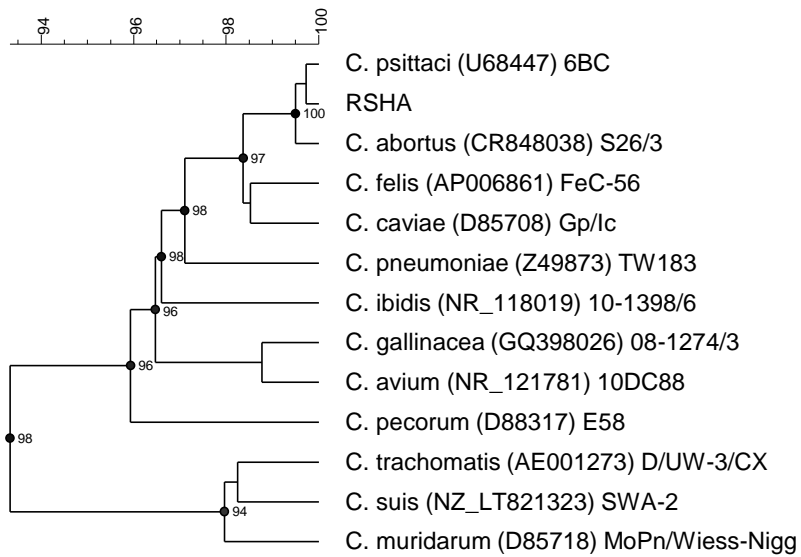


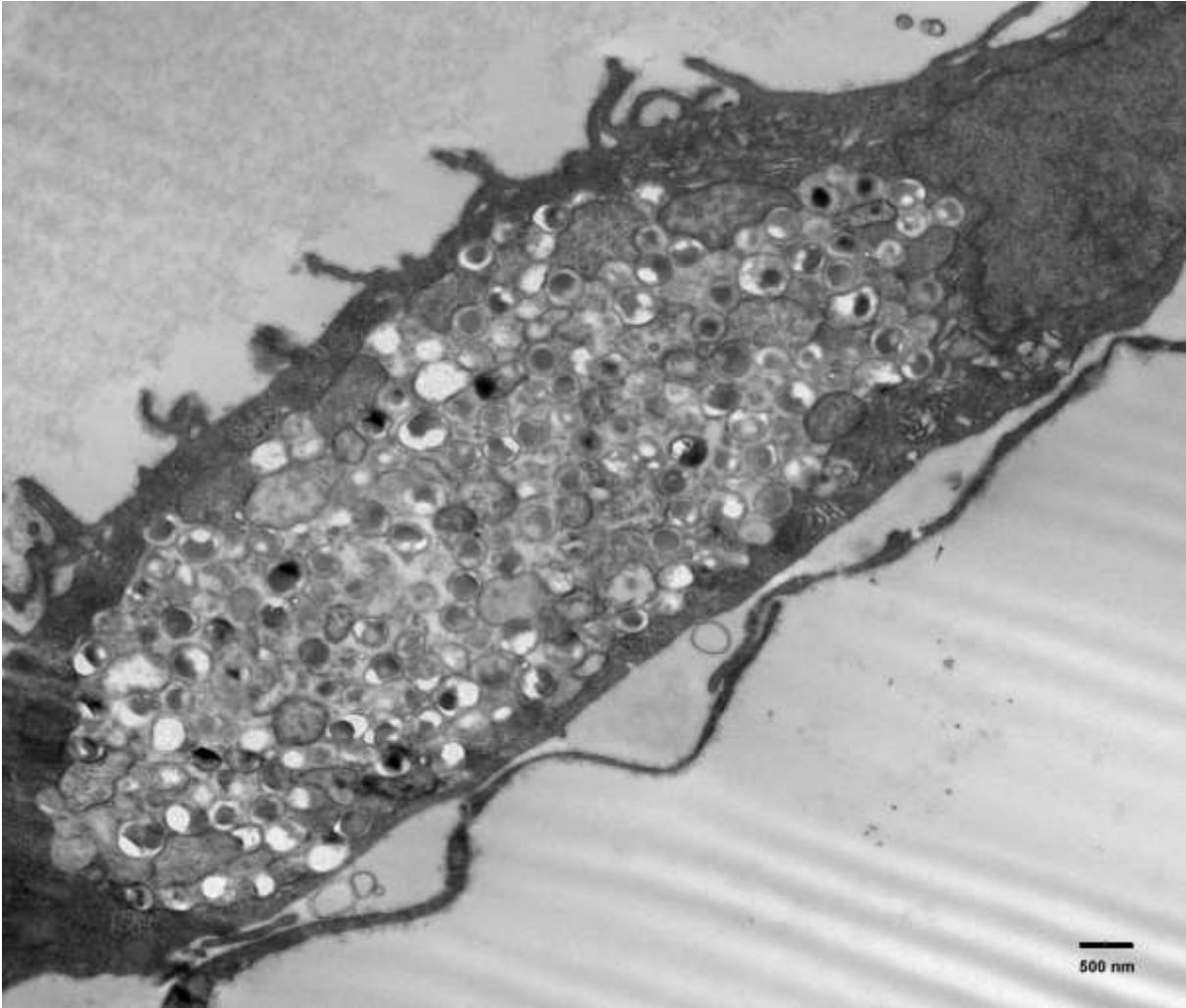
0.05

16S



23S





	RSHA	<i>C. psittaci</i> 6BC	<i>C. abortus</i> S26/3	<i>C. caviae</i> GPIC	<i>C. felis</i> Fe/C-56	<i>C. avium</i> 10DC88	<i>C. gallinacea</i> 08-1274/3	<i>C. ibidis</i> 10-1398/6	<i>C. pecorum</i> E58	<i>C. pneumoniae</i> TW-183	<i>C. muridarum</i> MoPn/Weiss-Nigg	<i>C. trachomatis</i> D/UW-3/CX	<i>C. suis</i> SWA-2
length	1,146,546	1,171,667	1,144,377	1,173,390	1,166,239	1,041,170	1,059,583	1,146,066	1,106,197	1,225,935	1,072,950	1,042,519	1,075,789
G+C mol-%	38.29	39.1	39.9	39.2	39.4	36.9	37.86	38.3	41.1	40.6	40.3	41.3	42.06
Genes (incl. pseudogenes)	977	1034	1028	1030	1024	956	962	963	985	1120	952	935	927
5S rRNA	1	1	1	1	1	1	2	1	1	1	2	2	2
16S rRNA	1	1	1	1	1	1	1	1	1	1	2	2	2
23S rRNA	1	1	1	1	1	1	1	1	1	1	2	2	2
tRNA	38	38	38	38	38	39	39	38	38	38	37	37	37
tmRNA	1	1	1	1	1	1	1	1	1	1	1	1	1
plasmid	1	1	0	1	1	1	1	1	0	0	1	0	1

	RSHA	<i>C. psittaci</i> 6BC	<i>C. abortus</i> S26/3	<i>C. caviae</i> Gp/lc	<i>C. felis</i> Fe/Pn-1	<i>C. avium</i> 10DC88	<i>C. gallinacea</i> 08-1274/3	<i>C. ibidis</i> 10-1398/6	<i>C. pecorum</i> E58	<i>C. pneumoniae</i> TW183	<i>C. muridarum</i> MoPn/Wiess- Nigg	<i>C. trachomatis</i> D/UW-3/CX	<i>C. suis</i> SWA-2
