Identification of "*Micrococcus candidus*" ATCC 14852 as a strain of *Staphylococcus epidermidis* and of "*Micrococcus caseolyticus*" ATCC 13548 and *Micrococcus varians* ATCC 29750 as Members of a New Species, *Staphylococcus caseolyticus*

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Comparative chemical, biochemical, and in vitro genetic analyses of "*Micrococcus candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, and *M. varians* ATCC 29750 have demonstrated that these strains were misidentified and that they should be assigned to the genus *Staphylococcus*. (Names in quotation marks are not on the Approved Lists of Bacterial Names, have not been validly published since 1 January 1980, and therefore do not have nomenclatural standing.) Deoxyribonucleic acid (DNA)-DNA-hybridization experiments and other physiological and biochemical data indicated that "*M. candidus*" ATCC 14852 is a strain of *Staphylococcus epidermidis*. High DNA homology values also revealed that "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 are related to each other at the species level. Although they differ from most staphylococci in their production of class II fructose-1,6-diphosphate aldolase and in their cytochrome composition, they are, on the basis of their cell wall compositions, the low guanine + cytosine contents of their DNAs, and the results of DNA-ribosomal ribonucleic acid hybridization studies, genuine members of the genus *Staphylococcus*. DNA-DNA hybridization experiments demonstrated that they are not closely related to any of the known *Staphylococcus* species. It is proposed that these organisms represent a new species, namely, *S. caseolyticus*. Strain ATCC 13548 is the type strain.

The separation of micrococci from staphylococci has been the subject of controversy for a long time (14, 23). Early taxonomists lumped them together, first into the genus *Micrococcus* (11) and later into the genus *Staphylococcus* (28). It was not until 1965 that a simple test system for their separation, the so-called oxidation/fermentation test, was introduced (30); it was based on the ability of staphylococci to produce acid anaerobically from glucose. Recent studies, however, have revealed that this test is not reliable in separating weakly anaerobic staphylococci, e.g., strains of *S. saprophyticus* and *S. xylosus*, from certain micrococci, such as strains of *M. varians*, that can also produce small amounts of acid from glucose under anaerobic conditions (9, 23). Some facultatively anaerobic micrococci, e.g., strains of *M. kristinae*, would be misidentified as staphylococci by relying upon the oxidation-fermentation test. Today, several criteria, such as deoxyribonucleic acid (DNA) base composition (16), cell wall composition (20, 21), menaquinone pattern (12), cytochrome pattern (7), and class of

fructose-1,6-diphosphate (FDP) aldolase (10), are available to distinguish staphylococci from micrococci. However, the determination of none of these characters is sufficiently simple to permit their routine use in the laboratory. Criteria for routine separation of staphylococci from micrococci are a special lysostaphin test (22), a phage adsorption test (26), a serological approach (27), and modified oxidase and benzidine tests (8). Moreover, selective media have been developed for the isolation of micrococci (2) and staphylococci (25).

In the present study we have undertaken routine and comparative chemical, biochemical, and in vitro genetic analyses of three gram-positive, catalase-positive cocci isolated from milk (1, 6, 11), which have, until now, been identified as members of the genus *Micrococcus*. These strains are "*M. candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, and *M. varians* ATCC 29750. (Names in quotation marks are not on the Approved Lists of Bacterial Names [29], have not been validly published since 1 January 1980, and therefore do not have

nomenclatural standing.) The last strain is of special interest because the structure and biosynthesis of its cell wall teichoic acid have been thoroughly elucidated (1, 18). However, according to our previous findings, micrococci should not contain teichoic acid in their cell walls (23, 24).

MATERIALS AND METHODS

Bacterial strains. "*M. candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, *M. varians* ATCC 29750, *S. aureus* ATCC 12600 (type strain), *S. capitis* ATCC 27840 (type strain), *S. epidermidis* ATCC 14990 (type strain), *S. hominis* ATCC 27844 (type strain), *S. sciuri* ATCC 29062 (type strain), *S. simulans* ATCC 27848 (type strain), and *S. warneri* ATCC 27840 (type strain) were obtained from the American Type Culture Collection, Rockville, Md. *S. saprophyticus* CCM 883 (type strain) and *M. luteus* CCM 169 are from the Czechoslovak Collection of Microorganisms, Brno, CSSR; *S. hyicus* subsp. *chromogenes* NCTC 10530 (type strain) is from the National Collection of Type Cultures, London, England; and *S. cohnii* DSM 20260 (type strain), *S. haemolyticus* DSM 20263 (type strain), and *S. xylosus* DSM 20266 (type strain) are from the Deutsche Sammlung von Mikroorganismen, Göttingen, FRG. *S. intermedius* H 11 (type strain) was received from V. Hajek, Palacky University, Olomouc, CSSR, and *Lactobacillus acidophilus* AM 63 was received from F. Gasser, Paris, France. All organisms with the exception of *L. acidophilus* were cultivated aerobically in peptone-yeast extract-glucose-NaCl broth (14). *L. acidophilus* was grown in the medium described by DeMan et al. (5). The incubation temperature was 32°C.

