Emended description of *Actinobacillus capsulatus* Arseculeratne 1962, 38^{AL}

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The taxonomic position of *Actinobacillus capsulatus*, a member of the family *Pasteurellaceae* found in rabbits, hares and hamsters, has been challenged. 16S rRNA gene (*rrs*) sequence data show the species to be heterogeneous. Using a polyphasic approach, 23 strains that were identified previously as belonging, or closely related, to *A. capsulatus* were analysed. Eighty characters were included in the phenotypic analysis. Phylogenetic analysis was done based on *rrs*, *rpoB*, *infB* and *recN* sequences. In addition, the *recN* sequence similarities were used to calculate the whole-genome sequence relatedness of all strains investigated as well as that with other members of the family *Pasteurellaceae*. The phenotypic analysis allowed identification of five groups. The major group of 17 strains could be classified as *A. capsulatus*. Two hamster isolates were closely related to *A. capsulatus* but differed in a few characters. Single isolates from a rabbit and snowshoe-hare were phenotypically related to *Actinobacillus suis*. One rabbit isolate was related to the genus *Mannheimia*, while another isolate could not be classified phenotypically with known taxa. The phylogenetic analysis confirmed the phenotypic grouping. In contrast to the *rrs*-based tree, the *A. capsulatus* strains clustered unambiguously with the type species and related species of the genus *Actinobacillus* in the *rpoB*-, *infB*- and *recN*-based trees. Genome similarity comparison using *recN* finally confirmed the high genomic relationship of the *A. capsulatus* strains with the type species and related species of the genus *Actinobacillus* and allowed a clear assignment of the other unrelated strains to the phenotypic and phylogenetic clusters outlined. The present findings allow the description of *A. capsulatus* to be emended and separate it more clearly from other species, both phenotypically and genotypically. The type strain of *A. capsulatus* is CCUG 12396^T (=Frederiksen 243^T=ATCC 51571^T=NCTC 11408^T=CIP 103283^T).

Actinobacillus capsulatus was first reported by Arseculeratne in 1962 as a cause of joint disease in laboratory rabbits in Sri Lanka (Arseculeratne, 1962). To the knowledge of the authors very few cases have been reported since then. Isolates of *A. capsulatus* from the uterus of rabbits, previously misclassified as *Actinobacillus equuli*, were reported by Blackall *et al.* (1997), while organisms closely related to *A. capsulatus* have been reported from hamsters (Krause *et al.*, 1989), free-ranging snowshoe-hares (*Lepus americanus*) (Zarnke & Schlater, 1988) and European brown hares (Bisgaard, 1993). Additional isolates were included in the studies of Bercovier *et al.* (1984) and Escande *et al.* (1984).

The GenBank/EMBL/DBJ accession numbers for the 16S rRNA (*rrs*), *infB*, *recN* and *rpoB* gene sequences determined in this study are given in Fig. 1 and Supplementary Figs S1–S3.

Phylogenetic trees based on *infB*, *rpoB* and *recN* genes and a table showing the phenotypic characters of the strains investigated are available as supplementary material in IJSEM Online.

The genus *Actinobacillus* Brumpt 1910 consists of 18 species (Olsen & Møller, 2005). The work of Dewhirst *et al.* (1992) on the 16S rRNA gene (*rrs*) phylogeny showed that a core group clusters around the type species *Actinobacillus lignieresii*, whereas other actinobacilli, including *A. capsulatus*, cluster outside this group. This core group is often referred to as *Actinobacillus sensu stricto* or 'true actinobacilli' (Olsen & Møller, 2005), even though a defined emended description of the genus is lacking. Here the core group of *Actinobacillus* is referred to as including the type species *A. lignieresii* and the species *Actinobacillus arthritidis*, *A. equuli*, *Actinobacillus hominis*, *Actinobacillus pleuropneumoniae*, *Actinobacillus suis* and *Actinobacillus ureae*. Based on the work of Dewhirst *et al.* (1992), an attempt to exclude *A. capsulatus* from the genus *Actinobacillus* began, even though DNA–DNA reassociation studies indicated that it is correctly named (Escande *et al.*, 1984; Mutters *et al.*, 1989). Phylogenetic analysis of members of *Actinobacillus* based upon partial sequences of the *infB* gene (encoding translation initiation factor 2) left

the position of *A. capsulatus* unresolved (Nørskov-Lauritsen *et al.*, 2004). However, phylogenetic studies of the family *Pasteurellaceae* based on *rpoB* (encoding the β -subunit of RNA polymerase) sequences grouped *A. capsulatus* within core *Actinobacillus* species (Korczak *et al.*, 2004). Clustering of the type strain of *A. capsulatus* with core *Actinobacillus* species was also seen by using multilocus sequence analysis (Kuhnert & Korczak, 2006).

