Investigation of taxa of the family *Pasteurellaceae* isolated from Syrian and European hamsters and proposal of *Mesocricetibacter intestinalis* gen. nov., sp. nov. and *Cricetibacter osteomyelitidis* gen. nov., sp. nov.

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Eleven strains from hamster of Bisgaard taxa 23 and 24, also referred to as Krause’s groups 2 and 1, respectively, were investigated by a polyphasic approach including data published previously. Strains showed small, regular and circular colonies with smooth and shiny appearance, typical of members of the family *Pasteurellaceae*. The strains formed two monophyletic groups based on 16S rRNA gene sequence comparison to other members of the family *Pasteurellaceae*. Partial *rpoB* sequencing as well as published data on DNA–DNA hybridization showed high genotypic relationships within both groups. Menaquinone 7 (MK7) was found in strains of both groups as well as an unknown ubiquinone with shorter chain length than previously reported for any other member of the family *Pasteurellaceae*. A new genus with one species, *Mesocricetibacter intestinalis* gen. nov., sp. nov., is proposed to accommodate members of taxon 24 of Bisgaard whereas members of taxon 23 of Bisgaard are proposed to represent *Cricetibacter osteomyelitidis* gen. nov., sp. nov. Major fatty acids of type strains of type species of both genera are C14:0, C14:0 3-OH/iso-C16:1 I, C16:1ω7c and C16:0. The two genera are clearly separated by phenotype from each other and from existing genera of the family *Pasteurellaceae*. The type strain of *Mesocricetibacter intestinalis* is HIM 933/7T (=Kunstyr 246/85T = CCUG 28030T = DSM 28403T) while the type strain of *Cricetibacter osteomyelitidis* is HIM943/7T (=Kunstyr 507/85T = CCUG 36451T = DSM 28404T).

Recommendations for health monitoring of rodents and rabbits as outlined by the Federation of European Laboratory Animal Science Associations (FELASA) include members of the family *Pasteurellaceae* (Nicklas et al., 2002). However, specific methods for isolation and identification were not stated, reflecting limitations for current classification, and this has left uncertainties with respect to procedures to identify and investigate host interactions of members of the family *Pasteurellaceae* associated with rodents and rabbit. The most frequently mentioned species of the family *Pasteurellaceae* reported in various rodent species is *Pasteurella pneumotropica* (the brackets indicate that the species probably needs reclassification within another genus). *Pasteurella pneumotropica*, described by Jawetz (1950), was initially isolated from pneumatic lesions in laboratory mice. Several other species and taxa classified within the family *Pasteurellaceae* have been reported from laboratory animals, representing serious differential diagnostic problems as discussed previously (Mutters et al., 1989; Bisgaard, 1993; Nicklas, 2007). Phylogenetic analysis based on 16S rRNA gene sequence comparison outlined a ‘rodent group’ within the family *Pasteurellaceae*, including *Pasteurella pneumotropica* and *Actinobacillus muris* (Dewhirst et al., 1993). Recently, a new genus, *Necropsobacter*, unrelated to *Pasteurella pneumotropica* and *Actinobacillus muris* was described that mainly included organisms from Guinea pigs as well as other rodents and rabbit (Christensen et al., 2011).
Table 1. Hamster isolates investigated

<table>
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<tr>
<th>Strain</th>
<th>Bisgaard taxon (Krause's group)</th>
<th>Host, isolation site and year of isolation</th>
<th>16S rRNA gene accession numbers</th>
<th>rpoB gene accession numbers</th>
<th>Reference</th>
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<td>HIM 933/7T (=Kunstyr 246/85T=CCUG 28030T=CCUG 36448T=HIM938/5T=MCCM466T=DSM 28403T)</td>
<td>24 (1)</td>
<td>Syrian hamster (Mesocricetus auratus), caecitis</td>
<td>KF875567 (AF024527, AF224302)*</td>
<td>KF875572</td>
<td>Krause et al. (1989)</td>
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<td>24 (1)</td>
<td>Hamster, intestine</td>
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<td>European hamster (Cricetus cricetus), osteomyelitis</td>
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<td>id</td>
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<td>Krause et al. (1989)</td>
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<td>1995010091</td>
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<td>Syrian Hamster</td>
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</tbody>
</table>

*Sequences under accession numbers AF024527 and AF224302 are identical.
†Identical to sequence listed.