Methods. Carbohydrate reactions were determined as described by Kloos et al. (15), except that phenol red was used as indicator instead of bromocresol purple. Proteolytic activity on casein was tested on calcium caseinate agar (E. Merck AG, Darmstadt, Germany, no. 5409). Inoculated plates were incubated at 32°C and examined after 3 and 6 days.

Preparation of cell walls and determination of peptidoglycan type were carried out as described by Schleifer and Kandler (21). Cell wall teichoic acids were extracted with 60% hydrofluoric acid and were characterized by hydrolysis with 2 N HCl at 100°C for 3 h, followed by gas chromatography of *N,O*-trifluoroacetylated products. The lysostaphin test was carried out as described by Schleifer and Kloos (22). The modified oxidase and benzidine tests used were developed by Faller and Schleifer (8). For the oxidase test, a 6% solution of tetramethylphenylenediamine (E. Merck AG) in dimethylsulfoxide was mixed with a loop of a bacterial culture grown for 15 to 18 h on blood agar (Standard I nutrient agar [E. Merck AG] plus 7% sheep blood). Within 2 min, micrococci as well as *S. sciuri* exhibit a dark-blue color.

For the modified benzidine test, one to two loopfuls from a bacterial colony were mixed with 0.5 ml of 2 N trichloroacetic acid and 0.5 ml of 2 N HClO₄, incubated for 3 min, and centrifuged. The pellet was suspended in 40 ml of a mixture of ice-cold acetone-2.4 N HCl (49:1, vol/vol) and stirred for 10 to 15 min. The solution was then passed through a small filter paper,

and the benzidine test was carried out by the method of Deibel and Evans (3). With this modified benzidine test, only bacteria containing cytochrome *c* react positively and turn blue (8). The class of aldolase was determined as described by Götz et al. (10). The cytochrome pattern was elucidated as previously reported (7). For labeling of DNA or ribosomal ribonucleic acid (rRNA), the bacteria were grown in broth in which yeast extract was replaced by 2 µCi of [6-³H]thymidine, or [5,6-³H]uracil per ml, respectively. Specific activities were in the range of 10⁴ to 10 × 10⁴ for [³H]DNA and of 10⁵ to 1.5 × 10⁵ for [³H]rRNA.

Extraction of labeled and unlabeled DNA was carried out as described by Meyer and Schleifer (19). DNA-DNA hybridization experiments were accomplished as described previously (13). DNA-rRNA hybridization studies and determination of the thermal stability of the DNA-rRNA hybrids were carried out by the method of De Ley and De Smedt (4; R. Kilpper-Bälz and K. H. Schleifer, FEMS Microbiol. Lett., in press).

The guanine plus cytosine (G+C) content of the DNA was determined by the thermal denaturation method of Marmur and Doty (17).

RESULTS AND DISCUSSION

The chemical and biochemical properties of "*M. candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, and *M. varians* ATCC 29750 were determined and compared with those of certain staphylococci (Table 1). "*M. candidus*" ATCC 14852 produced acid anaerobically from glucose and, like a typical staphylococcus, was susceptible to lysostaphin. "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 produced almost no acid in the oxidation-fermentation test and were susceptible to lysostaphin only after the concentration of lysostaphin was increased from 200 µg/ml to 500 µg/ml.

The assignment of these three strains to the genus *Staphylococcus* was also indicated by their DNA base compositions, their peptidoglycan types, and the presence of teichoic acid in their cell walls. The cell wall teichoic acid of "*M. candidus*" showed the same composition as that of *S. epidermidis*, whereas the teichoic acids of the other two strains were atypical. They contained only small amounts of glycerol.