Comparison of *rrs* gene sequences of strains deposited as *A. capsulatus* indicates that the taxon is heterogeneous, possibly reflecting the inclusion of strains that were not isolated from rabbits, strains that had been misclassified or sequences that had been wrongly annotated, such as the horse isolate CCUG 19799^T that was originally deposited as *A. capsulatus* but was classified recently as the type strain of *A. equuli* subsp. *haemolyticus* (Christensen *et al.*, 2002). To investigate the reasons behind the diversity observed and to clarify the classification of *A. capsulatus*, a strain collection representing isolates from various animal species and several continents was reinvestigated using a polyphasic approach. A total of 23 strains that had been characterized previously as, or closely related to, *A. capsulatus* (Table 1) were analysed phenotypically and genotypically.

A total of 80 characters were used for phenotypic analysis of each strain using tests adopted mainly from Bisgaard *et al.*

(1991) with reference to ‘Cowan and Steel’s Manual’ (Barrow & Feltham, 1993).

Sequencing of *rrs*, *rpoB* and *infB* genes, as established phylogenetic markers for the family *Pasteurellaceae*, was used to investigate the relationship between strains based on previously described protocols by which about 1360, 520 and 1340 bp, respectively, of the *rrs*, *rpoB* and *infB* genes were determined (Kuhnert *et al.*, 2002, 2004; Korczak *et al.*, 2004). In addition, *recN* gene sequences were used as a representative target for determining whole-genome sequence similarity as described by Kuhnert & Korczak (2006), with 1340 bp of the gene being sequenced. Whole-genome similarity values were calculated based on the formula: $SI_{\text{genome}} = -1.30 + 2.25(SI_{\text{recN}})$ of Zeigler (2003), where SI is sequence identity. The *recN* sequences were also included in the phylogenetic analysis.

The results from the analysis of the 80 phenotypic characters are shown in Supplementary Table S1 available in IJSEM Online. Characters that differentiate the strains investigated are given in Table 2. Phenotypic analysis allowed separation of the 23 strains into five groups. The main group consisted of 17 strains that exhibited the same phenotypic features as the *A. capsulatus* type strain (CCUG 12396^T) and were therefore classified as *A. capsulatus*. Two hamster isolates (CCUG 23125 and CCUG 26442) were closely related to *A.*

Table 1. Strains of *Actinobacillus capsulatus* and related strains investigated

Strain	Source of isolation	Country*
CCUG 12396 ^T	Joint, rabbit	SL
CCUG 23125 (=Kunstyr 570/85)	Osteomyelitis, hamster	D
CCUG 26442 (=MCCM 468=Kunstyr 570/85 =CCUG 37034=CCUG 37035)	Osteomyelitis, hamster	D
CCUG 37036 (=Kunstyr 640/89)	Sepsis, kitten	D
CCUG 37038 (=Wuthe DS 1089/92)	Lung, rabbit	D
CCUG 37798 (=SVA B707/97)	Wound, rabbit	S
CCUG 37956	Nose, rabbit	S
266/2693	Uterus, rabbit	B
266/3356 (=516/76)	Rabbit	DK
266/5603	Nares, rabbit	B
266/5695	Unknown	B
266/7370	Conjunctiva, hare	B
P244	Rabbit	SL
P796	Rabbit, lung	B
P224	Rabbit, lung	DK
J3-241	Respiratory tract, hare	USA
E1668/1	Uterus, rabbit	AUS
E1668/3	Uterus, rabbit	AUS
E1668/4	Uterus, rabbit	AUS
BK2999.1	Nose, rabbit	B
BJ4105.3	Pus, rabbit	B
R46	Nose, rabbit	B
R80	Intestine, rabbit	B

*AUS, Australia; B, Belgium; D, Germany; DK, Denmark; S, Sweden; SL, Sri Lanka.