No recent reports exist for members of the family Pasteurellaceae isolated from hamsters including their taxonomic position. In the present study, a collection of isolates representing the family Pasteurellaceae obtained from hamsters held as conventional laboratory animals was subjected to extended phenotypic characterization. Some of the strains were investigated previously by Krause et al. (1989) and classified as groups 1 and 2, and subsequently classified as taxa 23 and 24 of Bisgaard, respectively (Bisgaard, 1993). In the following, we refer to Krause’s groups 1 and 2 as taxa 24 and 23 of Bisgaard, respectively (Bisgaard, 1993). In the following, we will refer to Krause’s groups 1 and 2 as taxa 24 and 23 of Bisgaard, respectively. Olsen et al. (2005) showed a deep phylogenetic position of the proposed type strain CCUG 28030T (of the novel species Mesorickettsia intestinalis gen. nov., sp. nov. in the current study) from hamster within the ‘Rodent’ 16S rRNA cluster. Finally, Busse et al. (1997) investigated the presence of polyamines in the hamster strains of Krause et al. (1989).

Eleven strains from hamsters including six from Krause et al. (1989) and five additional strains were investigated (Table 1). Searches for sequences in public databases were performed by BLAST (Altschul et al., 1997). Determination of pairwise similarity was performed by the WATER program of EMBOSS (Rice et al., 2000). Multiple alignments and neighbour-joining phylogenetic analysis including calculation of bootstrap support were performed by using Clustal X 2 (Larkin et al., 2007) and MEGA5 (Tamura et al., 2011) was used for graphical representation of trees. Determination of the partial rpoB sequence of all 11 strains was performed according to previously described protocols (Korczak et al., 2004; Korczak & Kuhnert, 2008). The rpoB gene sequence analysis confirmed the existence of taxa 23 and 24 of Bisgaard and further showed identical sequences for all members of taxon 23, whereas strain 1986057021 diverged slightly (99.0 % similarity) from the other strains of taxon 24, otherwise with identical sequences (Fig. S1, available in the online Supplementary Material). The similarity between the two groups was 83.6 % based on the partial region of rpoB compared. The closest similarities at the genus level within the family Pasteurellaceae were between strain HIM 933/7T of taxon 24 and Necropsobacter rosorum with 86.6 % similarity; 87.6 % similarity was observed between HIM943/7T of taxon 23 and the type strain of Bibersteinia trehalosi.

On the basis of the rpoB sequence comparison, five strains were selected for 16S rRNA gene sequencing as reported previously (Christensen et al., 2002; Angen et al., 2003) with at least 1368 nt of the 16S rRNA gene sequenced for four strains. It was only possible to generate a short sequence from strain 1995010091 (1103 nt) and this was
excluded from the multiple alignment (see below). In addition to the 16S rRNA gene sequences determined in the current investigation, published sequences were included of type strains of type species of genera of the family Pasteurellaceae, as well as of type strains of [Actinobacillus] muris and [Pasteurella] pneumotropica type Jawetz and the reference strain of biovar Heyl. The 16S rRNA gene sequence based phylogenetic comparisons documented that strain HIM943/7T of taxon 23 was monotypic and that strains of taxon 24 of Bisgaard formed a monophyletic group compared with other genera of the family Pasteurellaceae (Fig. 1). The lowest sequence similarity within the groups was 98.8 %, found between strains HIM 933/7T and 1986057021. The closest relative to taxon 24 was the type strain of Haemophilus haemolyticus with 95.2 % similarity. The only representative of taxon 23 (strain HIM 943/7) was unrelated to the other members of the family Pasteurellaceae and to the strains of taxon 24. The short sequence from strain 1995010091 (1103 nt) showed a similarity to strain HIM 943/7 of 99.0 %. The older 16S rRNA gene sequence of CCUG 28030 T (AF224302) included some ambiguous positions and showed 98.9 % similarity to the sequence of HIM933/7T, which was the reason why we excluded sequence AF224302 from the phylogenetic analysis. The closest relative to taxon 23 was Mannheimia glucosida with 95.2 % sequence similarity. The similarity between the taxa 23 and 24 was 93.9 % (strains HIM 933/7 and HIM 943/7).