The results of a phage adsorption test support the transfer of "*M. candidus*" ATCC 14852 to the genus *Staphylococcus* (27). "*M. candidus*" ATCC 14852 contains, like most staphylococci, a class I FDP aldolase, which can be inhibited with sodium borohydride but not with ethylenediaminetetraacetate. On the other hand, "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 reveal, like most other bacteria, a class II FDP aldolase. In this respect they are similar to *S. intermedius* H 11, which, contrary to previous reports (10), contains a class II FDP aldolase (S. Fischer and K. H. Schleifer, unpublished data). With regard to the oxidase and

TABLE 1. Chemical and biochemical properties of "*Micrococcus candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, *M. varians* ATCC 29750, and various staphylococci^a

Characters	" <i>M. candidus</i> " ATCC 14852	" <i>M. caseolyticus</i> " ATCC 13548	<i>M. varians</i> ATCC 29750	<i>S. epidermidis</i> ATCC 14990	<i>S. sciuri</i> ATCC 29062	<i>S. intermedius</i> H 11
Anaerobic acid from glucose (O/F-test)	+	(+)	(+)	+	(+)	+
Lysostaphin susceptibility (500 µg/ml)	+	(+)	(+)	+	+	+
G + C content of DNA (mol %)	34.5	38.0	39.0	33.5	36.5	36
Acid (aerobically) from:						
Glucose	+	+	+	+	+	+
Galactose	+	(+)	+	+	+	-
Mannose	+	-	-	+	-	+
Maltose	+	+	+	+	+	-
Fructose	+	+	+	+	+	+
Mannitol	-	-	-	-	+	-
Xylose	-	-	-	-	-	-
Sucrose	+	-	+	+	+	+
Trehalose	-	+	+	-	+	+
Proteolytic activity on casein	(+)	+	+	(+)	+	+
Modified oxidase test	-	+	+	-	+	-
Modified benzidine test	-	+	+	-	+	-
Class of FDP aldolase	I	II	II	I	I	II
Peptidoglycan type	Lys-Gly ₄ , Ser	Lys-Gly ₄ , Ser	Lys-Gly ₄ , Ser	Lys-Gly ₄ , Ser	Lys-Ala- Gly ₄	Lys-Gly ₄ , Ser
Cell wall teichoic acid composition	Glycerol, glucose, GlcNAc	Glucose, GalNAc, small amounts of glycerol and GlcNAc	GlcNAc, small amounts of glycerol ^b	Glycerol, glucose, GlcNAc	Glycerol, GlcNAc	Glycerol, GlcNAc

^a Parentheses around symbols indicate a weak reaction. Abbreviations: GalNAc, *N*-acetylgalactosamine; GlcNAc, *N*-acetylglucosamine; O/F, oxidation/fermentation.

^b Atypical teichoic acid: poly-(*N*-acetylglucosamine 1-phosphate) according to Archibald et al. (1).

modified benzidine tests, "*M. candidus*" ATCC 14852 behaved like most staphylococci, whereas "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 reacted positively in both tests and in this respect resemble micrococci or *S. sciuri*.

On the basis of cell wall composition, utilization of sugars and sugar alcohols, and other characters listed in Table 1, "*M. candidus*" seems to be rather closely related to *S. epidermidis*. DNA base and cell wall compositions of "*M. caseolyticus*" and *M. varians* ATCC 29750 indicate their relationship to the genus *Staphylococcus*, whereas the occurrence of class II FDP aldolase and positive oxidase and benzidine tests are rather unusual properties for staphylococci. The latter criteria are correlated with the possession of cytochrome *c*. This was confirmed by a determination of the cytochrome pattern (Table 2). "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 resemble *S. sciuri* with respect to cytochrome composition, that is, the

occurrence of two cytochromes of type *c* (7). Thus, "*M. caseolyticus*," *M. varians* ATCC 29750, and *S. sciuri* react positively in the modified oxidase and benzidine tests, as do micrococci, but they differ from them in their cytochrome composition since micrococci contain only one type of cytochrome *c* and in addition cytochrome *d* (7).

DNA-DNA homology studies indicated the genetic relationship between "*M. candidus*," "*M. caseolyticus*," *M. varians* ATCC 29750, and staphylococci. The results of the DNA-DNA hybridization experiments are presented in Table 3. On the basis of the high DNA homology values, "*M. candidus*" ATCC 14852 has to be regarded as a member of the species *S. epidermidis*. The hybridization values of above 80% indicate that "*M. caseolyticus*" and *M. varians* ATCC 29750 are related to each other at the species level (Table 1). The DNA homology values with the other staphylococci studied were

TABLE 2. Absorption maxima of cytochromes present in "*M. candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, *M. varians* ATCC 29750, and various staphylococci