Table 2. Phenotypic characters that differentiate the strains investigated

Taxa: 1, *A. capsulatus*; 2, hamster isolates CCUG 23125 and CCUG 26442; 3, rabbit isolate R46; 4, rabbit isolate P224; 5, rabbit isolate R80; 6, snowshoe-hare isolate J3-241. +, 90% or more of the strains (or strain) positive within 1–2 days; (+), 90% or more of the strains (or strain) positive within 3–14 days; –, 10% or less of the strains (or strain) positive within 14 days; d, 11–89% of the strains are positive; w, weakly positive.

Character	1	2	3	4	5	6
Urease	+	+	–	–	+	+
β -Haemolysis (bovine blood)	–	–	–	–	–	+
CAMP (bovine blood)*	w	–	–	–	w	+
Growth on MacConkey agar	d	–	–	–	+	–
Presence of yellowish pigment	–	–	–	–	w	w
(+)-L-Arabinose	d	–	(+)	+	–	+
myo-Inositol	–	–	(+)	(+)	–	–
(–)-D-Mannitol	+	+	+	+	–	+
(–)-D-Sorbitol	+	–	+	+	–	–
(–)-L-Fucose	–	–	w	(+)	–	–
(+)-D-Mannose	+	+	+	–	+	+
Glycosides	+	+	+	–	+	+
β -Glucosidase	+	+	+	–	+	+
Lactose	+	+	–	(+)	+	+
β -Galactosidase	+	+	–	+	+	+
(+)-D-Melibiose	+/(+)	+	(+)	–	+	+
Trehalose	+	+	+	–	+	+
Raffinose	+	+	+	–	+	+
α -Galactosidase	+	+	+	–	+	+
α -Glucosidase	d	+	+	–	+	–
β -Xylosidase	–	–	–	–	+	+

*CAMP is an abbreviation of the first letters of the surnames of the authors who described the test (Christie *et al.*, 1944).

†Aesculin negative.

capsulatus, but differed from it in CAMP, (+)-L-arabinose, (–)-D-sorbitol, α -glucosidase and growth on MacConkey agar. One rabbit (R80) and the snowshoe-hare (J3-241) isolates were related to *A. suis*. Strain R80 represents a non-haemolytic and (+)-L-arabinose-negative isolate, whereas isolate J3-241 represents a (–)-D-mannitol-positive and α -glucosidase-negative isolate of *A. suis* (Christensen & Bisgaard, 2004). The two isolates P224 and R46 were both negative for urease and therefore differed in a key character from the core group of *Actinobacillus* (Christensen & Bisgaard, 2004). Whereas isolate P224 was related to *Mannheimia granulomatis*, only differing in (+)-L-arabinose and β -glucosidase, strain R46 could not be identified further phenotypically.

Based on the extended phenotypic characterization, *A. capsulatus* differs slightly from the characters listed in Olsen & Møller (2005). Growth on MacConkey agar appears to be isolate-dependent and most strains will not grow on this

medium. Also, oxidase and catalase reactions are isolate-dependent, with most strains being positive for both. Comparing characters used for identifying taxa of the core group of *Actinobacillus* described by Christensen & Bisgaard (2004) the following results were obtained. Catalase, oxidase, glycerol, (+)-L-arabinose and α -glucosidase (PNPG) are isolate-dependent with most strains being positive. β -Haemolysis, (–)-D-arabinose, (–)-L-fucose, inulin and β -xylosidase (ONPX) are negative. Acid is produced from (+)-D-xylose, (+)-D-mannose, cellobiose, β -glucosidase (NPG), lactose, β -galactosidase (ONPG), (+)-D-melibiose, trehalose, raffinose and α -galactosidase. These characters also allow separation of *A. capsulatus* from the other species within the genus.