The fatty acids of strains CCUG 28030 T and CCUG 36451 T were investigated by the Culture Collection, University of Göteborg, Sweden (CCUG). The major fatty acids were

Fig. 1. Phylogenetic relationships between the strains of the family Pasteurellaceae isolated from hamster and proposed to represent Mesocricetibacter intestinalis gen. nov., sp. nov. and Cricetibacter osteomyelitidis gen. nov., sp. nov. and representative members of the family Pasteurellaceae based on neighbour-joining analysis of 16S rRNA gene sequences. Support for monophyletic groups by bootstrap analysis are indicated as numbers out of 100. Strains in bold type have been sequenced in the present investigation. The bar represents sequence variation considering the model for nucleotide substitution (Jukes & Cantor) and tree shape used in the neighbour-joining analysis.
C_{14:0}, C_{14:1} 3-OH/iso-C_{16:1} I, C_{16:1}07c and C_{16:0} with minor amounts of C_{12:0}, C_{18:2}06,9c, anteiso-C_{18:0} and C_{18:1}09c (Table S1). The fatty acid composition did not allow for separation of the two strains or for separation from the existing genera of the family Pasteurellaceae.

The DNA G+C (mol%) content was determined by Krause et al. (1989) who reported 47.5–48.7% for taxon 24 and 41.9 and 42.0% for taxon 23 of Bisgaard.

Analysis of respiratory quinones was carried out by the Identification Service, DSMZ, Braunschweig, Germany. Menaquinone 7 (MK7) was found in both strains as well as an unknown ubiquinone with chain length shorter than 6, not previously reported. Krause et al. (1989) reported the presence of demethylmenaquinone – an observation not confirmed in the current study. MK7 has been reported in low amounts in some species of the genus Avibacterium (Kroppenstedt & Mannheim, 1989; Kainz et al., 2000) and in moderate amounts in members of the genera Actinobacillus, Mannheimia and Bibersteinia (Kroppenstedt & Mannheim, 1989). MK8 and ubiquinone with chain length of 8 were found by Engelhard et al. (1991) in the genus Gallibacterium and this separates the genus from the taxa 23 and 24 of Bisgaard (Table S2).

DNA–DNA reassociation of 19% was reported by Krause et al. (1989) between strains HIM 933/7^T of taxon 24 and HIM 943/7^T of taxon 23. Within taxon 24, 94 and 100% reassociation was found between HIM 933/7^T and strains HIM 942/8 and HIM 948-5/6, respectively, and 98% DNA–DNA reassociation was found between strain HIM 943/7^T of taxon 23 and HIM 948-3/4 of taxon 23. The taxa 23 and 24 of Bisgaard therefore represent separate species and genera based on the threshold of 70% DNA–DNA reassociation for species separation stated by Wayne et al. (1977) and the fact that more than 55% DNA–DNA reassociation for species separation was observed for the species of the same genera (Müters et al., 1989). In accordance with these data, rRNA–DNA reassociation was below the genus level between strain HIM 933/7^T and other taxa investigated and the strain belonged to a rRNA cistron different from that of the type strain of [Pasteurella] pneumotropica (De Ley et al., 1990).