RSHA		0.9872	0.9663	0.9658	0.9702	0.9396	0.9477	0.9073	0.8567	0.8696	0.8550	0.8315	0.8295
<i>C. psittaci</i> 6BC	93.67		0.9860	0.9698	0.9665	0.9235	0.9413	0.8865	0.8831	0.8961	0.8546	0.8428	0.8332
<i>C. abortus</i> S26/3	92.47	92.58		0.9565	0.9567	0.8983	0.9233	0.8565	0.8832	0.9039	0.8358	0.8347	0.8213
<i>C. caviae</i> Gp/lc	81.70	81.26	80.26		0.9510	0.9007	0.9114	0.8488	0.8921	0.9114	0.8441	0.8341	0.8198
<i>C. felis</i> Fe/Pn-1	81.20	80.84	79.82	82.00		0.9276	0.9475	0.8836	0.8739	0.8769	0.8433	0.8303	0.8365
<i>C. avium</i> 10DC88	73.80	73.86	73.57	74.04	73.63		0.9864	0.9329	0.8114	0.8094	0.8060	0.7658	0.7786
<i>C. gallinacea</i> 08-1274/3	73.24	73.34	73.33	73.71	73.19	81.09		0.9258	0.8332	0.8325	0.8217	0.7885	0.8001
<i>C. ibidis</i> 10-1398/6	70.92	70.87	70.55	70.81	70.64	69.93	69.74		0.7293	0.7106	0.8077	0.7698	0.7728
<i>C. pecorum</i> E58	68.89	68.84	68.75	69.00	68.86	68.49	68.34	67.81		0.9022	0.7761	0.7899	0.7761
<i>C. pneumoniae</i> TW183	69.78	69.57	69.50	69.85	69.67	68.97	68.93	68.40	69.32		0.7969	0.7883	0.7855
<i>C. muridarum</i> MoPn/Wiess-Nigg	68.30	68.60	68.58	68.72	68.46	68.30	68.26	67.80	67.13	67.57		0.9722	0.9770
<i>C. trachomatis</i> D/UW-3/CX	68.54	68.37	68.29	68.47	68.23	68.01	68.01	68.07	67.26	67.54	79.95		0.9718
<i>C. suis</i> SWA-2	68.02	68.36	68.38	68.22	68.21	67.80	67.93	67.68	67.06	67.35	81.53	78.84	