A phylogenetic analysis was carried out with all strains. Trees were built in BioNumerics v. 4.5 (Applied Maths) using the Jukes–Cantor correction for matrix calculation and neighbour-joining for generating the tree. Previous investigations have shown that the *rrs* gene often represents a phylogeny that is different from that derived from protein-encoding housekeeping genes, especially in the case of *A. capsulatus* (Korczak *et al.*, 2004, 2006; Kuhnert & Korczak, 2006). We therefore built two separate trees. Fig. 1 shows the classical *rrs*-derived tree and Fig. 2 a consensus tree derived from the matrices of individual trees of the *infB*, *rpoB* and *recN* gene sequences. The three individual trees are available as Supplementary Figs S1–S3, respectively, in IJSEM Online. Calculated using the Pearson correlation, the three trees showed a high degree of congruence between each other (>92%), whereas the congruence of each of the three trees with the *rrs* tree was only around 70%. In the *rpoB*-, *infB*- and *recN*-based trees, the phenotypic group of 17 *A. capsulatus* strains clustered within the core of *Actinobacillus* species, as was also seen in the consensus tree (Fig. 2). This cluster of 17 strains was very homogeneous, except with respect to strains CCUG 37798, 266/2693 and P796 in the *rpoB* gene-derived tree where these strains formed a cluster outside the main *A. capsulatus* branch. The same cluster of 17 *A. capsulatus* strains was found in the *rrs* gene-based tree; however, it was clearly outside the core *Actinobacillus* species cluster (Fig. 1). Strains CCUG 37798, 266/2693 and P796 also clustered separately in the *rrs* gene-derived tree. A remarkable observation was the sequence heterogeneity within the *A. capsulatus* cluster. The variability of the *rrs* sequences of *A. capsulatus* was as high as 3.3%, which is normally considered as a sequence difference that allows separation of species (Stackebrandt *et al.*, 2002). In contrast, the *rpoB*, *infB* and *recN* sequence heterogeneity within the cluster of 17 *A. capsulatus* strains was as low as 2.7 (including the three divergent isolates), 0.4 and 0.5%, respectively. This is remarkable since the variability of *rpoB* and *infB* as well as *recN* is normally much higher than that of the *rrs* gene, which is more conserved. The reason for this anomaly in this case is not clear but it might indicate that the *rrs* gene in *A. capsulatus* is prone to relatively high mutation rates and/or horizontal gene transfer that is known to occur with *rrs* genes (Yap *et al.*, 1999; Acinas *et al.*, 2004). This might also

Fig. 1. Phylogenetic tree based on the *rrs* gene. The Jukes–Cantor correction was applied for the distance matrix and neighbour-joining for tree construction. Percentage bootstrap values based on 500 simulations were calculated and are indicated at major branch points. Bar, 2% sequence divergence. *Genome sequence available at www.genome.ou.edu

Fig. 2. Consensus tree based on three genes. Individual trees based on *rpoB*, *infB* and *recN* sequences were used to generate a combined tree, built using BioNumerics. The Jukes–Cantor correction was applied for the distance matrix and neighbour-joining for tree construction. Cophenetic correlations are given, indicating the reliability of the branching compared to the actual genetic relatedness of the taxa. Numbers at nodes are percentage bootstrap values based on 500 simulations. Bar, 4% sequence divergence. The individual trees are available as Supplementary Figs S1–S3 in IJSEM Online.

explain why *A. capsulatus* clusters outside the core group of *Actinobacillus* species in the *rrs* gene-based phylogeny, whereas in all the other trees it evidently belongs to this cluster. Therefore, this example shows that the analysis of *rrs* gene sequences, as helpful as they are, in some cases might lead to false classification if taken as the gold standard without additional genetic and phenotypic characterization in a polyphasic approach.

The hamster isolates formed a branch of their own in all trees. In contrast to the *A. capsulatus* strains, they clustered very closely with the core group of *Actinobacillus* species in the *rrs* tree as well. Their *rrs*, *rpoB*, *infB* and *recN* sequences showed 100 % identity, in agreement with their matching phenotypic profiles. These two strains were deposited twice with CCUG but can be traced to the same source and both seem to represent the original strain Kunstyr 570/85.

The two isolates that resembled *A. suis* phenotypically (J3-241 and R80) clustered with *A. suis*, as seen in the consensus tree (Fig. 2). This clustering was seen repeatedly within the individual *rpoB*, *infB* and *recN* trees, but not within the *rrs* tree, in which these isolates are closer to *A. hominis*, and the type strain of *A. suis* clusters between the two *A. equuli* subspecies (Fig. 1). However, the resolution of the *rrs* gene is known not to allow discrimination between these closely related *Actinobacillus* species (Christensen & Bisgaard, 2004).

The phylogenetic analysis of strain P224, which was phenotypically related to *M. granulomatis*, placed this strain within that genus in all trees, but without clear species association.

Strain R46 appeared to be phylogenetically unrelated to the other isolates analysed as well as to any other member of the family *Pasteurellaceae* and cannot be clearly assigned to any specific cluster, either in the consensus tree or in any of the individual trees.