To provide the descriptions of the taxa 23 and 24 of Bisgaard (1993), isolates were subjected to phenotypic characterization as reported previously (Bisgaard et al., 1991; Christensen et al., 2007). In the current study, reinvestigations were performed using 40 biochemical criteria tested by conventional tests. In these tests, acid formation from carbohydrates was tested in phenol-red broth base (Difco) supplemented with 1% of the respective carbohydrate and read after incubation for 5 days at 37 °C. All other reactions were read after 18–24 h of incubation or as recommended by the author cited below. Hydrolysis of aesculin was tested in aesculin broth (Merck). Urease, indole and amino acid decarboxylase tests were performed as recommended by Kilian (1976). The requirement for growth factors was tested with filter paper discs containing 12.5 μg of NAD (Roche Diagnostics) or 25 μg haemin (Sigma) on Mueller–Hinton Agar (Heipha). The ability to synthesize porphyrins from δ-aminolaevulinic acid was demonstrated under UV light in a dark room and by addition of Kovac’s reagent (Merck) as described by Kilian (1976).

The taxa 23 and 24 by Bisgaard (1993) can be separated by urease activity and acid formation from (+)-L-arabinose, dulcitol and maltose (Table 2). In addition, they can be separated from all genera of the family Pasteurellaceae by phenotype (Table 2). The presence of Q8 and MK8 in members of the genus Gallibacterium separates this genus from the characteristic MK7 of taxa 23 and 24 (Table S2). On the basis of distinct phylogenetic, phenotypic and chemotaxonomic characteristics of taxa 23 and 24 of Bisgaard we propose two new genera of the family Pasteurellaceae, each with a single species. Taxa 24 and 23 of Bisgaard share a range of characteristics with other members of the family Pasteurellaceae as stated in the descriptions of the genera below. The genus names are based on their predominant hosts, and species names chosen from their main habitats. The following descriptions are based on Krause et al. (1989), unpublished data referred to in Bisgaard (1993), and control experiments performed in the current study.

**Description of Mesocricetibacter gen. nov.**

*Mesocricetibacter* (me.so.cri.ce.ti’bact.ter. N.L. masc. n. *Mesocricetus* a hamster genus; N.L. masc. n. *bacter* rod; N.L. masc. n. *Mesocricetibacter* a rod-shaped bacterium isolated from the hamster genus *Mesocricetus*).

Members of the genus are Gram-negative staining, pleomorphic rods, facultatively anaerobic, non-motile at both 22 and 37 °C and positive for oxidase. They do not show *in vitro* satellite growth, referred to as V-factor or NAD requirement. Porphyrin is synthesized by all isolates. They are fermentative in Hugh & Leifson’s medium with (+)-D-glucose. Catalase, Simmons’ citrate test as well as malonate (base) and H_2S/TSI tests are all negative. Tetrathionate and nitrate are reduced. Positive for urease and alanine amino peptidase. Growth is not observed with KCN and the Voges–Proskauer test is negative, whereas the methyl red test is weakly positive. Tests for arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase and phenylalanine deaminase are all negative. Indole is formed. The alkaline phosphatase test is weakly positive. Growth is observed on MacConkey agar. The gelatinase test and hydrolysis of Tween 20 and 80 are negative. Gas is formed from (+)-D-glucose. Acid is formed from (+)-D-ribose, (+)-D-xyllose, (-)-D-mannitol, (-)-D-fructose, (+)-D-sorbitol, (+)-D-galactose, (+)-D-mannose and sucrose. Acid is not formed from i-erythritol, (-)-L-sorbose, (+)-L-arabinose, adonitol, xylitol, (+)-L-arabitol, cellobiose, dulcitol, (-)-L-fucose, maltose, raffinose, stachy, dextrin, aesculin or salicin. The ONPG test is positive and α-glucosidase negative. Tests for α-fucosidase, α-galactosidase, β-glucuronidase, α-mannosidase and β-xyllosidase are all
Table 2. Phenotypic separation of the two genera isolated from hamster from the existing genera of the family Pasteurellaceae