Cytochromes present in:					
" <i>M. candidus</i> " ATCC 14852	" <i>M. caseolyticus</i> " ATCC 13548	<i>M. varians</i> ATCC 29750	<i>S. epidermidis</i> ATCC 14990	<i>S. sciuri</i> ATCC 29062	<i>S. intermedius</i> H 11
<i>a</i> -605	<i>aa</i> ₃ <i>c</i> -549 <i>c</i> -553	<i>aa</i> ₃ <i>c</i> -549 <i>c</i> -554	<i>a</i> -606	<i>aa</i> ₃ <i>c</i> -549 <i>c</i> -554	<i>a</i> -601
<i>b</i> -552			<i>b</i> -552		<i>b</i> -552
<i>b</i> -556			<i>b</i> -555		<i>b</i> -556
<i>b</i> -559	<i>b</i> -560	<i>b</i> -558	<i>b</i> -559	<i>b</i> -559	<i>b</i> -560
<i>b</i> -567	<i>b</i> -565	<i>b</i> -564	<i>b</i> -566	<i>b</i> -565	<i>b</i> -567

rather low (10 to 14%) but were significantly higher than the values between staphylococci and an unrelated gram-positive bacterium of low G+C content, such as *L. acidophilus* (below 10%). The occurrence of cytochromes of type *c* and the presence of class II FDP aldolase instead of class I is rather unusual within staphylococci. Until now, only one of these characters could be found in any of the other staphylococci examined. Cytochromes of type *c* were detected in *S. sciuri*, and class II FDP aldolase was detected in *S. intermedius*. DNA-DNA hybridization studies revealed that representatives of these species, however, are not more closely related to "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 than to any of the other

staphylococci investigated. Comparison of the highly conserved cistrons coding for RNA by DNA-rRNA hybridization techniques unequivocally demonstrated the relationship of "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 to various staphylococci (Table 4). The staphylococci investigated form, together with the three misidentified micrococci, a clearly defined rRNA homology group. The midpoints of the thermal denaturation curves for heterologous DNA-rRNA hybrids within this group were rather similar to those of homologous hybrids, whereas hybrids between nucleic acids of *M. luteus* and staphylococci, "*M. caseolyticus*," or *M. varians* ATCC 29750 exhibited markedly lower thermal stability (Table 4).

TABLE 3. DNA-DNA hybridization studies among "*M. candidus*" ATCC 14852, "*M. caseolyticus*" ATCC 13548, *M. varians* ATCC 29750, and various type strains of staphylococci^a

[³ H]DNA in solution	Filter-bound DNA											
	" <i>M. caseolyticus</i> "	<i>M. varians</i>	" <i>M. candidus</i> "	<i>S. epidermidis</i>	<i>S. aureus</i>	<i>S. hyicus</i>	<i>S. sciuri</i> ATCC 29062	<i>S. saprophyticus</i>	<i>S. xylosus</i>	<i>S. hominis</i> ATCC 27844	<i>S. capitis</i> ATCC 27840	<i>L. acidophilus</i>
" <i>M. caseolyticus</i> " ATCC 13548	100	82	14	10	11	10	10	—	14	13	12	1
<i>M. varians</i> ATCC 29750	87	100	14	10	13	11	12	14	13	—	—	2
<i>S. epidermidis</i> ATCC 14990	12	12	83	100	23	15	10	19	19	24	23	1
<i>S. aureus</i> ATCC 12600	11	9	28	22	100	17	11	18	19	14	13	1
<i>S. hyicus</i> subsp. <i>chromogenes</i> NCTC 10530	12	11	—	13	15	100	—	—	—	—	—	—
<i>S. saprophyticus</i> CCM 883	—	14	21	22	22	—	—	100	—	—	—	—
<i>S. xylosus</i> DSM 20266	12	12	—	25	23	—	—	—	100	—	—	—
<i>S. simulans</i> ATCC 27848	13	12	—	23	22	—	—	—	—	—	—	—
<i>S. intermedius</i> CCM 5739	11	14	19	14	19	—	—	—	—	—	—	—
<i>S. cohnii</i> DSM 20260	19	12	—	—	—	—	—	—	—	—	—	—
<i>S. warneri</i> ATCC 27840	10	11	—	—	—	—	—	—	—	—	—	—
<i>S. haemolyticus</i> DSM 20263	8	12	—	—	—	—	—	—	—	—	—	—
<i>L. acidophilus</i> AM 63	5	3	8	5	3	—	—	—	—	—	—	100

^a The percentage of radioactivity bound in the heterologous reaction was normalized to the percentage of radioactivity bound in the homologous reaction and expressed as a homology value. Reassociation conditions were employed corresponding to approximately 25°C below the thermal melting point of the DNA, (3× SSC [SSC = 0.15 M NaCl plus 0.015 M sodium citrate] containing 10% formamide, 60°C). —, Not determined.