Analysis of representative housekeeping genes was shown recently to be useful for the prediction of whole-genome relatedness within the family *Pasteurellaceae* (Kuhnert & Korczak, 2006). The sequence of the *recN* gene was shown to be sufficient to obtain an approximation of genetic relatedness between species and genera. We therefore calculated the genome similarity values based on the *recN* gene for all strains analysed and cross-compared them with all available species of the family. Table 3 shows some of the values obtained from this comparison that are relevant for our study. All 17 strains that clustered phenotypically and phylogenetically as *A. capsulatus* had similarity values between each other of close to, or identical with, the maximal possible value of 0.95. The type strain of *A. capsulatus* has been shown previously to share high *recN*-based similarity values, mostly above 0.7, with core members of *Actinobacillus* (Kuhnert & Korczak, 2006). This was also observed for each of the other 16 *A. capsulatus* strains analysed (data not shown) and is further reflected by

Table 3. Final classification and whole-genome similarity values calculated from *recN* sequences of strains investigated in this study and the most related species

Strains: 1, *A. capsulatus* CCUG 12396^T; 2, *A. suis* ATCC 33415^T; 3, *M. granulomatis* ATCC 49244^T; 4, *Mannheimia glucosida* CCUG 38457^T; 5, *Mannheimia haemolytica* NCTC 9380^T; 6, *Mannheimia ruminalis* CCUG 38470^T; 7, *M. varigena* CCUG 38462^T.

Strain	1	2	3	4	5	6	7
<i>A. capsulatus</i> CCUG 12396 ^T	0.95	0.77	0.29	0.27	0.26	0.29	0.28
<i>A. capsulatus</i> CCUG 37036	0.94	0.77	0.29	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> CCUG 37038	0.94	0.76	0.29	0.27	0.27	0.29	0.27
<i>A. capsulatus</i> CCUG 37798	0.95	0.77	0.28	0.27	0.27	0.29	0.28
<i>A. capsulatus</i> CCUG 37956	0.94	0.76	0.29	0.27	0.27	0.29	0.27
<i>A. capsulatus</i> 266/2693	0.95	0.77	0.28	0.27	0.27	0.29	0.28
<i>A. capsulatus</i> 266/3356	0.95	0.77	0.29	0.27	0.27	0.29	0.27
<i>A. capsulatus</i> 266/5603	0.95	0.77	0.28	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> 266/5695	0.95	0.77	0.28	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> 266/7370	0.94	0.76	0.29	0.27	0.27	0.29	0.27
<i>A. capsulatus</i> P244	0.95	0.77	0.28	0.27	0.26	0.29	0.28
<i>A. capsulatus</i> P796	0.95	0.77	0.28	0.27	0.27	0.29	0.28
<i>A. capsulatus</i> E1668/1	0.94	0.77	0.29	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> E1668/3	0.94	0.77	0.29	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> E1668/4	0.94	0.77	0.29	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> BK2999.1	0.95	0.77	0.28	0.27	0.26	0.28	0.27
<i>A. capsulatus</i> BJ4105.3	0.95	0.77	0.28	0.27	0.27	0.29	0.28
<i>Actinobacillus</i> sp. CCUG 23125	0.70	0.69	0.29	0.29	0.30	0.30	0.27
<i>Actinobacillus</i> sp. CCUG 26442	0.70	0.69	0.29	0.29	0.30	0.30	0.27
<i>A. suis</i> J3-241	0.76	0.94	0.27	0.25	0.25	0.29	0.28
<i>A. suis</i> R80	0.77	0.95	0.28	0.25	0.26	0.30	0.28
<i>Mannheimia</i> sp. P224	0.30	0.31	0.46	0.48	0.48	0.53	0.63
Unclassified strain R46	0.34	0.35	0.24	0.30	0.30	0.30	0.28

the uniformly high values all the *A. capsulatus* strains showed with *A. suis* (Table 3). The hamster isolates had values of 0.7 with the *A. capsulatus* strains, clearly outside the species border of about 0.85. However, they showed high similarity values with all species of the core group of *Actinobacillus*, ranging from 0.64 with *A. lignieresii* to 0.75 with *A. equuli*, definitely within the range of the genus, i.e. above 0.4 (data not shown). The two strains that were closely related to *A. suis* also showed very high similarity values with the type strain of *A. suis*, confirming the results of the phenotypic and phylogenetic analysis. Similarly, results obtained with strain P224 confirmed classification with *Mannheimia* as the highest values were obtained with species from the genus *Mannheimia*, clearly above the 0.4 threshold level (Table 3). The highest similarity value was obtained with *Mannheimia varigena* but was still clearly below the species level. Finally, strain R46, which could not be classified phenotypically or phylogenetically, showed the highest similarity value with [*Haemophilus*] *parasuis* (0.37), but without clear association with any established genus.