Genera: 1, Mesocricetus bactera gen. nov. (from Syrian hamster); 2, Cricetibacter gen. nov. (from European hamster); 3, Haemophilus sensu stricto (Kilian, 2005; Norskov-Lauritsen et al., 2005; Winslow et al., 1917; Zinnemann & Biberstein, 1974); 4, Actinobacillus sensu stricto (Brumpt, 1910; Christensen & Bisgaard, 2004); 5, Lonepinella (Osawa et al., 1995); 6, Mannheimia (Angen et al., 1999); 7, Pasteurella sensu stricto (Trevisan, 1887; Christensen & Bisgaard, 2006); 8, Phocoenobacter (Foster et al., 2000); 9, Gallibacterium (Bisgaard et al., 2009); 10, Volucribacter (Christensen et al., 2004); 11, Histophilus (Angen et al., 2003); 12, Avibacterium (Blackall et al., 2005); 13, Nicolettia (Kuhnert et al., 2004); 14, Bibersteinia (Blackall et al., 2007); 15, Aggregatibacter (Norskov-Lauritsen & Kilian, 2006); 16, Basfia (Kuhnert et al., 2010); 17, Chelonobacter (Gregersen et al., 2009); 18, Necropsobacter (Christensen et al., 2011); 19, Biaegardia (Foster et al., 2011); 20, Otadoridibacter (Hansen et al., 2012). +, At least 90% of strains positive within 1–2 days; −, less than 10% of the strains positive within 14 days; d, 11–89% of the strains positive; w, weakly positive. All tests performed at 37 °C. ND, no data available.

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<td>Growth on MacConkey agar</td>
<td>+‡</td>
<td>−†</td>
<td>ND</td>
<td>+</td>
<td>−†</td>
<td>ND</td>
<td>d</td>
<td>d</td>
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<td>ND</td>
<td>+</td>
<td>+</td>
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<td>ND</td>
<td>+</td>
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DNA G+C content (mol%) 47.5–48.7* 41.9–42.0* 39‡ 35.5–43.7‡ 37.5‡ 39.2 37.7–43.9 41.5 39.9–42.3 40.8 ND 44.2–47 ND 42.6 42–44 42.5 47.2 52.5 39.5 36.2

*Data from Krause et al. (1989).
†Not part of formal genus description.
‡Data from current study.
§X-factor, referring to the dependence on haemin for growth in vitro and V-factor related to dependence on NAD (or related substances) for growth in vitro.
||Negative reaction listed in table of Osawa et al. (1995).
negative. The DNA G+C content is 47.5–48.7 mol% according to Krause et al. (1989). Menaquinone 7 (MK7) is found in the type strain of the type species as well as an unknown ubiquinone with a chain length shorter than 6. The major fatty acids are C14:0, C16:0 3-OH/iso-C16:1 I, C16:1ω7c and C16:0. According to Busse et al. (1997), 1,3-diaminopropane is the dominant polyamine and putrescine, cadaverine, spermidine and spermine are found in low amounts in strain Kunstyr 246/85T. The type species is Mesocricetibacter intestinalis.

**Description of Mesocricetibacter intestinalis**

*Mesocricetibacter intestinalis* (in.tes.ti.na’lis. N.L. masc. n. intestinalis pertaining to the intestine).

After 24 h of aerobic incubation at 37 °C on bovine blood agar, β-haemolysis is not observed. Isolates on bovine blood agar form greyish, shiny, regular and circular colonies with smooth appearance. Adherence to the blood agar may occur. Colonies of strain HIM933/7T are 0.5–1.0 mm in diameter increasing in size to 1.5 mm after 48 h of incubation. Colonies of 1991003092 have a diameter of 1 mm after 24 h and 4 mm after 3 days and are flat, smooth and greyish and shinier compared with HIM933/7T. In addition to the properties listed for the genus, acid formation from glycerol and meso-inositol are late. Acid production from mucate is variable with a positive reaction for the type strain. Acid formation from (+)-l-rhamnose is variable with a positive reaction of the type strain. Acid formation from raffinose is variable with a negative reaction of the type strain. Acid formation from (−)-d-arabinose is variable with a late positive reaction for the type strain. Acid is not formed from (−)-l-xylene, (−)-l-sorbos, (−)-l-melibiose, (−)-l-melezitose, (−)-l-glycogen, inulin, amygdalin, arbutin, gentiobiose and (−)-l-turanose. Acid formation from lactose is mainly negative, including in the type strain, but may be late positive (strain P. pn. 86). The reaction of β-glucosidase is negative. Isolates have mainly been obtained from Syrian hamster.