TABLE 4. Thermal stability of DNA-rRNA hybrids^a

Filter-bound DNA	[³ H]rRNA in solution	
	<i>S. aureus</i> ATCC 12600	<i>S. epidermidis</i> ATCC 14990
<i>S. aureus</i> ATCC 12600	78.0	76.3
<i>S. epidermidis</i> ATCC 14990	76.2	77.7
" <i>M. candidus</i> " ATCC 14990	76.6	77.3
" <i>M. caseolyticus</i> " ATCC 13584	75.5	74.5
<i>M. varians</i> ATCC 29750	74.7	73.8
<i>S. sciuri</i> ATCC 29062	72.7	72.8
<i>M. luteus</i> CCM 169	62.5	61.9

^a Results are expressed as the midpoint of the thermal denaturation curve of DNA-rRNA hybrids (4). Conditions of hybridization experiments were 2× SSC containing 20% formamide, 50°C.

On the basis of the low G+C contents of their DNAs, their cell wall compositions, the DNA homology values, and the results of DNA-rRNA hybridization studies, the assignment of "*M. caseolyticus*" ATCC 13548 and *M. varians* ATCC 29750 to the genus *Staphylococcus* is warranted. As demonstrated by DNA-DNA hybridization studies, they are not closely related to any of the known species of the genus *Staphylococcus* and they are here regarded as belonging to a new species, namely, *Staphylococcus caseolyticus*.

Description of *Staphylococcus caseolyticus* sp. nov. (case-oly'ti-cus. L. noun caseus cheese; Gr. adj. lyticus able to loose; M.L. adj. caseolyticus casein-dissolving.)

Cocci, 0.8 to 1.2 μm in diameter, occurring predominantly in pairs and clusters, occasionally singly. Gram positive. Nonmotile. Nonspore-forming. Colonies are slightly convex, circular, usually entire, 2 to 5 mm in diameter, smooth, glistening, and opaque. Pigment occurs as a yellow ring around the edge of the colonies. Growth is predominantly aerobic; under anaerobic conditions, growth is rather weak. A small amount of L-(+)-lactic acid is produced from glucose under anaerobic conditions.

The strains failed to produce coagulase. They were catalase positive and also reacted positively in the modified oxidase and benzidine tests. Both strains produced acid aerobically from glucose, maltose, fructose, ribose, galactose, and lactose; strain 29750 also produced acid from sucrose. No acid was produced from mannose, mannitol, xylose, xylitol, or turanose.

The strains were resistant to lysozyme and were susceptible only to a high concentration (500 μg/ml) of lysostaphin.

The cell wall peptidoglycan type is L-Lys-Gly₄, L-Ser. The cell wall teichoic acids are atypical, since they contain only small amounts of glycerol. The G+C content of the DNA is 38 to 39 mol%.

S. caseolyticus can be distinguished from all other known staphylococci primarily on the basis of carbohydrate reaction pattern, novobiocin susceptibility, cell wall composition, positive oxidase reaction, weak lysostaphin susceptibility, low acid production under anaerobic conditions, and the presence of class II FDP aldolase.

Type strain: ATCC 13548. A description of this strain is presented below.

Cells: Spheres, 0.8 to 1.2 μm in diameter, occurring predominantly in pairs and clusters. Nonmotile and nonsporeforming. Gram positive.

Agar colonies: Circular entire, 3 to 5 mm in diameter, low convex, smooth with glistening surface, sticky consistency. Opaque pale cream with yellow edge.

Catalase, benzidine, and oxidase tests are positive.

Chemoorganotrophic; metabolism is respiratory. Cytochromes of type *c* are present in the electron transport system. Under anaerobic conditions, there is almost no growth. A class II FDP aldolase is produced. Coagulase is not produced. Sheep blood is not hemolyzed. Acetoin is not produced. Nitrate is reduced. Casein is hydrolyzed. Susceptible to novobiocin (<1.6 μg/ml). Acid is produced aerobically from glucose, fructose, ribose, maltose, lactose, galactose, and trehalose. No acid from mannose, mannitol, xylose, xylitol, turanose, or sucrose.

Cell wall peptidoglycan: L-Lys-Gly₄, L-Ser.

Cell wall teichoic acid composition: glucose and N-acetylgalactosamine.

Only small amounts of N-acetylglucosamine and glycerol are present. G+C content of the DNA: 38 mol%.

REPRINT REQUESTS

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