In conclusion, a polyphasic approach carried out on a set of strains that were classified previously as *A. capsulatus* showed that this species contains heterogeneous and misclassified isolates. There was an excellent correlation

between results obtained from extended phenotypic and phylogenetic investigations as well as calculated whole-genome similarity values based on the *recN* gene sequence. With all three approaches, the majority of the strains were clearly classified as representing *A. capsulatus*. Two hamster-derived strains were shown to be identical and to represent the same isolate, which forms a species of its own within the genus *Actinobacillus*. Two other strains could be classified as atypical *A. suis*. Finally, one strain was shown to represent a species of the genus *Mannheimia* and one strain could not be classified further within the family *Pasteurellaceae* and might belong to a new genus. This study allows an emended description of the species *A. capsulatus*.

Emended description of *Actinobacillus capsulatus* Arseculeratne 1962, 38^{AL}

Actinobacillus capsulatus (cap.su.la'tus. L. n. *capsula* a small chest, capsule; M.L. masc. adj. *capsulatus* encapsulated).

Cells are non-motile, Gram-negative, small coccoid or pleomorphic rods. Colonies on bovine blood agar are regular, circular, slightly raised, greyish and 1.0–1.5 mm in diameter after 24 h incubation at 37 °C. Haemolysis is normally not observed on calf blood agar but may be observed, with the type strain being non-haemolytic. Weakly CAMP positive using bovine blood. Catalase and oxidase reactions may vary but, in most cases, are positive, including the type strain. Fermentative with (+)-D-glucose in Hugh & Leifson's medium. Symbiotic growth (NAD requirement) is not observed. Porphyrin test is positive. No growth is observed on Simmons' citrate agar and acid is not produced from mucate. An alkaline reaction is not observed in malonate broth. H₂S is not produced in TSI and growth is not observed in KCN. Methyl red and Voges-Proskauer tests at 37 °C are negative. Nitrate is reduced without gas formation. Urease and alanine aminopeptidase tests are positive, whereas tests for arginine dihydrolase, lysine- and ornithine decarboxylase, phenylalanine deaminase, indole, gelatinase, Tweens 20 and 80 and pigment formation are negative. Phosphatase is produced and growth may occur on MacConkey agar, although rarely, with the type strain not growing on this medium. Acid is not produced from *meso*-erythritol, adonitol, (+)-D-arabitol, xylitol, (-)-D-arabinose, (-)-L-xylose, dulcitol, *myo*-inositol, (+)-D-fucose, (-)-L-fucose, (+)-L-rhamnose, (-)-L-sorbose, (+)-D-melezitose, (+)-D-glycogen, inulin, (+)-D-turanose and β -N-CH₃-glucosamid. Acid is produced from (-)-D-ribose, (+)-D-xylose, (-)-D-mannitol, (-)-D-sorbitol, (-)-D-fructose, (+)-D-glucose (without gas), (+)-D-galactose, (+)-D-mannose, cellobiose, lactose, maltose, (+)-D-melibiose, sucrose, trehalose, raffinose, dextrin, arbutin and salicin. Most isolates, including the type strain, produce acid from glycerol, (+)-L-arabinose, aesculin, amygdalin and gentiobiose. β -Glucosidase (NPG), β -galactosidase (ONPG) and α -galactosidase are produced whereas α -fucosidase (ONPF), α -mannosidase, β -glucuronidase (PGUA) and β -xylosidase (ONPX) are negative. Most isolates, including the type strain, produce α -glucosidase

(PNPG). The major polyamine compound is 1,3-diaminopropane (DAP), common to the majority of members of *Pasteurellaceae* with no characteristic minor compound (Busse *et al.*, 1997). *recN*-based genome similarity with the type species *A. lignieresii* is 0.71, whereas using the genes *recN*, *rpoA* and *thdF* this value is 0.74 (Kuhnert & Korczak, 2006).

Isolated from various pathological lesions in rabbits, septicaemia in a kitten and conjunctiva of a hare. The type strain is CCUG 12396^T (= Frederiksen 243^T = ATCC 51571^T = NCTC 11408^T = CIP 103283^T), which was isolated from a joint of a rabbit in Sri Lanka. The DNA G + C content of the type strain is 42.4 mol% (Kuhnert & Korczak, 2006) and the genome size is 1.9 GDa (Krause *et al.*, 1989).

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