The type strain is HIM 933/7T (=Kunstyr 246/85T=CCUG 28030T=DSM 28403T), isolated from caecitis of a Syrian hamster.

**Description of Cricetibacter gen. nov.**

*Cricetibacter* (cri.ce.ti.bac’ter N.L. masc. n. Cricetus a hamster genus; N.L. masc. n. bacter rod; N.L. masc. n. cricetibacter a rod-shaped bacterium isolated from the hamster genus Cricetus).

Members of the genus are Gram-negative staining, facultatively anaerobic, pleomorphic rods, non-motile at 22 and 37 °C and positive for oxidase. They do not show in vitro satellite growth, referred to as V-factor or NAD requirement. Porphyrin is synthesized by all isolates. The methyl red reaction is weakly positive and Voges–Proskauer test negative. A fermentative reaction is observed in Hugh & Leifson’s medium with (+)-D-glucose. The catalase, Simmons’ citrate, malonate (base), H2S/TSI and mucate (acid) tests are all negative. Indole is formed, and the alkaline phosphatase and alanine aminopeptidase tests are positive. Tetrathionate is not reduced. The urease test is negative. Nitrate is reduced. Tests for arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, phenylalanine deaminase, Tweens 20 and 80 and gelatinase are all negative. Acid is formed from (+)-D-xylene, (−)-l-arabinose, dulcitol, (−)-D-fructose, (−)-D-mannitol, (−)-D-sorbitol (+)-D-galactose, (−)-D-fructose, (−)-D-mannose, maltose, sucrose and dextrin while acid formation is late from glycerol. Acid formation is not registered from (−)-l-sorbos, xylitol, (−)-l-melezitose, l-erythritol, adonitol, (−)-l-fucose, (−)-D-glycogen, trehalose, inulin, starch, salicin, arbutin, amygdalin, gentiobiose, (−)-l-turanose, cellobiose or aesculin. Growth is not observed on MacConkey agar. Tests for ONPG, α-galactosidase, α-mannosidase, β-glucoronidase, α-galactosidase, β-glucosidase and α-xylosidase reactions are all negative. The DNA G+C content is 41.9–42.0 mol% (Krause et al., 1989). The major fatty acids are C14:0, C16:0 3-OH/iso-C16:1 I, C16:1ω7c and C16:0. Menaquinone 7 (MK7) is found in the type strain of the type species of the genus as well as an unknown ubiquinone with a chain length shorter than 6. According to Busse et al. (1997), 1,3-diaminopropane makes up some 94% of the polyamine content, while putrescine, spermidine and spermine are found in low amounts in Kunstyr 507/85T, the type strain. Cricetibacter osteomyelitidis is the type species of the genus.

**Description of Cricetibacter osteomyelitidis**

*Cricetibacter osteomyelitidis* (os.te.o.my.e.li’ti.dis. N.L. gen. n. osteomyelitidis of osteomyelitis, inflammation of bone marrow).

Colonies on blood agar have a diameter of 1.0–1.5 mm after 24 h of aerobic incubation and 2–3 mm after 3 days of incubation at 37 °C. Colonies are shiny, regular, circular, yellowish in colour and non-haemolytic. Adherence to the agar has not been observed. In addition to the characteristics described for the genus, acid formation is not observed from (−)-l-xylene or melibiose. Acid formation from myo-inositol and (+)-l-rhamnose is late positive (reaction after 3 days). Acid formation from (−)-l-glucose but may be late positive (strain HPA37). Acid formation from (−)-d-arabinose is late positive or positive including the type strain. Acid formation from (+)-l-lactose is negative or late positive (strain HPA37). Acid formation from (−)-d-arabinose is late positive or positive including the type strain. Acid formation from (+)-D-glucose may be late positive (strain HPA37). Gas is formed from (+)-D-glucose but may be absent (strain 199501009). The type strain is HIM943/7T (=Kunstyr 507/85T=CCUG 36451T=DSM 28404T), isolated from osteomyelitis of European hamster.
Acknowledgements

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References


